Hotspot of new megafauna found in the Central Amazon (Brazil): the lower Rio Aripuanã Basin

Marc G.M. van Roosmalen

¹MVRS Marc van Roosmalen Stichting, Leiden, The Netherlands; e-mail: marc.mvrs@gmail.com

ABSTRACT

Here I announce the discovery of a whole new ecosystem in the central-southern part of the Brazilian Amazon: the Rio Aripuanã Basin. Overall, it seems to have created more ecological niches than any other river basin in the Amazon, in particular so to aquatic and non-volant terrestrial mammals. This is plausibly explained for by the unique geo-morphological history of the region. During the Pliocene and Early Pleistocene the entire area to the southeast of the Rio Madeira contained one huge clear-water system that was drained toward the south into the Atlantic Ocean. In the course of several million years a biome quite different from the rest of Amazonia could evolve in this drainage system. Living relicts from ancient times that happened to survive in isolation here, are: a dwarf manatee here described as Trichechus pygmaeus n. sp., a dolphin locally called "boto roxo" that is suspected to be closer related to marine Rio Plata dolphins Pontoporia blainvillei (Gervais et d'Orbigny, 1844) than to Amazonian dolphins of the genus Inia (d'Orbigny, 1834), a black dwarf tapir (Tapirus pygmaeus Van Roosmalen, 2013, with T. kabomani Cozzuol et al., 2013 as junior name), a dwarf marmoset Callibella humilis Van Roosmalen et Van Roosmalen, 2003, a new monospecific genus of Callitrichidae that stands at the base of the phylogenetic tree of all extant marmosets (i.e., Cebuella Gray, 1866, Mico Lesson, 1840, and Callithrix Erxleben, 1777), a giant striped paca here described as Agouti silvagarciae n. sp., and an arboreal giant anteater spotted in the wild but remains to be collected and described (Myrmecophaga n. sp.). A number of other, more advanced mammalian species discovered in the Rio Aripuanã Basin, among which a third species of brocket here described as Mazama tienhoveni n. sp., evolved after a dramatic vicariance took place about 1-1.8 MYA (million years ago), the break-through of the continental watershed by the proto-Madeira River during one of the glacial epochs of the Middle Pleistocene. It marked the birth of the modern fast-flowing Rio Madeira, in terms of total discharge the biggest tributary of the Amazon proper and the second strongest river barrier in the entire Amazon Basin. Furthermore, current threats to the environment in this sparsely inhabited and poorly explored river basin will be addressed. We intend to have this 'lost world' preserved as a UNESCO Natural World Heritage Reserve through the divulgation of new, hitherto not yet identified mammals that it appears to harbor.

KEY WORDS Brazilian Amazon; nova species; Rio Aripuanã Basin.

Received 15.06.2014; accepted 12.12.2014; printed 30.03.2015 Proceedings of the 2nd International Congress "Speciation and Taxonomy", May 16th-18th 2014, Cefalù-Castelbuono (Italy)

INTRODUCTION

Overall, the Rio Aripuanã Basin (Fig. 1) seems to have created more ecological niches than

any other basin in the Amazon, in particular to aquatic and terrestrial mammals. In terms of species evolution and phylogeography the Rio Aripuanã Basin distinguishes itself from Amazonia west of the Rio Madeira and north of the Rio Amazonas by harboring:

- Five sympatric species of peccaries (Tayassuidae: *Tayassu* G. Fisher, 1814; *Pecari* Linnaeus, 1758), instead of two species elsewhere in the Amazon;

- Three sympatric species of brocket deer (Cervidae: *Mazama* Rafinesque, 1817), including a new species we here describe as *M. tienhoveni* n. sp., instead of two species elsewhere in the Amazon;

- Two sympatric species of coati (Procyonidae: *Nasua* Storr, 1780), including a newly identified red-coated pair-living coati we here resurrect as *N. solitaria* Schinz (ex Wied, MS), 1821, as Spix & Martius (1823-1831) refer to it in their account "Reise in Brasilien in den Jahren 1817-1820", instead of only one gregarious species elsewhere in the Amazon;

- Two sympatric species of giant anteater (Edentata: *Myrmecophaga* Linnaeus, 1758), including a new species being tree-dwelling and climbing by its hind feet, instead of only one grounddwelling species elsewhere in the Amazon;

- Two sympatric species of lowland tapir (Tapiridae: *Tapirus* Brünnich, 1772), including a new species in 2013 described by me as *T. pygmaeus* (with *T. kabomani* Cozzuol et al., 2013 as a junior synonym), instead of only one species elsewhere in lowland Amazonia;

- Two sympatric species of jaguar (Felidae: *Pan-thera* Oken, 1816), including a new larger-sized species reported to hunt in pairs, its coat being all-black but a white throat, instead of only one species elsewhere in the Amazon;

- Two sympatric species of paca (Rodentia: *Agouti* Lacépède, 1799), including a new species here described as *A. silvagarciae* n. sp., being larger-sized, its coat orange-brown with white stripes instead of dots, instead of only one species elsewhere in the Amazon;

- Two sympatric species of porcupine (Rodentia-Erethizontidae: *Coendu* Lacépède, 1799), including a new species described as *C.* (*Sphiggurus*) *roosmalenorum* Voss et Da Silva, 2001 belonging to the *vestitus* group of small-bodied dwarf porcupines formerly known only from the Andean Mountains in Colombia, instead of only one species elsewhere in lowland Amazonia;

- Two sympatric species of woolly monkey (Primates: *Lagothrix* Humboldt, 1812), including

L. nigra n. sp. that is all-black, small, and ranging in atypical small social groups (Van Roosmalen, 2013a; 2014; 2015; Van Roosmalen & Van Roosmalen, 2014), instead of only one species elsewhere in lowland Amazonia;

- Two sympatric species of Amazonian marmoset (Primates, Callitrichidae), including a new species, first described as *Callithrix humilis* Van Roosmalen, Van Roosmalen, Mittermeier et De Fonseca, 1998, and later as a new genus, *Callibella* Van Roosmalen et Van Roosmalen, 2003, which is much smaller, does not show any territorial behavior, and occurs in sympatry with *Mico manicorensis* Van Roosmalen, Van Roosmalen, Mittermeier et Rylands, 2000, instead of only one species elsewhere in the Amazon east of the Rio Madeira;

- Two sympatric species of a large-bodied river dolphin (Delphinidae), including a new species locally called "boto roxo" that we suspect to belong to the marine genus *Pontoporia* Gray, 1870, it being smaller, having an overall bluish-grey colored skin, lacking a distinct melon (and therefore maybe foraging by eye-sight and not by echo location), living in pairs with a single offspring, and restricted to the clear-water habitat of the lower Rio Aripuanã, instead of only one species elsewhere in the Amazon Basin;

- Two sympatric species of freshwater manatee, including a new species described in this work as *Trichechus pygmaeus* n. sp., it being less than half the size and one-fifth of the body weight of common Amazonian manatees *T. inunguis* (Natterer, 1883), and its skin deep black instead of grey, instead of only one species elsewhere in lowland Amazonia downstream of rapids and waterfalls;

- A number of newly identified large-fruited, large-seeded, synzoochorically dispersed trees and lianas that are demographically confined to the terra firme forests east of the Rio Madeira (Van Roosmalen, 2013b). These woody plants seem to have co-evolved with scatter hoarding rodents belonging to the genera *Dasyprocta* Illiger, 1811 (agoutis) and *Myoprocta* Thomas, 1903 (acouchis), among which we identified some possibly new species;

- Primate diversity, here defined as the total number of taxa that occur in sympatry within a 10x10 km quadrant of land overlying both banks of a river at certain latitudes, is the highest for the Rio Madeira at the longitude of the mouth of the Rio Aripuanã, reaching at least 25 (!) valid species. That



Figure 1. Study area. Central Amazon (Brazil): the Rio Aripuanã Basin (shaded area).

exceeds with at least two species the hitherto highest primate diversity (in total 23 valid species) found west of the Madeira River, along the Rio Purús at its confluence with the Rio Tapauá (Van Roosmalen, 2013a; 2015; Van Roosmalen & Van Roosmalen, 2014).

- The Rio Aripuanã is a clear-water river draining the area north of the Chapada dos Parecís, a mountain range that is part of the crystalline Pre-Cambrian Brazilian Shield. Together with the clear- water Rios Tapajós-Juruena, Teles-Pires, and Xingú, the Rio Aripuanã seems to harbor relicts of a highly species-rich endemic Miocene freshwater mollusk (shellfish or bivalve) fauna with extant shells, oysters and mussels only to be found east of the Madeira River (Hoorn & Wesselingh, 2010).

RESULTS

New mammalian species descriptions from the Rio Aripuanã Basin, Brazilian Amazon

1. New species of living brocket deer (Mammalia Cervidae) from the Rio Aripuanã Basin

Up to recently, only two members of the Neotropical Odocoileinae (brocket deer), a subfamily of the Cervidae (deer), from lowland Amazonia were known to science, belonging to the extant genus *Mazama* (Wilson & Reeder, 1993): the red brocket *M. americana* (Erxleben, 1777), and the grey brocket M. nemorivaga (F. Cuvier, 1817). The latter has being recently (Rossi, 2000) distinguished from M. gouazoupira (G. Fischer, 1814), which species is said to range south of Amazonia on the open savannas and shrub savannas (cerrado) of Central Brazil, Bolivia, Paraguay, N Argentina and Uruguay. Although the evolutionary history of brocket deer dates back almost 20 million years ago (MYA), Duarte et al. (2008) suggest that in the Late Pliocene, approximately 2.5-3 MYA, the uplift of the Panamanian land bridge allowed deer to spread south, as participants in the "great American interchange" between North and South America. According to Duarte et al. (2008), these were the first deer to enter the South-American continent, and their surprising success in South America may be attributed to the absence of other ruminants (Webb, 2000).

Class Mammalia Order Artiodactyla or Cetartiodactyla (if whales are to be included) Family Cervidae Goldfuss, 1820

Subfamily Odocoileinae Pocock, 1923

Genus Mazama Rafinesque, 1817

Mazama tienhoveni Van Roosmalen et Van Hooft

EXAMINED MATERIAL. Two skins in possession of hunters from the village of Tucunaré along the lower Rio Aripuanã were examined. Moreover, a complete skull and mandible still in the flesh from an adult female specimen, and one spike from an adult male specimen were obtained from them in the course of the year 2006. The settlement of Tucunaré is situated along the Paraná do Santa Maria, a shortcut from the community of Santa Maria to that of Tucunaré, along the left bank of the middle Rio Aripuanã, State of Amazonas, Brazil (05°45'S, 60°15'W). Holotypus: Specimen MR204, complete head with partly damaged mandible (Fig. 3), adult female, on May 12, 2006 killed for food by a local hunter along the left bank of the Rio Aripuanã near the settlement of Tucunaré, skull, spike (Fig. 4) and skin (Fig. 5). The type specimen MR204 is deposited as INPA4273, Mammal Collection of the National Institute for Amazon Research, Manaus, Amazonas, Brazil.



Figures 2–9. *Mazama tienhoveni* n. sp. Figure 2. *M. tienhoveni* n. sp. drawing reconstructed from plate depicting *M. nemorivaga* (Eisenberg, 1989). Fig. 3. Skinned head of a holotype female fair brocket deer *M. tienhoveni* n. sp. Fig. 4. Two spikes of *M. nemorivaga* and one (the smallest) of *M. tienhoveni* n. sp. Fig. 5. Skin of *M. tienhoveni* n. sp. from Tucunaré village, Rio Aripuanã. Figs. 6–8. skull and mandible of gray brocket deer *M. nemorivaga* (MPEG1969). Fig. 9. Distribution map for *M. tienhoveni* n. sp.

DESCRIPTION OF HOLOTYPUS. Measurements. Two skins obtained from hunters along the lower Rio Aripuanã were measured. Body weight not taken but according to local hunters ranges from 20-25 kg. Skull length 185 mm, mandible length 145 mm. Diastema length in skull 53 mm. Condylobasal length 167 mm. Palatal length 114 mm. Length of nasals 55 mm. Interorbital constriction 41 mm. Zygomatic breadth (= breadth across zygomatic arches) 80 mm. Breadth of braincase 55 mm. Length of upper tooth-row 53 mm. Length of lower toothrow 58 mm. Breadth of M² 12 mm, breadth of M2 8 mm. Dental formula: I 0/3, C (1)/1, P3/3, M 3/3.

Length of spikes (including the coronet) 55 mm.

VARIABILITY. No paratypes have been collected thus far.

ETYMOLOGY. We would like to name the species for Dutch lawyer and naturalist Pieter Gerbrand van Tienhoven (1875-1953), co-founder of a mainstream conservation organisation in the Netherlands (Natuurmonumenten) and one of the founding fathers of the International Union for the Conservation of Nature and Natural Resources (IUCN): Van Tienhoven's fair brocket deer, *M. tienhoveni* n. sp. Van Tienhoven's fair brocket deer *M. tienhoveni* n. sp. is locally known as "veado branco", which means "white brocket deer". This way locals distinguish it from *M. americana* commonly known as "veado vermelho" or "veado capoeira", which means "red brocket" or "secondary-growth brocket", referring to its overall orange-red color and preference for edge habitats and forest clearings, and from *M. nemorivaga* locally known as "veado roxo", which means "purplish-grey brocket".

DISTRIBUTION. The geographical distribution of Van Tienhoven's fair brocket is thought to be restricted to the lower and middle part of the Rio Aripuanã Basin, but it might well be distributed across the entire interfluvium delineated by the Rio Madeira in the west, the Rio Tapajós-Juruena in the east, the Rio Amazonas in the north and the Rio Guaporé in the south. Since it seems to be confined to terra firme rainforest habitat, we assume that its real distribution is much smaller and does not extend into the northern part of the Rios Madeira/Tapajós interfluvium, where many open savannas and extensive floodplains are found. We have observed the species in the wild only along both banks of the Rio Aripuanã.

ECOLOGY. Van Tienhoven's fair brocket, M. tienhoveni n. sp., seems to be restricted to dense terra firme (upland) rain forest, where it lives solitary or in pairs. It occupies rather small territories and occurs in the Rio Aripuanã Basin in sympatry with the locally much rarer grey brocket *M. nemorivaga*, and the greater red brocket *M. americana*. The latter, however, occurs more frequently in disturbed areas with secondary growth and edge habitats, and in open areas such as white-sand savannas, which are common in the region. Nothing is known about Van Tienhoven's fair brocket, its ecology, and habits in the wild. The author has seen it only a few times in the wild during the dry season, while it was visiting the *Bactris maraja* (palm) dominated margins of muddy ponds, mud pools and saltlicks. These can be found locally in the middle of the rain forest at sometimes long distances from any substantial water supply, such as rivers, streams, lakes and ponds.

PHYLOGENY. DNA was extracted from a skin sample from each of the two brocket species, *M. tienhoveni* n. sp. and *M. nemorivaga*, both collected from the forests along the left bank of the Rio Aripuanã. Partial mitochondrial cytochrome b DNA sequences of 233 bp (sites 133-365) and 295 bp (sites 108-402) in length were obtained for respectively Mazama tienhoveni n. sp. and M. nemorivaga with the conserved primers L14841 and H15149 (Kocher et al., 1989). DNA extractions, PCR reactions, and DNA sequencing were performed according to standard laboratory protocols. The sequences are deposited in Genbank under the accession numbers: GQ268320 (M. tienhoveni n. sp.) and GQ268321 (M. nemorivaga). Unfortunately, we did not have a skin sample from a specimen of the third sympatric brocket M. americana. However, different cytochrome b DNA sequences from this species and all other currently known Amazonian deer species could be obtained from Genbank (Genbank accession numbers given in Fig. 10). Most of these sequences have been used in a recent phylogenetic study on the South American deer (Duarte et al., 2008). We generated a minimum-evolution (ME) distance tree by adding our two sequences to those used in Duarte et al., 2008. Furthermore, we included Genbank sequences not used in that study, belonging to various South-American deer species, and excluded those with a large number of missing data in the 133-365 bp region of cytochrome b. The ME-tree was constructed with MEGA 4 (Tamura et al., 2007). We used the substitution model K2P (Kimura, 1980) with a constant rate applied and with Rangifer tarandus (Linnaeus, 1758) being outgroup, as has also been done in Duarte et al., 2008. The tree is based on the 133-365 bp region of cytochrome b with unresolved nucleotides deleted by pairwise deletion. Divergence times were estimated assuming separation between Blastocerus/Pudu and *Mazama/Odocoileus* 5 MYA (Duarte et al., 2008).

Mazama tienhoveni n. sp. and Genbank sequence AY886753, not being used in Duarte et al. (2008) although being from a brocket classified as *M. gouazoupira*, formed a distinct clade that diverged from the other South American deer species (average sequence divergence: 8.3%) 5 MYA (Fig. 10). This would imply that *M. tienhoveni* n. sp. diverged already before the uplift of the Panamanian land bridge and invaded South America during the "great American interchange" between both continents. A distinct clade not only supports the separate species status of *M. tienhoveni* n. sp., it also indicates that Genbank sequence AY886753 was wrongly identified as *M. gouazoupira*. The latter

observation is not unlikely, as low levels of morphological differentiation in the genus *Mazama* have caused numerous errors in species identification in the past (Duarte et al., 2008). Genbank sequence AY886753 should either be attributed to *M. tienhoveni* n. sp. or to a separate species in its own right, which is very well possible considering the fact that it diverged 2-3 MYA from the *M. tien-hoveni* n. sp. sequence. This divergence seems to have occurred, more or less coinciding with the uplift of the Panamanian land bridge.

REMARKS. *Mazama tienhoveni* n. sp. differs from the two other known Amazonian species, the



Figure 10. Linearized minimum-evolution tree showing phylogenetic relationships among South American deer derived from a 233 bp fragment of the mitochondrial cytochrome b. The scale on top corresponds to the time scale in millions of years while the scale below corresponds to the observed mean sequence divergence using the substitution model K2P. Bootstrap values (1000 replicates, > 50%) are denoted above nodes. Numbers behind taxon names correspond to Genbank accession numbers.

Greater Red Brocket *M. americana* and the Gray Brocket M. nemorivaga, in being intermediary in size, but with 55 mm total length and coronet diameter 24x30 mm having the shortest but most robust spikes (mean spike length 74 mm and coronet diameter 21x22 mm in M. nemorivaga). Most of the body is overall light brown colored, grading toward almost white on the sides and ventrally, whereas the dorsal parts of *M. americana* are of a (deep) reddish brown color, grading ventrally into a more rusty color, and those of M. nemorivaga are dull or pale vellowish or gravish brown to chestnut brown, grading ventrally into yellowish or whitish (Husson, 1978). The males of *M. tienhoveni* n. sp. do not have the distinct crest of hairs on the forehead as M. nemorivaga has, neither do the males of Mazama americana. Head-body length is not known yet, but M. tienhoveni n. sp. is said to be intermediary in size between M. nemorivaga, being 760-1015 mm (N=6) (Rossi, 2000), with shoulder height 480 mm (Duarte, 1996), and M. americana being 1120–1135 mm. The short tail is 75 mm long, dorsally has the same color of the back but shows a conspicuous white tuft at the end, being predominantly white below, whereas the tail in M. americana is 160-200 mm long, including the tuft, and 60-106 mm in M. nemorivaga. Furthermore, hind foot length (with hoof) in M. americana is 313-318 mm and ear length is 94–100 mm, and 82-93 mm in M. nemorivaga (Husson, 1978; Rossi, 2000). Weight of adult specimens is reported less than 15 kg in M. nemorivaga, 25-40 kg in M. americana, and about 20-25 kg in M. tienhoveni n. sp., according to local hunters. M. tienhoveni n. sp. can be distinguished from other brocket deer by its intermediary-sized head and various other intermediary skull characters (Table 1). Overall, the cranium of M. tienhoveni seems more related to that of *M. nemorivaga* than that of M. americana, but it differs clearly from Mazama nemorivaga in the following mean cranial measurements: greatest skull length 185 versus 174 mm; palatal length 114 vs. 105 mm; length of nasals 55 vs. 50 mm; interorbital constriction 41 vs. 39 mm; zygomatic breadth 80 vs. 73 mm; braincase breadth 55 vs. 53 mm; alveolar breadth of the upper second molar 12 vs. 11.3 mm; alveolar breadth of the lower second molar 8 vs. 7.4 mm; and length of mandible 145 vs. 134 mm.

The divergence time between *M. tienhoveni* n. sp. and the two other brocket deer, derived from partial cytochrome b DNA sequences, is estimated

Skull	M. americana	M. nemorivaga	M. tienhoveni	
Greatest or condylobasal length (=length anterior tip of I ¹ to rear of condyles)	(n=11) 221	(n=5) 174	(n=1) 185	
Basal length (= length anterior tip of I ¹ to proximal end of condyles)	210	162	167	
Palatal length	137	105	114	
Length of nasals	65	50	55	
Interorbital constriction	47	39	41	
Zygomatic breadth (breadth across zygomatic arches)	97	73	80	
Breadth of braincase	63	53	55	
Length of diastema	70	52	53	
Alveolar length of upper tooth-row	63	52	53	
Alveolar breadth of M ²	14.6	11.3	12	
Length of mandible (=length from I' to rear of processus condylicus)	172	134	145	
Alveolar length of lower tooth-row	72	59	58	
Alveolar breadth of M2	9.7	7.4	8	
Length of spikes	101 (n=5)	55		
Distance between spikes	36 (n=5)	35 (n=2)		
Diameter of coronet	21-22 RA (n=2)		24-30 RA	

Table 1. Skull measurements (in mm) of *Mazama americana* (N=11; NHML), *M. nemorivaga* (N=5; NHML), and *M. tienhoveni*; *M. tienhoveni* n. sp. is represented by the holotype - an adult female from Tucunaré, Rio Aripuanã, State of Amazonas.

at 5 million years before present, which is well before the uplift of the Panamanian land bridge. As in other brocket deer, Van Tienhoven's fair brocket seems to live solitary or in pairs. In view of recent developments in the Rio Aripuanã Basin where it lives and due to its limited distribution, we consider Van Tienhoven's fair brocket highly endangered.

CONSERVATION STATUS. All three brocket species, occurring in sympatry in the Rio Aripuanã Basin, are favorite game to the locals. Hunting the 'blond' or fair brocket *M. tienhoveni* n. sp. is said to be more successful. Along the lower Rio Aripuanã, it is said to be the most commonly encountered type of brocket, at least in terra firme (upland) rain forest, whereas greater red brocket are more often found near forest edges and clearings, such as fields and plantations. Although human occupation in this part of the Amazon is very low nowadays, this situation might soon change. In the Rio Aripuanã region unprecedented illegal extraction of timber, gold and gravel is taking place, ironically after the whole lower Rio Aripuanã region was declared a State of Amazonas Sustainable Development Reserve (Reserva de Desenvolvimento Sustentável - RDS do Baixo Rio Aripuanã). Recent road building through the area has as objective to connect the town of Manicoré on the right bank of the Rio Madeira with the now booming town of Apuí at the border of the Tenharim Savanna and the State of Mato Grosso, areas of large-scale industrialized soybean agriculture. As recently as the year 2006, gold was found where the road from Novo Aripuanã crosses the Rio Juma, a clear-water tributary of the right-bank Rio Aripuanã. A crowd of over 10,000 gold diggers then settled in. Locals told us that ever since commercial hunters flocked into the area.

They use trained dogs for the hunt on game species as giant peccary Pecari maximus Van Roosmalen et al., 2007, Van Tienhoven's fair brocket M. tienhoveni n. sp., and both dwarf tapir Tapirus pygmaeus Van Roosmalen, 2013 (also known as T. kabomani Cozzuol et al., 2013 - a junior name) and lowland Brazilian tapir Tapirus terrestris (Linnaeus, 1758) to feed hungry settlers and gold-miners. Taking increasing hunting pressure and the species's limited distribution into account, M. tienhoveni n. sp. is considered highly endangered. It is recommended to include this new species in the IUCN Global Red List, based on criterion D (very small or restricted population). Besides Van Tienhoven's fair brocket, the Rio Aripuanã region seems to harbor a number of other faunal elements new, or possibly new, to science. Identified so far are a new species of peccary Pecari maximus (Van Roosmalen et al., 2007), a new species of dwarf porcupine Coendu (Sphiggurus) roosmalenorum (Voss & Da Silva, 2001), and at least four new primate species (Van Roosmalen et al., 1998; Van Roosmalen et al., 2000; Van Roosmalen et al., 2002; Van Roosmalen and Van Roosmalen, 2003). Among these primates, the black-crowned dwarf marmoset Callibella humilis Van Roosmalen et al., 1998 represents a complete new genus first seen and collected by me in 1996. Most surprisingly, up to today not a single area exists in the region that is effectively protected by Brazilian environmental law. Given the uniqueness of the region in terms of biodiversity and its current status of biological terra incognita, we here suggest UNESCO to urge the Brazilian Government to declare the entire lower Aripuanã Basin a Natural World Heritage Reserve.

2. New species of living rodent from the Rio Aripuanã Basin: the giant striped paca (Mammalia Agoutidae)

Up to recently only two members of the Neotropical family Agoutidae (pacas), synonymous to Cuniculidae, were known to occur in the Americas belonging to the extant genus *Agouti* (Wilson & Reeder, 1993): the spotted common paca *Agouti paca* (Linnaeus, 1766), which species ranges in C+S America from San Luis Potosi, SE Mexico, to Paraguay, the Guianas, and S Brazil (the species was introduced into Cuba) and occupies suitable lowland habitats, and the mountain paca *A. taczanowskii* (Stolzmann, 1865), a species from the high cloud forest (altitudes between 2,000-3,000 m) of Andean regions of Peru, Ecuador, Colombia, and NW Venezuela (Eisenberg, 1989; Eisenberg & Redford, 1999).

Class Mammalia Order Rodentia Family Agoutidae Gray, 1821 Subfamily Agoutinae or Cuniculinae Genus *Agouti* Lacépède, 1799

Agouti silvagarciae Van Roosmalen et Van Hooft

EXAMINED MATERIAL. Holotypus: adult female, complete head (Fig. 13), killed for food by a local hunter on May 28, 2006, along the left bank of the Rio Aripuanã near the settlement of Tucunaré. Paratypus: stuffed specimen found under number MPEG 22302 in the mammal collection of the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil, its provenance not given (Fig. 14). Headbody length 750 mm. The heads were preserved on spirit (Fig. 13). Grain shot had severely damaged the skull of the giant paca specimen making it impossible to take cranial measurements.



Figures 11–16. Fig. 11. Plate from Eisenberg (1989) depicting the common spotted paca *Agouti paca*; Fig. 12. The common spotted paca *A. paca* as depicted in Emmons & Feer (1990). Fig. 13. Heads of freshly killed common spotted paca *A. paca* (at bottom) and Silva Garcia's striped giant paca *A. silvagarciae* n. sp. (at top). The skulls and mandibles of these specimens are stored at Tucunaré village, Rio Aripuanã, State of Amazonas, Brazilian Amazon. Figs. 14, 15. Stuffed specimen of striped giant paca *A. silvagarciae* n. sp. found by the first author in the collection of Museu Paraense Emílio Goeldi under MPEG 22302 - without locality and misidentified as *A. paca*. Fig. 16. Skull of the common spotted paca *A. paca* found by the first author in the collection of Tapirinha. Skull length 147 mm, skull width 97 mm.

DESCRIPTION OF HOLOTYPUS. The general dorsal pelage color of the common spotted paca Agouti paca is uniformly chestnut or mummy brown to almost black, usually with a striking pattern of four horizontal lines of white or light yellowish dots on each side of the body, the two middle ones at least extending all the way from the neck to the rump. In these two middle rows, the spots in the middle part may be fused to an uninterrupted stripe. The lower of the rows of spots is only visible in the extreme anterior and posterior parts, as the middle part is fused with the white ventral surface of the body. One or two of the upper rows of spots are shorter than the other rows; they are visible only in the posterior half of the body. The hairs are stiff and shiny. The dark brownish hairs show a lighter

median line. The dorsal surface of the head is of the same color as the back, but the hairs are shorter and less stiff. On the snout, there are long stiff whiskers. The upper whiskers are blackish and the lower are white, the color difference being quite striking. Similar stiff whisker-like hairs, though fewer, are implanted below and slightly in front of the ears; here too, upper hairs are blackish brown, lower ones white. The ears are relatively large; a tuft of blackish and yellowish longer hairs is implanted before the opening of the ear. The throat and the cheeks are uniformly cream-colored, as is the entire ventral surface of the body. The line of demarcation between the dark dorsal and the whitish ventral color is distinctly marked. The outside of the legs is of the same brown color as the dorsal surface of the body; the inside of the legs is yellowish white basally, brown or brownish distally. The tail is vestigial, very short, and hardly noticeable. There are four toes with nails both on the fore- and hindfeet. In the forefeet, the nail of the thumb is very small, the others are well developed and of equal size. In the hind-feet, the three middle nails are large and of about the same size, while the nails of the inner and outer toes are markedly smaller and implanted higher, the inner nail being again somewhat smaller than the outer one. In the female there is on each side one pectoral mamma, at about the level of the bases of the front legs. Dental formula: I1/1, C0/1, P1/1, M3/3. The skull of an adult common paca is immediately characterized by the zygomatic arch that has grown out to an enormously swollen, distinctively sculpted bony plate, which is about two-third the length of the palate; this plate is strongly produced downward, in lateral view obscuring the teeth and the basal part of the mandible. Anteriorly, this plate encloses a deep and very large cavity at each side of the very narrow palate in front of the tooth-rows. In comparison to other rodents, the teeth are placed far backward. The palate ends at the line between the last and the penultimate molars. The infra-orbital opening has become a narrow canal almost entirely enclosed by bone. The outer surface of the zygomatic arch is covered with a honey-comb of irregular bony ridges, giving it a strongly rugose appearance. These rugosities extend also onto the larger parts of the nasals, frontals and parietals; in full-grown specimens the sutures between these bones are not or only partly visible. Even in newborn and juvenile specimens, the zygomatic arch is relatively high, but still smooth. The external measurements of three adult specimens of Agouti paca from Suriname on which the above mentioned description is based, are: head-body length 650; 676; 662 mm; tail length 18; 17; 19 mm; hind foot (including nail) 119; 117; 113 mm; ear length 46; 41; 48 mm; weight 9.2; 9.1; and 9.5 kg (Husson, 1978). Eisenberg (1989) gives headbody length averages 600-795 mm, vestigial tail length 19 mm, hind foot 188 mm, ear length 45 mm and weight 7.5 kg. He also states that the adult male is about 15% larger than the adult female. Silva Garcia's giant paca A. silvagarciae n. sp. from the Rio Aripuanã Basin has been reported by locals to weigh between 12–15 kg, its general color is bright orange brown. Average weight of the sympatric common paca *A. paca* in the Rio Aripuanã Basin is reported to be 5–6 kg. The head of the giant paca shot near Tucunaré settlement measures 155 x 80 mm (compared to 115 x 80 mm in the common paca specimen shot the same night at the same locality of Tucunaré) (Fig. 13). The eight upper whiskers are black and about 110 mm long, the eight lower whiskers are white, stronger and stiffer than the upper ones and 105-110 mm in length (similar to those in the common paca). Three out of four lateral rows show the white spots (almost) completely fused (Figs. 14, 15).

Measurements. Body weight was not taken from the holotype specimen of *A. silvagarciae* n. sp., but according to local hunters body weight ranges from 12-15 kg. The head of the giant paca shot near Tucunaré settlement measured 155 x 80 mm, whereas that of the adult common paca shot at the same locality the same night measured only 115 x 80 mm (Fig. 13).

VARIABILITY. Paratype: stuffed specimen of striped giant paca *A. silvagarciae* n. sp. found under number MPEG 22302 in the mammal collection of the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil, misidentified as *A. paca*, its provenance not given (Figs. 14, 15). Head-body length 750 mm.

ETYMOLOGY. This paca is named in honor of the author's spouse Antonia Vivian Silva Garcia. During our visit to the community of Tucunaré she heard the villagers talk about the two types of paca the locals there distinguish, one specimen of each a local hunter had shot for food that very night. Undoubtedly, the two species of paca must therefore be considered (micro)-sympatric.

Vernacular name: *A. silvagarciae* n. sp. is known locally as "paca concha", which means "shellfish paca". This way, locals distinguish it from the common paca *A. paca* that is known as "paca pintada" ("spotted paca").

DISTRIBUTION. Members of the genus *Agouti* are distributed from southern Mexico to northern Argentina in suitable lowland habitats. The geographical distribution of the giant paca is thought to be restricted to the interfluvium confined by the Rio Amazonas in the north, the Rio Madeira in the west, the Rio Ji-Paraná or Rio Guaporé in the south, and the Rio Tapajós-Juruena in the east (Fig. 1). We have observed the species in the wild only along both banks of the Rio Aripuanã. Type locality of

<i>Agouti paca</i> Rg n° Sex	23902	18233 ?	17756 -	21889 -	21891 -	21892 -	18013 ?	18017 ?	М
Greatest length mm	139	143	143	142	148	148	136	141	143
Condylobasal length	129	138	144	136	145	139	128	137	137
Basal length	123	131	136	128	138	133	121	129	130
Palatal length	77	82	86	82	86	85	75	82	82
Length of nasals	45	fused	56	44	50	47	46	50	48
Zygomatic breadth	92	96	104	87	100	95	-	92	95
Hght zygomatic arch	46	50	60	39	56	47	37	47	48
Lgth zygomatic arch	80	87	102	80	98	86	72	82	86
Interorbital constr.	45	42	44	40	45	45	37	40	42
Braincase breadth	45	43	47	45	49	46	44	43	45
Mastoid breadth	61	57	65	60	65	62	59	55	61
Bullae lgth x bdth	20x15	18x14	18x17	21x17	17x14	20x18	20x14	19x17	19x16
Height of rostrum	39	40	42	39	41	42	37	40	40
Diastema	44	48	51	46	51	50	42	46	47
Alveolar length P-M ³	28	30	29	28	32	28	29	30	29
Breadth of m ²	7.1	7.2	7.9	8.0	7.4	7.3	7.0	7.6	7.4
Length of mandible	97	87	103	-	-	-	93	96	95
Alveolar length P-M3	30	31	32	-	-	-	31	33	31
Breadth of M3	7.5	6.8	8.5	-	-		7.2	8.0	7.6

Table 2. Cranial measurements (in mm) of eight specimens of the common spotted paca *Agouti paca* from Suriname (zoological collection of the NHML, Leiden, the Netherlands) on which our description is based. With "height of zygomatic arch" is meant the greatest height; with "breadth of the braincase" is meant the width of the skull at the level just above the external auditory meatus. Also, the total length of the zygomatic arch is noted being the distance between the extreme anterior and posterior borders. The length of the mandible was measured from the processus angularis. Mean skull length 143 mm, mean mandible length 95 mm. Diastema length in skull 47mm. Condylobasal length 137 mm. Palatal length 82 mm. Length of nasals 48 mm. Interorbital constriction 42 mm. Zygomatic breadth (= breadth across zygomatic arches) 95 mm. Breadth of M³ 7.6 mm. Dental formula: I 1/1, C 0/0, P1/1, M 3/3.

A. silvagarciae n. sp. is the Rio Aripuanã, close to the settlement of Tucunaré, situated along the Paraná do Santa Maria, a shortcut from the community of Santa Maria to that of Tucunaré, sitting on the left bank of the middle Rio Aripuanã, State of Amazonas, Brazil (05°45′ S, 60°15′ W).

ECOLOGY. Pacas of both species are nocturnal and have their hiding-places in hollow fallen tree trunks. They always carefully make two entrances to their burrows, so that they can escape when hunted down by dogs. Pacas usually live close to rivers and creeks. When pursued by dogs, they frequently take refuge in the water. Notwithstanding its fat body, it manages to walk on the bottom of any substantial water body. The formidable teeth and enormous masticatory muscles of pacas enable them to break open the hardest fruits and seed kernels. In contrast to the agouti, the paca digs burrows that are sometimes interconnected with others.

The giant paca A. silvagarciae n. sp. is assumed to be restricted to dense terra firme upland rain forest, where it lives solitary or in pairs. It occupies rather small territories and occurs in the Rio Aripuanã Basin in sympatry with the locally much more common spotted paca A. paca. The latter, however, is more frequently found along edges, such as roadsides, streams and creeks, in disturbed areas with secondary growth, and in open areas on white-sand savannas common in the region. Nothing is known about its ecology and habits in the wild. I myself have seen it in the wild only a few times during the dry season while visiting the Bactris maraja Mart (palm) dominated margins of muddy ponds, mud pools and saltlicks. These can be found locally in the middle of the rain forest,

often at long distances from any substantial water body, such as rivers, streams, lakes or ponds.

PHYLOGENY. One complete mitochondrial Dloop and two nuclear SINE PRE-1 DNA sequences of Silva Garcia's giant paca were carried out and compared with Genbank sequences of the sympatric common paca (*A. paca*). The results (15.5% difference between species) clearly support the distinction into valid species. As genetic distances based on partial mtDNA cytochrome b sequences (283 bp) in Bovidae are estimated 1.25% = 1 MYS, divergence time between *A. paca* and *A. silvagarciae* n. sp. is estimated at about 10 million years. The giant paca therefore seems to have derived from ancestral pacas in the Late Miocene to Early Pliocene.

Remarks. This second species of paca from the Brazilian Amazon is distinctly bigger than the morphologically most related species that occurs in the Amazon, the common spotted paca *A. paca*. One complete mitochondrial D-loop and two nuclear SINE PRE-1 DNA sequences of the giant paca compared with that of the sympatric common paca (*A. paca*) supports the distinction. Divergence time is estimated at 10 million years. As in the common paca, giant pacas are nocturnal and reported to live solitary or in pairs. In view of recent developments in the interfluves where it lives, due to its limited distribution and for being a prime target to local hunters, we consider Silva Garcia's giant paca

Several specimens of stuffed pacas in the zoological collection of Museu Paraense Emílio Goeldi, Belém, Pará, identified as common pacas, are suspected to represent giant pacas, hereafter named *A. silvagarciae* n. sp. (Figs. 14, 15). This assumption is based on the orange-brown skin color, the pattern of horizontal white stripes instead of spots, total body length, weight, and cranial measurements. Unfortunately, none of them has been given a proper geographic locality.

CONSERVATION STATUS. The two paca species occurring sympatrically in the Rio Aripuanã Basin are favorite game to the locals. Although human occupation in this part of the Amazon is very low nowadays, this situation may change in the near future. In the Rio Aripuanã region unprecedented extraction of timber and gravel is taking place. Recent road building through the area is intended to connect the town of Manicoré on the right bank of the Rio Madeira with the boomtown of Apuí located at the border of the Tenharim Savanna and the State of Mato Grosso, areas of large-scale industrialized soybean agriculture. In view of these developments, we fear that commercial hunters using trained dogs will focus first on large animals, such as the giant paca Agouti silvagarciae n. sp., to feed hungry settlers and gold-diggers. Taking increasing hunting pressure and the species's limited distribution into account, I consider A. silvagarciae n. sp. on the verge of extinction. It is recommended to include this new species in the IUCN Global Red List, based on criterion D (very small or restricted population). Besides the giant paca, the Rio Aripuanã region is thought to harbor a number of other mega-faunal elements new to science. I have identified so far a new species of peccary Pecari maximus (Van Roosmalen et al., 2007), a new species of dwarf porcupine Coendu (Sphiggurus) roosmalenorum (Voss & Da Silva, 2001) - and seven new primate species, four of which are already officially described [Van Roosmalen et al. (1998); Van Roosmalen et al. (2000); Van Roosmalen et al. (2002); Van Roosmalen & Van Roosmalen (2003)]. Among these primates, the dwarf marmoset Callibella humilis represents a new primate genus first seen and collected by me in 1996. Most surprisingly, not a single area protected by Brazilian environmental law exists in the region. Given the uniqueness of the region in terms of biodiversity and its current status of biological terra incognita, we here suggest UNESCO to urge the Brazilian Government to declare the entire region a Natural World Heritage Reserve.

3. New species of living manatee (Mammalia Trichechidae) from the Rio Aripuanã Basin - shallow clear-water adapted dwarf manatee is on the verge of extinction

Manatees (Mammalia Trichechidae) are fully aquatic mammals of the ancient Order Sirenia. Worldwide there are two extant genera, *Trichechus* Linnaeus, 1758 and *Dugong* Lacépède, 1799. The Amazonian manatee *T. inunguis* (Natterer in Pelzeln, 1883) is the only species strictly adapted to fresh-water environments. However, here we announce the discovery of a second taxon from the Amazon that is also adapted to fresh-water habitat. Class Mammalia Order Sirenia Family Trichechidae Genus *Trichechus* Linnaeus, 1758

Trichechus pygmaeus Van Roosmalen et Van der Vlist

EXAMINED MATERIAL. Holotype: skull with lower jaw of adult male is numbered CCM181, Zoological Collection of the Brazilian Institute for Amazon Research (INPA), Manaus-Amazonas, Brazil, collected eight km upstream from the mouth of the Rio Arauazinho (Fig. 17), a left bank tributary of the lower Rio Aripuanã, State of Amazonas, Brazil (06°16′94″S, 60°20′87″W), 25.IX.2002, M.G.M. van Roosmalen legit.

DESCRIPTION OF HOLOTYPUS. Holotype skull length 24 cm, greatest width 15 cm. Mandible length 15.5 cm. Rostrum length 6.5 cm. Frontal bones convex, greatest width 5.1 cm. Cheek teeth (fully erupted molars) 4, maxillar molars 0.9 x 0.9 cm (Fig. 18), mandibular molars 0.8 x 0.6 cm. Skull roof 5 cm wide, lacking parasagittal crests. Braincase volume approximately 210 cc.

VARIABILITY. The species description is based on two adult males and generalized in accordance with reports from local hunters. Both adult male dwarf manatees have been examined, each measuring 130 cm in length, 90 cm in circumference, and weighing about 60 kg. The skin is overall pitch-black with a circular to tear-shaped white patch on the abdomen reported to be so in both the sexes, measuring in the captive male ca. 52 cm long and 26 cm in diameter. The flippers measured 32x11 cm and the paddle 36x40 cm. Snout comparatively short, circumference 46 cm, 19 cm in diameter, beset with long, stiff bristle hairs. Whole body is thinly beset with bristle-hairs (see also Fig. 19).

ETYMOLOGY. Pygmaeus in Latin means "short", "very small" or "dwarf", reflecting as such the fact that the new taxon of manatee is a dwarf compared with the common Amazonian manatee *T. inunguis*. Vernacular name: "Dwarf manatee", or "peixeboi anão". It is locally known as "pretinho", which means "little black fellow". This way, the locals distinguish it from the common Amazonian freshwater manatee *T. inunguis* widely known as



Figure 17. Landsat images of the Rio Arauazinho, branching off in three directions, one lengthy branch coming from the south running parallel with the Rio Aripuanã, one short branch coming straight from the north, and one main branch coming from the northwest. The latter drains the extensive wetlands along the watershed with the upper Rio Mariepaua, which harbor the last remaining population of *T. pygmaeus*.



Figure 18. (Above) Maxillary molars of a young juvenile male *T. inunguis* (Inpa Pb248) compared with those of the holotype adult male *T. pygmaeus* n. sp. (below).

"peixe-boi comum" (Portuguese for "common fish cow").

DISTRIBUTION. Currently known distribution restricted to the Rio Arauazinho Basin, a clearwater tributary of the left-bank Rio Aripuanã, State of Amazonas, Brazil. Dwarf manatees may also occur in the headwater region of the Rio Mariepaua, the wetlands of which are interconnected with those of the northernmost branch of the Rio Arauazinho.

COMPARISONS. The new taxon is assigned to the genus *Trichechus*, because it possesses a number of traits in common with the parapatric, though in ecological respect allopatric Amazonian manatee, *T. inunguis*, from which it differs by its total adult body length 130 cm (280-320 cm in *T. inunguis*), and weight ca. 60 kg (350-500 kg in *T. inunguis*) (Domning & Hayek, 1986). Growth curves of free-ranging Amazonian manatees (*T. inunguis*) in Brazil

are described by Vergara-Parente et al., 2010. Age estimates and biometrics from 60 Amazonian manatees captured between 1993 and 2006 by local residents of the mid-Solimões and Pirativa Rivers in the Brazilian Amazon are given as follows: length at birth for T. inunguis is estimated at 133.2 cm (average = 113.0 cm; SD = 34.4 cm) for males, and 131.0 cm (average = 124.7 cm; SD = 22.0 cm) for females. A maximum length of 299.4 cm is given in males, and 256.1 cm in females. Therefore, both the adult male holotype T. pygmaeus n. sp. and the adult male dwarf manatee that we kept alive for over four months in an enclosure by fencing off a bend in the Rio Arauazinho, had the same total body length as just-born infants of the common manatee T. inunguis. Moreover, the skin in T. inunguis is evenly dark grey colored, with individually very variable irregular elongated white stripes on the abdomen in females and only a few small



Figure 19. Adult dwarf manatee male kept for over four months in a fenced-off river bend of the Rio Arauazinho where it was fed with its local natural food; note the saturated eumelanin black skin, relatively short head, short trunk and flippers, the bristle hairs on the snout, and the large, tear-shaped albinotic white patch on the abdomen.

irregular white blotches in males (Da Silva, pers. comm.). Dwarf manatees, in contrast, are saturated eumelanin coal black, the black pigmentation most likely being an adaptation to its preferred habitat, fast flowing shallow clear-water streams, protecting them from skin burn by UV radiation (Fig. 19). Common Amazonian manatees that are evolutionarily adapted to murky silt-laden white-water or low visibility dark-brown stained black-water, kept in clear-water tanks at INPA, Manaus, have to be protected from severe skin burn by blocking off any direct sunlight (Da Silva, pers. comm.). Male T. pygmaeus n. sp. have a white tear-shaped, ca. 52 cm long patch on the abdomen, greatest width 26 cm (Fig. 19). Flippers of the captive male measuring 32 x 11 cm were too short to reach the mouth. In contrast, the flippers of T. inunguis are proportionately longer in the animals kept at INPA. They are used to push floating stems and foliage toward the trunk and into the mouth. The snout of adult T. pygmaeus n. sp. is beset with long bristle hairs (Fig. 19), whereas that of infants T. inunguis kept at INPA is smooth lacking bristle hairs. The large white ventral patches reported in both sexes of T. pygmaeus n. sp. perhaps have been selectively evolved as protection against stingray attacks (an irregular black-and-white belly pattern may deceive its visual perception) during horizontal browsing of pastures of *Eleocharis minima* Kunth (Cyperaceae) and *Thurnia* spp. (Thurniaceae). These aquatic herbs grow on the sandy bottom of the mostly shallow clear-water Arauazinho River. Those pastures offer ideal hiding places for stingrays of all sizes (Fig. 22).

The holotype skull of T. pygmaeus n. sp. is 24 cm long and 15 cm wide, the rostrum is 6.5 cm in length and lacks the expanded nasal basin of adult T. inunguis. The skull of T. inunguis measures 34 x 19 cm and the rostrum 11.5 cm (Figs. 20, 21). Frontal bones in the holotype skull of an adult male T. pygmaeus n. sp. are convex and 5.1 cm wide, whereas in T. inunguis they are concave and only 4 cm wide (Fig. 21 - note that the skull of the juvenile male T. inunguis, INPA Pb248, is not damaged, but falls apart along the fissures). The skull roof lacks the parasagittal crests of T. inunguis, and the braincase volume in both taxa is about equal being ca. 210 cc. Therefore, it is much larger in T. pygmaeus relative to its total body size. The total number of cheek teeth (fully erupted molars) in each jaw quadrant is 4 in the holotype T. pygmaeus n. sp. (indicating a trend to neotony), but 6(-8) in T. inunguis (Domning & Hayek, 1986). Furthermore, they are much smaller-maxillary molars are 0.9 cm in diameter in T. pygmaeus, and 1.3 cm in diameter in T. inunguis (Fig. 21). While the 3-4 anterior molars in juvenile T. inunguis are hardly worn in comparison to the just erupted posterior molar, this is strikingly different in the holotype T. pygmaeus with the 3 anterior molars strongly worn, thus showing indisputably its adult status (Fig. 18). The skull of the holotype male T. pygmaeus compared with a similar-sized skull (23 x 15 cm) of a young male T. inunguis (INPA Pb248) reveals the following major differences: 1/ the skull of T. pygmaeus n. sp. is thick, robust and solid (the cranial sutures, especially the basisphenoidbasioccipital one, are fully fused), whereas the skull bones of the young T. inunguis are thin and not fused yet, so that its skull falls apart along the fissures; 2/ the frontal bones in T. pygmaeus n. sp. are convex and 5.1 cm wide, whereas in T. inunguis they are concave and only 3.8 cm wide; and 3/ the 3-4 anterior molars in T. pygmaeus are fully worn, whereas in young T. inunguis only three cheek teeth are fully erupted.

The latter are sharply crested and do not show any rate of abrasion (Figs. 18, 21). We have sequenced a fragment of 410 bp of the left domain of the mitochondrial control region (D-loop), using DNA extracted from a skin sample of a living specimen. We used the same primers as were used for T. manatus and T. inunguis in Garcia-Rodriguez et al. (1998). The resulting sequence was identical to the most frequent T. inunguis haplotype-haplotype T, frequency 31% (Garcia-Rodriguez et al., 1998). At first sight, this result seems to be discrepant with the valid species status allocated by us to the dwarf manatee. We first thought this result could be explained by the relatively slow control region mutation rate in manatees, being only 1.5%/1 million years (equivalent to 1 point mutation/163,000 years) between lineages as compared to 8-15%/1million years in most terrestrial mammals (Garcia-Rodriguez et al., 1998). This would indicate a maximum divergence time of 485,000 years before present (p=0.05). Within such a long space of time, sub-specific and even specific dwarfism is possible. For example, episodes of invasion and subsequent dwarfing affected many



Figure 20. Comparing skull and mandible of *Trichechus inunguis* adult female Inpa Pb197; *T. pygmaeus* adult male holotype Inpa CCM181; and *T. manatus* (illustration taken from Husson, 1978). Note the convex and wider frontals in *T. pygmaeus*, and the comparatively greater resemblance of its skull to that of *T. manatus*.



Figure 21. Comparing skull, mandible and cheek teeth (fully erupted molars) of *Trichechus inunguis* adult female Inpa Pb197; *T. pygmaeus* n. sp. adult male holotype Inpa CCM181; and *T. inunguis* juvenile male Inpa Pb248. Note the strikingly different wearing pattern when comparing the cheek teeth of the adult male *T. pygmaeus* n. sp. and the juvenile *T. inunguis*.

insular fossil Elephantidae species from islands in the Mediterranean and Wallacea Seas. Some of these have become dwarfs in less than 5,000 years (Lister, 1993; Lahr & Foley, 2004). Also, Wrangel Island mammoths diminished by about 65% in body size within at most 5,000 years after the severing of the Late Pleistocene land bridge to Eurasia (Lister, 1993). Early Pleistocene large elephants, with which the Sirenians are closely related, swam and walked from the European mainland to the island of Crete. There, they evolved into a 90 kg weighing dwarf species *Elephas creticus* Bate, 1907 (Caloi et al., 1996). It could be hypothesized that common Amazonian manatees once accidentally got trapped in the Rio Arauazinho Basin isolated from the main population in the Rio Aripuanã Basin. Forced to survive in (to the species inappropriate) clear-water habitat, these colonizers may have drastically changed their diet and adopted a different foraging technique. In addition, they might have dwarfed under strong selective pressure of limited food resources. Nowadays, hybridization between the two extant taxa will not take place easily, for dwarf manatee's preferred habitat, diet and foraging strategy is completely different from that of the common Amazonian manatee. However, a local from San Antonio village once reported having seen twenty years ago a group of seven dwarf manatees ("Pretinhos") swimming along the fishing nets he had put up along a sandy beach at Prainha, right bank of Rio Aripuanã, during the peak of the dry season. If true, in theory female dwarf manatees that accidentally drift into the Aripuanã River during the flood season and are not able to return to the Rio Arauazinho (because its mouth has fallen dry earlier than expected), may be fertilized by male T. inunguis. The latter are said to hibernate during the dry season in deep pools in the main Aripuanã River. Even if hybridization would take place only once in the course of tens of thousands of years, some gene flow between populations of both taxa would significantly obscure their true divergence time. Accordingly, we believe that the dwarf manatee should be placed at the base of the phylogenetic tree of all freshwater-adapted manatees. In this quadrant of the Amazon Basin south of the Rio Amazonas and east of the Rio Madeira, it might have adapted to clear-water wetland habitat already in Late Miocene to Early Pliocene, times in which the landscape east of the

proto-Madeira was predominately drained by clearwater rivers and streams - until the Late Pleistocene vicariance that marked the birth of the modern fastflowing Rio Madeira. According to this geophysical scenario, common Amazonian manatees may have derived from archetypical ancestral dwarf manatees during the Pliocene by adapting to black- and white-water floodplain systems. This could have happened after the Amazon reversed its course about 8 MYA and began to drain the East-Andean region into the Atlantic Ocean. At the same time, this evolutionary scenario would explain for the horizontal feeding posture of dwarf manatees in which they stand on their flippers while browsing on aquatic vegetation growing on the bottom of fast-flowing clear-water streams. The horizontal posture of dwarf manatees during feeding and foraging resembles that of marine manatees from which they could have derived during Late Miocene to Early Pliocene, when the Andean uplift was crucial for the evolution of Amazonian landscapes and ecosystems reconfiguring drainage patterns, creating a vast influx of sediments into the Amazon Basin, and boosting its biodiversity (Hoorn & Wesselingh, 2010).

ECOLOGY AND CONSERVATION. Along the lower and middle Rio Aripuanã T. inunguis is during the flood season commonly found in the deep, slowmoving, rather turbid dark waters of the Rio Aripuanã, its floodplain and deep back-water lakes. The latter are filled with black-water coming from local streams that drain nearby alluvial sand savannas. T. pygmaeus n. sp., on the contrary, occurs exclusively in the shallow, fast-flowing, clear waters of the Rio Arauazinho Basin. During the rainy season, the water level of the lower Arauazinho rises over 7 m annually, and the dark rather turbid waters from the Aripuana River then inundate the riparian forest (igapó) fringing the lower Arauazinho. Dwarf manatee's preferred food, most importantly Eleocharis minima R. Br. grass (Cyperaceae), dies off for lack of sunlight. Its rhizomes survive and hibernate in the dark during the flood season. According to locals living in a small community at the mouth of the Arauazinho, and confirmed by us during surveys of the entire Rio Arauazinho Basin in 2006 (on foot) and 2011 (by dugout canoe), shortly before the Rio Aripuanã starts flooding the igapós, a number of dwarf manatees migrate back to the headwater wetlands,



Figure 22. The lower Rio Arauazinho showing the dwarf manatee's preferred habitat: shallow fast-flowing transparent waters with *Eleocharis minima* meadows growing on arenite white-sand substrate. At places shown above, where the river becomes shallow and flows faster, abundantly growing meadows of *E. minima* attract dwarf manatees from as far upriver as the head-water wetlands in the northwest (see Fig. 17). During the entire dry season (July to January), this amphibian herb belonging to the family of Cyperaceae provides the dwarf manatee with its preferred staple food. Then, the Rio Arauazinho is teeming with stingrays in all sizes representing a true danger, for dwarf manatees expose their bellies while standing on their flippers browsing pastures of *E. minima*. Dwarf manatees are reported to associate with "jaraqui" fish *Semaprochilodus insignis* (in a picture above seen swimming near a *Paleosuchus caiman*). The fish's sharp eye-sight together with the manatee's extraordinarily keen sense of hearing seem to provide both species with the perfect audio-visual protection against electric eel and potential predators, such as anaconda, jaguar and man fishing with bow and arrow or harpoon.

swamps and lakes located in the northwest (Fig. 17). From there, they had wandered down during the dry season while feeding upon *Eleocharis minima* meadows that grow locally on a thin layer of arenite sand overlying the pre-Cambrian sandstone bedrock (Fig. 22). During the wet season the entire population is believed to hibernate there while feeding upon *Eleocharis minima*, two aquatic coarse-leaved *Thurnia* Hook.f. species belonging to the aquatic plant family Thurniaceae, one *Cabomba* Aubl. (Cabombaceae) species locally called "camarão", a wild variety of rice (*Oryza* sp.) and several algae (called "sulape"). All these aquatic

food plants grow abundantly in the narrow but locally deep river itself and in the wetlands it drains, that contain numerous clear-water lakes, ponds and swamps dominated by *Mauritia flexuosa* L.f. palms. During the dry season, some animals browsing *Eleocharis minima* meadows may descend as far as seven km from the mouth of the Rio Arauazinho. Before it flows into the Rio Aripuanã, the Arauazinho widens into a 0–30 cm deep lake. During the summer *T. inunguis* cannot enter and *T. pygmaeus* cannot leave the mouth and lower course of the Rio Arauazinho. Therefore, the two parapatric manatee taxa cannot hybridize. Performing above-substrate browsing in a horizontal feeding posture, dwarf manatees appear to have adapted to feeding on (semi-)aquatic herbs that grow attached to the sandy bottom of shallow, fast-flowing clear-water streams. Its seasonally available preferred staple food is *Eleocharis minima*, a Cyperaceae grass that grows in submersed pastures up to 1 m below the surface on a shallow arenite-sandy substrate overlying the sandstone bedrock.

It has edible leaves and rhizomes that the dwarf manatee easily pulls whole from the sandy substrate with its trunk and lips. Chewing the entire plant including the sand-containing rhizomes seems to be responsible for the strong abrasion of the molars as seen in adult T. pygmaeus n. sp. (Figs. 20, 21). In contrast, T. inunguis feeds on floating and submerged plants in deeper waters (>2 m deep), being consumed in situ or, in the case of floating plants, taken below the surface and manipulated into the mouth by the flippers, preferentially if depth allows in a vertical position. While foraging in shallow waters, dwarf manatees when detecting people walking or canoeing along the riverbank immediately seek seclusion in the deep pools found in river bends. There, they stay underwater for three minutes at the most. When on ease, they slowly come to the surface and take a breath every 30-55 seconds.

Trichechus inunguis, when persecuted, can stay underwater up to 20 minutes without breathing. According to the locals and confirmed by our own observations, dwarf manatees tend to associate with schools of "jaraquí" fish (Semaprochilodus insignis - Prochilodontidae) while browsing on Eleocharis minima. This polyspecific association helps to protect them against defensive shocks from electric eels, and attacks of potential predators such as over 8 m long anacondas and spotted jaguars (Fig. 22). Dwarf manatees are considered critically endangered due to their most restricted geographical and ecological range, small population size (we estimate it to be less than 100 individuals), value as game, and their extremely vulnerable and delicate preferred habitat, clear-water streams and wetlands. The skull of the type specimen is recovered from game occasionally killed with bow and arrow and eaten by the locals. Habitat favorable to dwarf manatees occurs, aside of the Rio Arauazinho, only in the basins of two other clear-water tributaries of the lower Rio Aripuanã - Rio Aracú and Rio Juma.

Trichechus pygmaeus n. sp., though, is not reported to exist there. The Rio Aracú Basin has been completely destroyed after a colonization scheme was implanted by the local government in the late 1970s. The Rio Juma Basin has been significantly affected after a goldmine was opened in 2006. Over 10,000 people flocked into the area polluting the Juma and Aripuana Basins using highpressure hose-pipes and large amounts of mercury. Illegal mining of gravel and gold, timber extraction, commercial hunting and fishing in the Rio Aripuanã Basin pose serious threats to the survival of both Amazonian manatee species. The discovery of T. pygmaeus adds to the uniqueness of the lower Aripuanã Basin and shows once more that it is a poorly explored hotspot of biodiversity and endemism. My biodiversity surveys conducted after the year 2000 indicate that the region harbors at least seven primates new to science, four of which being described, including the new genus Callibella never reported or collected before (Van Roosmalen et al., 1998; Van Roosmalen et al., 2000; Van Roosmalen et al., 2002; Van Roosmalen & Van Roosmalen, 2003; 2014; Van Roosmalen, 2013b; 2015). Disturbingly, there is not a single officially protected area in the entire basin.

CONCLUSION. Trichechus pygmaeus n. sp., the dwarf manatee, represents a second taxon of living fresh-water manatees and the smallest (130 cm in length) of all extant sirenians. The new species differs from the other known western Atlantic manatees, *T. inunguis* and *T. manatus*, in being two to three times smaller, with a more streamlined, less bloated appearance, a deep black instead of dark greyish skin, a large symmetrical, circular to tearshaped white patch on the abdomen in at least the males (and reported equally in the females), a shorter head and shorter flippers, the tips of which do not reach the mouth (Fig. 19).

In September 2002, the author collected a complete skull of a recently killed adult male. Two years later, he could film, photograph, examine, and study for the first time an adult male dwarf manatee while keeping it alive for over four months in its natural habitat. It then escaped and returned to its natural environment. Figure 23 shows the fenced-off river bend along the lower course of the Rio Arauazinho in which we kept, fed and observed for

over four months a solitary adult male dwarf manatee that was captured by a local from Arauazinho while feeding on *Eleocharis minima* at about seven km from the confluence with the Aripuanã River. Floating vegetation was systematically refused. Food plants we brought in from the nearby river consequently had to be fixed onto the sandy bottom of his pan in order to be recognized as food, browsed and eaten in a horizontal feeding posture.

Nine years later, Van Roosmalen and Van der Vlist conducted an expedition by canoe and found

the last existing population of dwarf manatees in the wetlands situated along the northern branch of the upper Rio Arauazinho near the watershed with the Rios Uruá and Mariepaua (Figs. 17, 22). Dwarf manatees were found to be fully adapted to foraging in fast-flowing shallow clear-water streams. Standing on their flippers they browse in a horizontal position on aquatic grasses and other non-floating plants that grow on or near the bottom. In contrast, the three times bigger common freshwater manatee *T. inunguis* is restricted to calm



Figure 23. The fenced-off river bend along the lower course of the Rio Arauazinho. Here we kept, fed, filmed and observed for over four months a solitary adult male dwarf manatee that was captured at seven km from the mouth of the Rio Arauazinho by a local from Arauazinho village.

waters of rivers and lakes of the black- and whitewater types offering limited visibility.

It feeds on floating aquatic plants and submersed foliage of floodplain (igapó and várzea) plant species. Mitochondrial control region DNA sequences revealed a haplotype identical to *T. inunguis.* We believe that this resulted from some gene flow that must have taken place in the past, as the two taxa are parapatric and only allopatric in ecological respect.

We consider the dwarf manatee at the verge of extinction, for only the headwaters of the northernmost branch of Rio Arauazinho, a 120 km long left-bank clear-water tributary of the Rio Aripuanã, are thought to harbor a viable relict population.

DISCUSSION

In phyto-sociological respect, the many scrub and open savannas on white-sand alluvial soils in the entire Rio Aripuanã Basin are unique and found nowhere else in the Amazon. Together with the adjacent low savanna forests their branching pattern seen on satellite images does indicate that the entire basin preceding the Late Pleistocene was drained southward - instead of northward like the Rio Aripuanã and its tributaries nowadays drain the area into the Madeira River, and through the Rio Madeira into the Amazonas and eventually into the Atlantic Ocean. The alluvial sand deposits of former Pliocene and Early Pleistocene creeks and rivers show a branching pattern in their headwaters, meaning toward their northernmost end. Toward the southernmost end of the basin, where the Rio Aripuanã later in the Pleistocene originated, is situated nowadays the Tenharim Savanna, a large continuous savanna area. It is located east of the city of Porto Velho, close to the Rio Jí-Paraná, a river that together with the Rio Guaporé drains the western part of the Brazilian Shield into the Rio Madeira. The huge Tenharim Savanna has been interpreted by geo-morphologists as the result of sedimentation in a Quaternary long-lived clearwater inner lake. If we look at the geo-morphological history of the Rio Aripuanã Basin, it is assumed that during part of the Miocene a large freshwater inland lake existed, called the Beni Lake.

This lake stretched westward across the Bolivian Amazon. The brackish-water marine molasses-lakes from the Oligocene might have turned in the Miocene into the fresh-water molasseslakes, and in the Pliocene into the sub-andine inner or inland lakes. During the Pliocene and Pleistocene these lakes filled with rainwater flowing down from the eastern foothills of the (by then) higher Andes Mountains (Hoorn & Wesselingh, 2010). In the Pleistocene era, three main drainage systems or basins were formed in former Amazonia: the whitewater basin influenced by the eroding volcanic Andes in the western part of Amazonia, drained by the proto-Amazon River flowing toward the Atlantic Ocean; the clear-water basin draining the south-east Amazonian crystalline Brazilian Shield with the watershed running across the Chapada dos Parecis toward the south through the proto-Beni, proto-Mamoré, and proto-Guaporé Rivers; thirdly, the black-water basin draining the northern Amazonian alluvial white-sand area through the proto-Rio Negro. During the Late Pleistocene oceanic levels repeatedly have dropped on a global scale and the sub-andine inner lakes were quickly emptied by the much stronger eroding power of the proto-Amazon rushing toward the Atlantic Ocean - its surface lying 100-120 m lower during the subsequent ice ages of the Pleistocene.

During the glacial periods of the Late Pleistocene (1-2 MYA) the ancient continental watershed running across the Chapada dos Parecís has been broken through by the proto-Madeira River, which in turn was connected with the mighty Amazon River. The Madeira/Amazonas drainage system, as a way of speaking, then 'sucked' its way through the watershed powered by huge water volumes on their way to the up to 120 m lower lying water table of the Atlantic Ocean. The vortex holes in what a geologist would call an "unripe riverbed" - in the 400 km long stretch of the upper Madeira River and a shorter stretch in the middle Rio Aripuanã, as well as in the Rio Roosevelt - tell the tale about a former battle over one watershed between two drainage systems, each draining one side of it. The proto-Madeira and Amazonas Rivers thus conquered the clear-water catchment area of the Brazilian Shield. From then on, they made a connection with what was left of the former Pantanal/Chaco Lake through the Mamoré, Beni, and Abuña Rivers. Thereafter, these white-water rivers began to leak the subandine Bolivian drainage system, this time to the north instead of to the east, connected as they now were with the Madeira and Amazon Rivers. The Pantanal/Chaco Lake was quickly emptied out to the east through the Madeira flowing into the Amazon and then into the Atlantic Ocean. In the northern part of the former Pantanal/Chaco Lake one or more clear-water lakes that had formed there since the Pliocene, were now also emptied out by the combined Rios Madeira/Amazonas drainage system.

One of these large clear-water lakes was situated exactly where nowadays the Tenharim Savanna is located, just north of the pre-andine watershed running across the Chapada dos Parecís. This Tenharim Lake was so far fed by rivers running in a north-south direction within what is nowadays the larger Rios Madeira/Amazonas/Tapajós-Juruena interfluvi-um (the Tenharim Lake was drained southward toward the Pantanal through the proto-Guaporé River). After the conquest of the watershed by the combined Madeira/Amazonas drainage system, rivers such as the Jí-Paraná, Roosevelt, Guariba, and Aripuanã began to flow north- and westward, this way draining the entire Aripuanã Basin directly into the Rio Madeira. Clear evidence that rivers like the Aripuanã and Roosevelt originated in a more recent geological era (the Late Pleistocene) is the occurrence of so-called "Strudellöchern" in the crystalline bedrock of the middle and upper courses of these rivers. In the Rio Aripuanã, south of Prainha, are nowadays found the unsurpassable Periquito Falls, among other extensive stretches of rapids and waterfalls. Moreover, the very deep deposits of gravel in the form of small brown rounded-off, polished pebbles that are laid down in calmer waters downstream of the rapids, assign to the afore-mentioned geological (vicariance) event of a Pleistocene watershed break-through.

Once the complex history of South-America's continental landscape and river systems, and, in particular, the relatively recent (Pliocene through Pleistocene) geo-morphological model of the Aripuanã River's drainage system is clearly understood, about all demographic and evolutionary odds of this river basin, that were hitherto considered 'hit and miss' distributions, may now be plausibly explained for. It seems that during a large part of the Pliocene and Early Pleistocene eras the entire pre-Aripuanã river drainage system with its predominantly clear-water habitats was effectively blocked off from Amazonia west and north of the proto-Madeira River, for it was drained by rivers flowing southward toward the eastern part of the late-Miocene sub-andine Pantanal/Chaco Lake, and from there into the Atlantic Ocean. The continental watershed built from pre-Cambrian crystalline rock, together with the (those days) extensive lacustrine habitats, effectively isolated this peripheral drainage system from sub-andine white-water river systems, that were drained by the proto-Madeira and Amazon Rivers. Over millions of years opportunities for allopatric divergence were provided, for no gene flow could take place between non-volant terra firme and aquatic fauna of the clear-water drainage system and the rest of Amazonia, which was drained to the far northeast into the Atlantic Ocean. A number of ground- as well as treedwelling vertebrates, but also aquatic (mostly mammalian and mollusk) fauna, could therefore evolve in seclusion. The first vicariance must have taken place already in the Early-Pliocene, about 5 MYA, when ancestral proto/archetypical forms of all-Amazonian generic groups (i.e., the marmosets, spider-, woolly-, capuchin-, saki-, titi-, night- and howling monkeys, tapirs, anteaters, rodents like porcupines, pacas, agoutis, and acouchis, manatees, and 'botos') have diverged from closely related species found in the rest of the Amazon - to the west and north of the proto-Madeira and Amazon Rivers.

A second, more dramatic vicariance took place during one or more of the glacial epochs of the Middle Pleistocene, about 1-1.8 MYA, the breakthrough of the continental watershed by the proto-Madeira, being in turn powered by the modern Rio Amazonas drainage system in times that ocean levels had dropped over 120 m. So far, this watershed had run across the Serra dos Parecis in the Brazilian State of Rondônia. This way, the modern Madeira River originated and, at the same time, the Rios Aripuanã, Ji-Paraná, Tapajós-Juruena, and, perhaps, also the Rios Xingú and Araguaia, although the headwaters of the latter two rivers are found in the 'cerrado' (white-sand savannas) of Mato Grosso. These rivers also cleared themselves a way through the watershed of the former clearwater north-south directed drainage system and

began to empty their waters into the modern Madeira and Amazonas Rivers. From then on, the Rio Madeira became the rather straight and fastflowing, second largest river barrier in the entire Amazon Basin, after the Amazon proper.

Ever since, no gene flow of terrestrial megafauna could take place to and from the western and northern Amazon. The Rios Aripuanã and Ji-Paraná first emptied out the former Tenharim Lake into the modern Madeira, there where for a long time lacustrine environments and wetlands had deposited white sand. The former clear-water drainage system left behind, aside of the Tenharim Savanna, many smaller patches of white-sand savanna and savanna forest on alluvial sandy soils deposited by former Pliocene and Early Pleistocene rivers and streams. Locally, new rivers arose and began to drain these areas dotted with white-sand savannas and stretches of savanna forest. That explains why they are of the black-water type. To name a few: the Rios Arauá, Mariepaua, Uruá, Manicoré, Atininga, Canumã, Sucundurí, Acarí. Some local rivers draining areas that do not contain alluvial white-sand deposits, but instead having heavily weathered pre-Cambrian arenite (sandstone) reaching the surface, remained of the clear-water type, such as the Rios Aracú, Arauazinho, and Juma. The entire former (Pliocene) clear-water drainage system, from then on, was intersected by new rivers draining the system in opposite (south-north) direction, most importantly the Rios Aripuanã, Tapajós- Juruena, Xingú, Teles-Pires, and Araguaia. In the course of several millions of years, a different biome could develop in this SE Amazon clear-water drainage system harboring a mixture of endemics and newcomers. The latter were ancestral forms of non-volant terrestrial mammals that, after cros- sing the Panamanian land bridge formed between 2.5-3 MYA, had migrated into the northern and western sub-andine regions of the Amazon. Subsequently, some managed to traverse the proto-Madeira River and established themselves in most of this ancient clear-water drainage system.

As such, newcomers such as ancestral collared and white-lipped peccaries, jaguars, pumas, small cats, canids, coatis and mustelids, lived side by side with endemics such as primates, rodents (squirrels, pacas, agoutis, acouchis, capybaras, spiny rats), marsupials (Didelphidae), edentates (anteaters, armadillos, sloths), tapirs, and porcupines. Not before the last glacial period of the Holocene, about 10,000 YA, some modern mega-fauna elements, among which the common spotted paca A. paca, that had evolved west and north of the strong geographic barrier formed by the non-meandering Rio Madeira, managed to circumvent the headwaters of the Rio Madeira. Thereafter, they migrated into the Rios Madeira/Tapajós interfluvium. They took either the northwestern route following the western border of the Tenharim Savanna, or the southeastern route circumventing the Tenharim Savanna along the southern border, or they migrated into the Rios Madeira/Tapajós interfluvium along both paths. So, they entered a different ecosystem full of phylogenetically related but formerly allopatric species endemic to the region. Consequently, the new-comers may then have outcompeted closely related species that occupied similar ecological niches, causing their extinction. Or, one species may have become genetically absorbed by the other through cross-breeding. Or, allopatric species may have diverged that much from one another in habitat and dietary preferences. foraging strategy and/or social and sexual behavior, that they were able to co-exist and live on in sympatry. The latter scenario may well explain, for instance, the sympatric occurrence in the Rio Aripuanã Basin of two different species of brocket deer (i.e., Mazama nemorivaga and M. tienhoveni n. sp.) and two different species of paca (i.e., the common spotted paca A. paca and Silva Garcia's striped giant paca A. silvagarciae n. sp.).

ACKNOWLEDGEMENTS

Molecular analyses were co-financed by the Treub Stichting (Society for the Advancement of Research in the Tropics), and performed at the Animal Breeding and Genomics Centre of Wageningen University, The Netherlands. The author received a grant for conducting biodiversity fieldwork in the Aripuanã region from the Van Tienhoven Foundation for International Nature Conservation. We are grateful to René Dekker and Hein van Grouw of The Netherlands Natural History Museum Naturalis in Leiden, who kindly provided their museum specimens for our comparative research on the genus *Mazama*.

REFERENCES

- Caloi L., Kotsakis T., Palombo M.R. & Petronio C., 1996. In: Shoshani J. & Tassy P. (Eds.), 1996. The Proboscidae: evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford, 234–239.
- Domning D.P. & Hayek L.C., 1986. Interspecific and intraspecific morphological variation in manatees (Sirenia: *Trichechus*). Marine Mammal Science, 2: 87–144.
- Duarte J.M.B., 1996. Guia de identificação de Cervídeos Brasileiros. FUNEP. Jaboticabal.
- Duarte J.M.B., González S. & Maldonado J.E., 2008. The surprising evolutionary history of South American deer. Molecular Phylogenetics and Evolution, 49: 17–22.
- Eisenberg J.F., 1989. Mammals of the Neotropics. The Northern Neotropics, Vol. 1. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago, 449 pp.
- Eisenberg J.F. & Redford K.H., 1999. Mammals of the Neotropics, Vol.3. The Central Neotropics: Ecuador, Peru, Bolivia, Brazil. Chicago: University of Chicago Press, Chicago, 609 pp.
- Emmons L.H. & Feer F., 1990. Neotropical rainforest mammals. A field guide. University of Chicago Press, Chicago, 281 pp.
- Garcia-Rodriguez A.I., Bowen B.W., Domning D., Mignucci-Giannoni A.A., Marmontel M., Montoya-Ospina R.A., Morales-Vela B., Ruding M., Bonde R.K., & McGuire P.M., 1998. Phylogeography of the West Indian Manatee (*Trichechus manatus*): how many populations and how many taxa? Molecular Ecology, 7: 1137–1149.
- Hoorn C. & Wesselingh F.P., 2010. Introduction: Amazonia, landscape and species evolution - a look into the past. Wiley-Blackwell, Oxford, 477 pp.
- Husson A.M., 1978. The Mammals of Suriname. Rijksmuseum van Natuurlijke Historie. Zoologische Monografieen. No. 2, E.J. Brill, Leiden, The Netherlands, xxxiv + 569 pp.
- Kimura M., 1980. A simple method for estimating evolutionary rates of base substitutions through compa- rative studies of nucleotide sequences. Journal of Molecular Evolution, 16: 1–20.
- Kocher T.D., Thomas W.K., Meyer A., Edwards S.V. & Paabo S., 1989. Dynamics of mitochondrial-DNA evolution in animals - amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences, 86: 6196– 6200.
- Lahr M.M. & Foley R.A., 2004. Palaeo-anthropology: Human evolution writ small. Nature, 431, 1043– 1044.

- Lister A.M., 1993. Mammoths in miniature. Nature, 362: 288–289.
- Rossi R.V., 2000. Taxonomia de Mazama Rafinesque, 1817 do Brasil (Artiodactyla, Cervidae). Master's thesis, Instituto de Biociências, Universidade de São Paulo, 1–174.
- Tamura K., Dudley J., Nei M. & Kumar S., 2007. MEGA4: Molecular evolutionary genetics analysis (MEGA) software version 4.0. Molecular Biology and Evolution, 24: 1596–1599.
- Van Roosmalen M.G.M., 2013a. Barefoot through the Amazon - On the path of evolution. Paperback, 500 pp. https://www.createspace.com/ 4177494
- Van Roosmalen M.G.M., 2013b. Wild fruits from the Amazon Vol. I. Paperback, 280 pp. https://www. createspace.com/4177494
- Van Roosmalen M.G.M., 2014. Distributions and phylogeography of Neotropical primates - A pictorial guide to all New World monkeys. Paperback, 71 pp. https://www.createspace.com/ 4596480
- Van Roosmalen M.G.M., 2015. Live from the Amazon. Elliot Editori, Rome, Italy, 608 pp.
- Van Roosmalen M.G.M. & Van Roosmalen T., 2003. The description of a new marmoset genus, *Callibella* (Callitrichinae, Primates), including its molecular phylogenetic status. Neotropical Primates, 11: 1–10.
- Van Roosmalen M.G.M. & Van Roosmalen T., 2014. On the origin of allopatric primate species and the principle of metachromic bleaching. Paperback, 146 pp. https://www.createspace.com/ 4549738
- Van Roosmalen M.G.M., Frenz L., Van Hooft P., De Iongh H.H. & Leirs H., 2007. A new species of living peccary (Mammalia: Tayassuidae) from the Brazilian Amazon. Bonner zoologische Beiträge, 55: 105–112.
- Van Roosmalen M.G.M., Van Roosmalen T., Mittermeier R.A. & De Fonseca G.A.B., 1998. A new and distinctive species of marmoset (Callitrichidae, Primates) from the lower Rio Aripuanã, State of Amazonas, central Brazilian Amazon. Goeldiana, Zoologia, 22: 1–27
- Van Roosmalen M.G.M., Van Roosmalen T., Mittermeier R.A. & Rylands A.B., 2000. Two new species of marmoset, genus *Callithrix* Erxleben, 1777 (Callitrichidae, Primates) from the Tapajós/Madeira interfluve, south central Amazonia, Brazil. Neotropical Primates, 8: 2–18.
- Van Roosmalen M.G.M., Van Roosmalen T. & Mittermeier R.A., 2002. A taxonomic review of the titi monkeys, genus *Callicebus* Thomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*, from Brazilian Amazonia. Neotropical Primates, 10 (Supplement): 1–52.
- Vergara-Parente J.E., Parente C.L., Marmontel M., Silva J.C.R. & Sá F.B., 2010. Growth curve of free-ranging *Trichechus inunguis*. Biota Neotropica, 10: 89–93.

- Von Spix J.B. & Von Martius C.F.Ph., 1823-1831. Reise in Brasilien in den Jahren 1817-1820. 3 Vols. + 1 Atlas. Verlag M. Lindauer, München, 1388 pp. Reprint 1967, Stuttgart.
- Voss R.S. & Da Silva M.N.F., 2001. Revisionary notes on Neotropical porcupines (Rodentia: Erethizontidae). 2. Review of the *Coendu vestitus* Group with descriptions of two new species from Amazonia. Novitates, American Museum for Natural History,

New York, 3351: 1-36.

- Webb S.D., 2000. Evolutionary history of new world deer. In: Vrba E.S. & Schaller G.B. (Eds.), 2000. Antilopes, Deer, and Relatives. Yale University Press, London, 38–64.
- Wilson D.E. & Reeder D.M. (Eds.), 1993. Mammal Species of the World. A Taxonomic and Geographic Reference. John Hopkins University Press, Baltimore, 1206 pp.