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ORIGINAL PAPER

Western Amazonia as a Hotspot of Mammalian Biodiversity Throughout the Cenozoic

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Abstract A state-of-the-art review of the Cenozoic fossil record from Western Amazonia is provided, based on literature and new data (regarding Paleogene native ungulates). It allows summarizing the evolution and dynamics of middle Eocene–Holocene mammalian guilds, at the level of species, families, and orders. Major gaps in the Western Amazonian mammal record occur in the pre-Lutetian and early Miocene intervals, and in the Pliocene epoch. Twenty-three orders, 89 families, and 320 species are recognized in the fossil record, widely dominated by eutherians from the middle Eocene onward. Probable Allotheria (Gondwanatheria) occur only in the earliest interval, whereas Metatheria and Eutheria are conspicuous components of any assemblage. Taxonomic diversity was probably fairly constant at the ordinal level (~12–14 orders in each time slice considered) and much more variable in terms of family and species richness: if most intervals are characterized by 40–50 co-occurring species and 19–31 co-occurring families, the early Miocene period illustrates a depauperate fauna (21 species, 17 families), strongly contrasting with the late Miocene climactic guild (82 species, 38 families). Recent mammalian taxonomic diversity from Western Amazonia (12 orders, 37 families, and 286 species) is at odds with all past intervals, as it encompasses only three orders of South American origin (Didelphimorphia, Cingulata, and Pilosa) but four North American immigrant orders (Artiodactyla, Perissodactyla, Carnivora, and Lagomorpha). In terms of taxonomic diversity, recent mammalian guilds are fully dominated by small-sized taxa (Chiroptera, Rodentia, and Primates). This overview also confirms the scarcity of large mammalian flesh-eaters in ancient Neotropical mammalian assemblages. The pattern and the timing of mammalian dispersals from northern landmasses into Western Amazonia are not elucidated yet.

Keywords Amazonian lowlands · Neotropics · mammalian guilds · Biochronology · Paleobiodiversity · Historical geography

Introduction

In spite of being intensively covered by either water or vegetation, Cenozoic deposits from Western Amazonia have yielded a wide range of fossil mammals, documenting three major lineages (Allotheria, Metatheria, and Eutheria). Most of these mammals are highly relevant to test major evolutionary and/or biogeographic hypotheses at either the Neotropical, South American, or Panamerican scale. Before the 1980s, specimens collected in Western Amazonian lowlands were primarily recovered as isolated or float remains, with poor stratigraphic constraints (e.g., Spillmann 1949; Willard 1966; Simpson and Paula-Couto 1981). Nevertheless, the fossil record has been widely substantiated in the meantime, thanks to considerable field efforts by international

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multidisciplinary teams, mostly focusing on Brazilian, Peruvian, and (to a lesser extent) Bolivian Amazonian lowlands (Fig. 1; see Antoine et al. 2016 for a review). In contrast, virtually no pre-Pleistocene mammal remain is known from Ecuadorian or Colombian Amazonian lowlands so far (Marshall et al. 1983; Webb and Rancy 1996).

This contribution aims at providing a state-of-the-art review of the Cenozoic mammalian record from Western Amazonia (mainly from Peru and Brazil), notably by incorporating new specimens of large Paleogene native ungulates (Figs. 2 and 3). Based on this Neotropical record, we summarize the evolution and dynamics of mammalian guilds in the same time and space at the ordinal, familiar, and specific levels (Fig. 4).

Material and Methods

We have primarily taken into account time-constrained localities from the concerned area, further privileging plurispecific assemblages described in the literature and/or new ones uncovered by our team. Detailed information about the inferred age of all localities (hypothesized standard age and reference to a South American Land Mammal Age [SALMA]) and their mammalian content (faunal lists) can be found in Supplemental Material.

We have restricted our locality sample to Western Amazonian lowlands as observed today, i.e., matching the Amazon hydrographic basin (eastern Bolivia, western Brazil, southeastern Colombia, southeastern Ecuador, and eastern Peru) and bordered to the east by the Carauari Arch (Mora et al. 2010). We have included a few data from subandean zone low-altitude localities of Bolivia (Río Yapacani and Quebrada Saguayo; Marshall et al. 1983) and Peru (Bagua-La Bocana and Upper Madre de Dios; Fig. 2). Species-rich Andean localities, such as Salla (Bolivia, late Oligocene), Quebrada Honda (Bolivia, late middle Miocene), or La Venta (Colombia, late middle Miocene), were not taken into account in our study, as they fall outside Western Amazonian lowlands today, even though the concerned areas were probably part of a single biogeographic

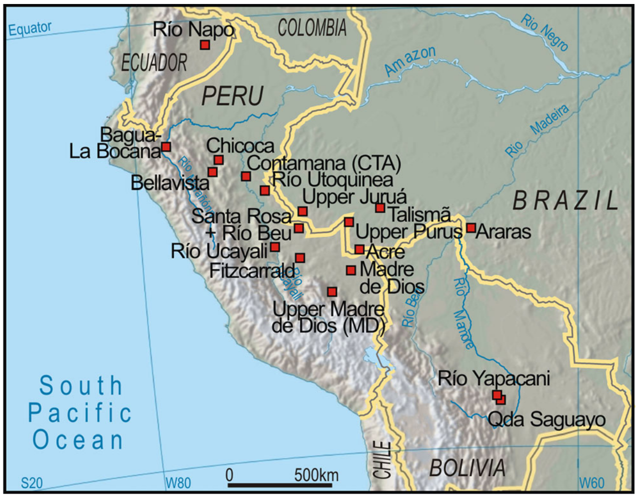

Fig. 1 Location map of Cenozoic mammal-bearing localities from Western Amazonia (Bolivia, Brazil, and Bolivia) mentioned in the text. Qda, Quebrada. Based on Marshall et al. (1983), Negri et al. (2010), Ribeiro et al. (2013), and Antoine et al. (2016)

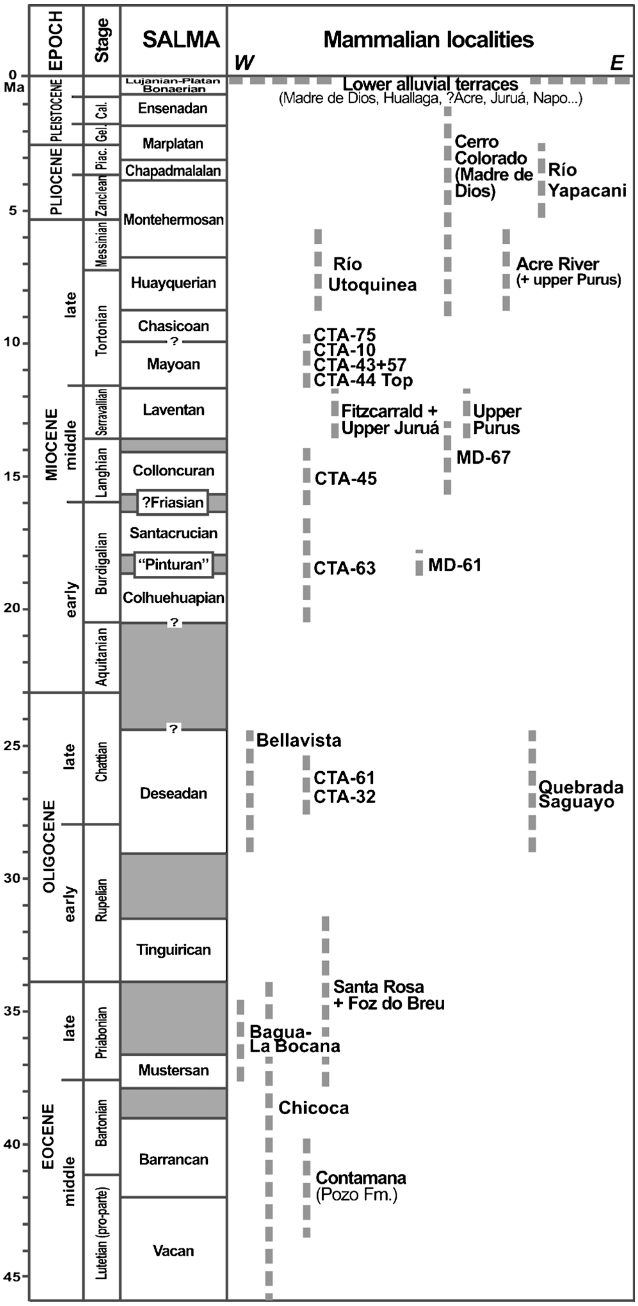

Fig. 2 Stratigraphic chart of Cenozoic mammal-bearing localities from Western Amazonia mentioned in the text. CTA, localities from Contamana; Fm., Formation; MD, localities from the Upper Madre de Dios. Based on Simpson and Paula Couto (1981), Antoine et al. (2012, 2013, 2016), Marivaux et al. (2012), Ribeiro et al. (2013), and Tejada-Lara et al. (2015)

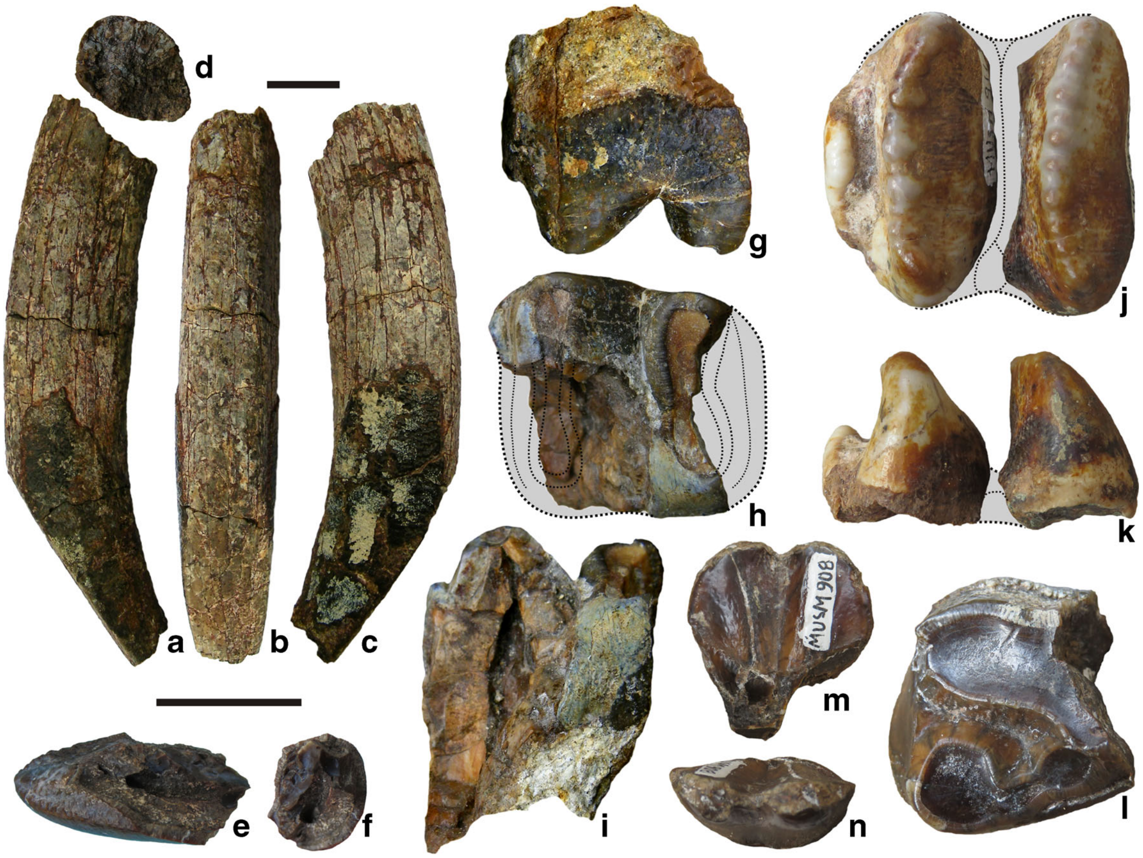

Fig. 3 Mammalian remains from Paleogene deposits of Peruvian Amazonia. **a-d** Astrapotheriidae indet., upper canine in lingual (a), mesial (b), and labial views (c), and cross-section (d). Bagua-La Bocana, Amazonas, late Eocene. **e-f** *Baguatherium jaureguii*, tip of an unworn anterior tooth, in buccal view (e) and cross section (f). Bagua-La Bocana, Amazonas, late Eocene. **g-i** *Pyrotherium macfaddeni*, right m1 in lingual (g), occlusal (h), and labial views (i). Bellavista, San Martín, late Oligocene (Deseadan). The occlusal outline is reconstructed based on Shockey and Anaya Daza (2004). **j-k** *Pyrotherium* cf. *macfaddeni*, right m3 in occlusal (j) and labial views (k). Surface collection, Río Beu, Ucayali, supposedly late Oligocene (Deseadan) in age. **l-n** Uruguaytheriinae indet., right P4 in occlusal view (l) and i3 in lingual (m) and occlusal views (n). Surface collection, Río Beu, Ucayali, supposedly late Oligocene (Deseadan) in age. Scale bars = 2 cm (a–d) and 1 cm (e–n)

province by that time (e.g., Marshall et al. 1983; Croft 2007; Tejada-Lara et al. 2015).

Biases in species-richness and relative abundance may be due to taphonomic factors (e.g., hydrodynamics or predation) and result in the over-representation and better taxonomic assignment of micromammals with respect to meso- and megamammals, particularly perceptible for early time intervals, as it adds to a sampling bias (due to intensive screen-washing; e.g., Contamana and Santa Rosa localities; Antoine et al. 2016). On the other hand, large mammals are widely overrepresented whereas micro- and meso-mammals are virtually absent from historical findings (e.g., Spillmann 1949; Willard 1966), especially in Pleistocene–Holocene fluvial deposits (e.g., Simpson and Paula-Couto 1981; Rancy 1991; Webb and Rancy 1996; Latrubesse and Rancy 1998), as they were merely resulting from surface collecting.

The evolution of mammalian guilds in Western Amazonia throughout the middle Eocene–Holocene interval is illustrated in Fig. 4. It was analyzed at the specific, familial, and higher levels (= order-group; for further information, see Antoine et al. 2016). Time intervals coincide mostly with successive sub-epochs or epochs (Gradstein et al. 2012): middle Eocene, late Eocene–early Oligocene, late Oligocene, early Miocene, middle Miocene, late Miocene, Pliocene (almost no attested record), and Pleistocene–Holocene. The concerned assemblages result from compiled taxonomic lists (either available in the literature or corresponding to original work), as detailed in the Supplemental Material.

Results

This section provides a group-based review of the Cenozoic mammalian record in Western Amazonia. To our knowledge, the earliest mammalian remain from Amazonian lowlands is an enamel fragment showing Hunter-Schreger bands originating from upper Paleocene marginal marine deposits in the Upper Madre de Dios, Peru (Mammalia indet., MD-85

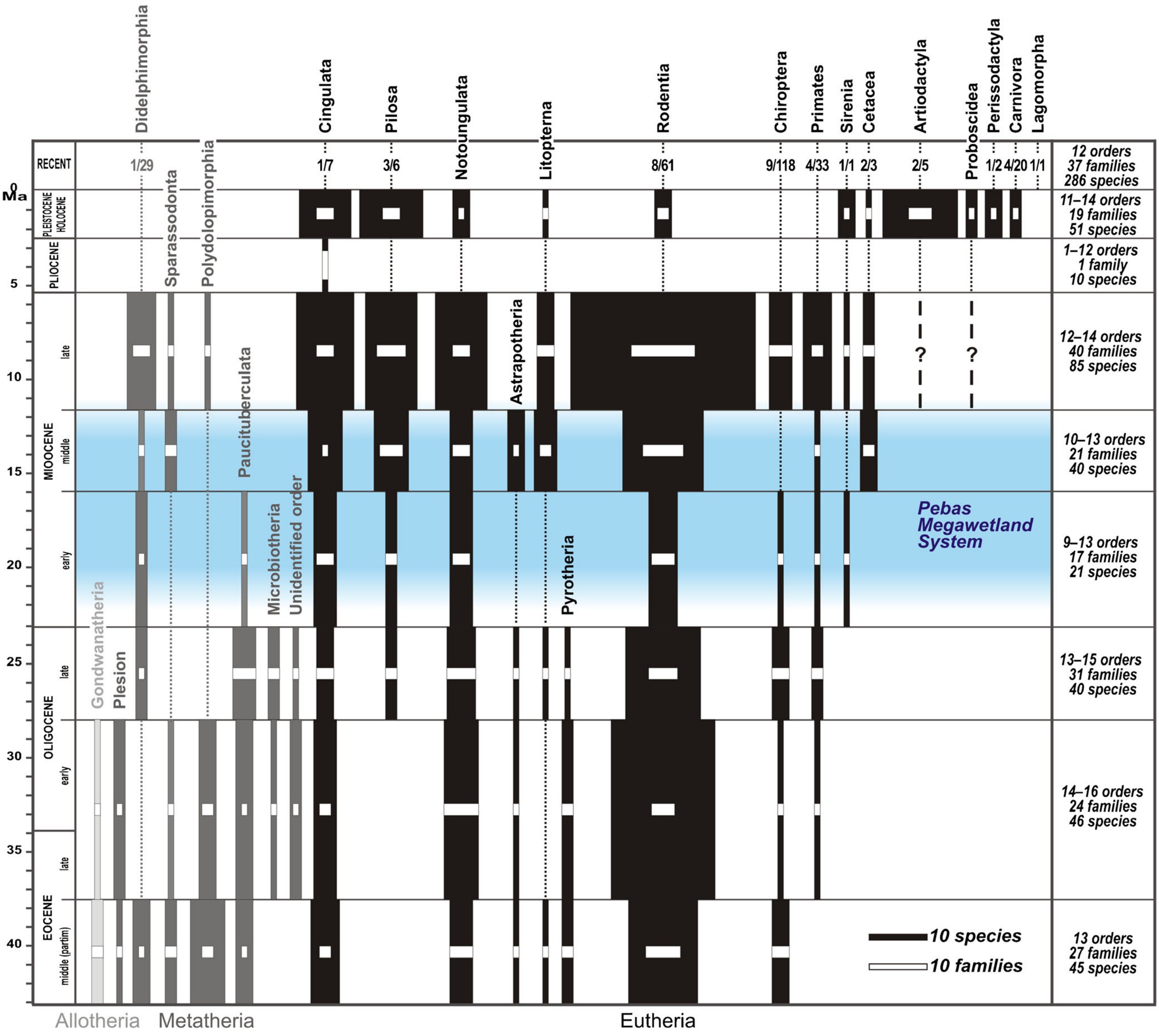

Fig. 4 Mammalian taxonomic diversity in Western Amazonia from the middle Eocene onward. Evolution of diversity through time, at the ordinal, familial, and specific levels within Allotheria, Metatheria, and Eutheria. Time intervals considered coincide with standard ages of fossil-yielding localities: middle Eocene, late Eocene + early Oligocene (most localities are not constrained enough to split that interval), late Oligocene, early Miocene, middle Miocene, late Miocene, Pliocene, Pleistocene–Holocene, and Recent. Many families are monospecific, mostly due to sampling biases (low specimen number per locality). See Supplemental Material for taxonomic lists and counts. Scale bars = 10 taxa (*grey or black*: species; *white*: families). For recent orders, numbers denote family/species diversity based on Eisenberg and Redford (2000). The temporal extension of the Pebas Mega-Wetland System is provided by Salas-Gismondi et al. (2015)

locality; Louterbach et al. 2014). Identifiable remains range from the late middle Eocene (Pozo Formation [Fm.], Contamana, Peru; Figs. 1 and 2; Antoine et al. 2012, 2016) to the Holocene (e.g., Rancy 1991; Latrubesse and Rancy 1998).

Three major mammaliaform groups are recorded in the Cenozoic of Amazonian lowlands: (1) probable Allotheria (Gondwanatheria) occur only in Contamana (CTA-27, late middle Eocene; unidentified ?sudamericid) and in Santa Rosa (?late Eocene-early Oligocene; unnamed taxon of uncertain affinities), which would coincide with both the last occurrences of this enigmatic group in South America and the only ones in northern South America (Goin et al. 2004, 2012; Antoine et al. 2012, 2016). In contrast, (2) Metatheria and (3) Eutheria are conspicuous components of any corresponding mammalian assemblage from the middle Eocene onward (Fig. 4).

Among Metatheria, probable herpetotheriids (*Rumiodon* spp.) were identified in the middle Eocene–?early Oligocene interval in the CTA-27 locality at Contamana and Santa Rosa

(Goin and Candela 2004; Antoine et al. 2016). Didelphimorphians (middle Eocene–late Miocene), documented by scarce dental remains, are either of uncertain affinities or referred to as marmosids (*Marmosa* (*Micoureus*) cf. *laventica*; MD-67, Upper Madre de Dios, middle Miocene; Antoine et al. 2012) and didelphids (unidentified didelphids and *Didelphis solimoensis*; Acre, late Miocene; Czaplewski 1996; Negri et al. 2010). Western Amazonia shelters 29 species of living didelphids (Eisenberg and Redford 2000). Sparassodonta remains are also scarce, small-sized (except the large canine from Fitzcarrald; Tejada-Lara et al. 2015), and requiring a taxonomic revision (four unidentified borhyaenoids are mentioned); the hathliacynids *Patene campbelli* and *Sipalocyon* sp. were recognized in Santa Rosa (late-Eocene-early Oligocene; Goin and Candela 2004) and in MD-67 (middle Miocene; Antoine et al. 2012; Fig. 4), respectively. Polydolopimorphians are abundant, small-sized, and quite diversified in the middle Eocene–early Oligocene interval (Pozo Fm. in Contamana, Santa Rosa locality; Figs. 2 and 4), with bonapartherioids-argyrolagoids (*Wamradolops* and close allies, plus *Hondonadia pittmanae*), and prepidolopids (*Incadolops ucayali* and two unidentified species; Goin and Candela 2004; Antoine et al. 2016). This range coincides with the climax of polydolopimorphians at middle and high latitudes (Goin et al. 2012). After this interval, a single late Miocene occurrence is attested for polydolopimorphians, corresponding to a lower molar of an argyrolagid recovered in CTA-44 (Mayoan SALMA; Antoine et al. 2016). Paucituberculatans are only recorded in the middle Eocene-early Miocene interval (Fig. 4; Supplemental Material). Santa Rosa and late middle Eocene localities from Contamana yielded palaeothentoids of uncertain affinities (*Sasawatsu* spp., *Perulestes* spp., and/or cf. *Perulestes*), whereas Deseadan SALMA localities from Contamana (Fig. 2) record abderitids (*Abderites* sp. and cf. *Abderites*), a possible palaeothentid, and a probable caenolestid (Goin and Candela 2004; Antoine et al. 2016). The only post-Paleogene paucituberculatan from Western Amazonia is an unidentified ?caenolestid in CTA-63 (early Miocene; Colhuehuapian–Santacrucian SALMAs; Antoine et al. 2016). Finally, two enigmatic metatherians were described in Santa Rosa (*Wirunodon chanku* and *Kiruwamaq chisu*; Goin and Candela 2004).

Eutherians have a far much better fossil record in Amazonian lowlands than allotherians and metatherians, in terms of both abundance and taxonomic diversity (Fig. 4; Supplemental Material). Fifteen orders are documented, either pertaining to South American natives (Cingulata and Pilosa, within Xenarthra; Notoungulata, Astrapotheria, Litopterna, and Pyrotheria among native ungulates), originating from remote landmasses (Rodentia, Chiroptera, and Primates), having aquatic habitats (Sirenia and Cetacea), or being North American invaders (Proboscidea, Artiodactyla, Perissodactyla, and Carnivora). Thus far, Lagomorpha have no fossil record in Western Amazonia.

Xenarthran remains consist of cingulates (Dasypodidae, Glyptodontidae, Pampatheriidae, and incertae sedis) and folivoran pilosans (mylodontoid and megatherioid sloths), whereas no vermilinguan pilosan is recorded (in contrast with recent times and with La Venta, middle Miocene of Colombia; Kay and Madden 1997). Cingulates are recognized in all intervals (Fig. 4), mainly on the basis of isolated and often fragmentary osteoderms, which in turn somewhat blur their taxonomic assignment (see discussion in Gaudin and Croft 2015). Dasypodids have a middle Eocene–Recent range, with conspicuous representatives such as *Stegosimpsonia* (late middle Eocene, Contamana; Antoine et al. 2016), *Parastegosimpsonia* (Santa Rosa; Ciancio et al. 2013), or *Anadasypus* (Acre, late Miocene; Ribeiro et al. 2013). Glyptodontids are first recorded in CTA-32 (late Oligocene; Fig. 2) with a close ally of *Neoglyptatelus* (Antoine et al. 2016) and they reach a climax by late middle Miocene times (Fitzcarrald; Supplemental Material; Tejada-Lara et al. 2015). *Glyptodon* and other glyptodontids (e.g., *Hoplophorus* and *Sclerocalyptus*) occur in Pleistocene localities from Brazil (Upper Juruá), Ecuador (Río Napo; Rancy 1991), and/or Peru (Río Ucayali) and isolated osteoderms are also recovered floating on river banks (e.g., Río Inuya, Peru; Willard 1966; Antoine et al. 2007). Pampatheriids have a fairly long and continuous range (late Oligocene–late Pleistocene). In particular, the unidentified pampatheriid from CTA-61 (late Oligocene, Deseadan SALMA; Fig. 2) may be among the earliest representatives of the family (Salas-Gismondi et al. 2011). Acre local fauna yields *Scirrotherium carinatum* (Góis et al. 2013 and references therein). *Vassallia minuta* occurs in Río Yapacani, Bolivia (Pliocene; Marshall et al. 1983). *Pampatherium* and *Holmesina* are recognized in Brazilian late Pleistocene deposits of Upper Juruá and Araras/Periquitos, respectively (Rancy 1991; Holanda et al. 2011; Góis et al. 2012). Other cingulates of uncertain affinities, such as *Yuruatherium tropicalis* (Santa Rosa; Ciancio et al. 2013) and *Eocoleophorus glyptodontoides* (CTA-29, Pozo Fm., late middle Eocene; Salas-Gismondi et al. 2011; Antoine et al. 2016) occur in Paleogene Peruvian localities (Supplemental Material). The latter species was previously restricted to the Oligocene locality of Tremembé, eastern Brazil; Oliveira et al. 1997) and the cingulate from CTA-29 may show closer affinities to a new taxon from the Paleogene fauna of Guabirotuba (southeastern Brazil; Sedor et al. in revision). The earliest sloths from Western Amazonia are unidentified late Oligocene mylodontoids (CTA-61; Antoine et al. 2016). Mylodontids occur throughout the post-Oligocene interval, with three associated genera in the late Miocene Acre assemblage (*Urumacotherium*, *Pseudoprepotherium*, and cf. *Ranculcus*; Ribeiro et al. 2013). *Oreomylodon wegneri*, *Lestodon armatus*, and

Catonyx sp. (*Scelidotherium* sp. in Rancy 1991) are recognized in Pleistocene deposits of Upper Juruá (Rancy 1991; Latrubesse and Rancy 1998). The late Pleistocene Río Napo assemblage in Ecuador yields *Mylodon* sp. (e.g., Rancy 1991). Holanda et al. (2011) mentioned a close ally of *Ocnotherium* in the late Pleistocene Rio Madeira Fm. (Araras/Periquitos, Brazil). The mylodontid *Octodontobradys* (often assigned to Orophodontidae among Mylodontoidea) is recorded in the Acre local fauna and CTA-57 (early late Miocene; Fig. 2). An early diverging megatherioid, cf. *Hapalops*, occurs in the ?early-middle Miocene Talismã locality (Purus River, Amazonas, Brazil; Ribeiro et al. 2013). The earliest megatheriids from Amazonian lowlands are the planopsine cf. *Planops* (Talismã; Ribeiro et al. 2013) and the megatheriine *Megathericulus* sp. (Fitzcarrald, late middle Miocene; Pujos et al. 2013). Small-sized *Megatherium* species and the large-sized *Eremotherium laurillardi* are recorded in most Pleistocene lowland localities from Peru, Brazil, and Ecuador (Rancy 1991; Pujos and Salas 2004; Supplemental Material). Megalonychids have a middle Miocene–Recent range, with *Pliomorphus*, a close ally of *Protomegalonyx* in the late Miocene of Acre (Ribeiro et al. 2013), and representatives of *Megalonyx* and *Ocnopus* in the Pleistocene of Upper Juruá (Rancy 1991). A single nothrotheriine occurrence is attested in the late Miocene of Acre (De Iuliis et al. 2011), with a sub-complete skeleton of *Mionothropus cartellei*, previously considered as Holocene in age (=*Nothropus priscus* in Frailey 1986). All other Pleistocene nothrotheriine occurrences in Western Amazonia are unclear (e.g., Rancy 1991; Webb and Rancy 1996). Three species of tree sloths (Bradypodidae and Megalonychidae) live today in the studied area.

South American native ungulates are a conspicuous element of most inventoried faunas (Supplemental Material). Four orders out of five are documented (Notoungulata, Astrapotheria, Litopterna, and Pyrotheria; Fig. 4). Xenungulata are not known in Amazonian lowlands primarily because they are restricted to the Paleocene–early Eocene interval (Gelfo et al. 2008; Woodburne et al. 2014), lacking any mammalian record in the studied area. Nevertheless, xenungulates may have roamed these lowlands during early Paleogene times, as both "etayoids" and carodniids have an early Eocene record in nearby regions, with *Etayoa bacatensis* in Bogotá, Colombia (Villarroel 1987) and *Carodnia inexpectans* in northwestern Peru (Antoine et al. 2015). Notoungulata are the most diversified native ungulate order in Western Amazonian assemblages, with a late Miocene climax (Fig. 4). They span the middle Eocene–Pleistocene interval, with Typotheria ("Archaeohyracidae," Interatheriidae, and Hegetotheriidae; middle Eocene–late Miocene) and Toxodontia (Toxodontidae, Leontinidae, and Notohippidae; middle Eocene–latest Pleistocene), the earliest records of which consist mainly of isolated teeth or tooth fragments (e.g., Antoine et al. 2012, 2016). "Archaeohyracids" are restricted to the late middle Eocene of Contamana (unidentified taxon, CTA-27; Antoine et al. 2012). Interatheriidae occur throughout the documented interval. They are mostly referred to as taxa of uncertain affinities (unidentified interatheriines in CTA-27, Santa Rosa, CTA-61, and CTA-57; Shockey and Anaya Daza 2004; Antoine et al. 2016); *Miocochilius anamopodus* is found in Fitzcarrald (Laventan; Tejada-Lara et al. 2015). The single occurrence of a hegetotheriid is *Prohegetotherium*? sp. from CTA-61 (Deseadan SALMA; Antoine et al. 2016). Toxodontia are much better represented, first by unidentified taxa (Contamana [Pozo Fm. localities], Santa Rosa, and La Bocana-Bagua; Shockey and Anaya Daza 2004; Antoine et al. 2016; this work), then by toxodontids, from Deseadan deposits (CTA-61) onward (Supplemental Material; MacFadden 2005). A systematic revision would be needed as multiple synonymies can be alleged among the Amazonian representatives of *Pericotoxodon*, *Gyrinodon*, *Trigodon*, *Palaeotoxodon*, *Paratrigodon*, *Trigodonops*, "*Plesiotoxodon*," and *Neotrigodon* (e.g., Ribeiro et al. 2013). Dental remains referred to as *Toxodon* sp. and/or *Mixotoxodon* sp., and/or *Trigodonops lopesi* are recorded until the latest Pleistocene in Bolivian, Brazilian, and Peruvian Amazonia (Rancy 1991; MacFadden 2005; Holanda et al. 2011). Leontiniids and notohippids are recognized in Paleogene deposits of Santa Rosa (unidentified leontiniid and ?*Eomorphippus*, respectively; Shockey and Anaya Daza 2004), in the early-middle Miocene locality 28 from the Upper Juruá (*Purperia cribatidens*; Ribeiro et al. 2013), and in late Miocene Acre localities (unidentified notohippid; Ribeiro et al. 2013).

Two families are documented among Astrapotheria: Trigonostylopidae (?*Trigonostylops* in CTA-27, late middle Eocene; Antoine et al. 2012, 2016) and Astrapotheriidae (late Eocene–middle Miocene). A large-sized astrapotheriid occurs in Bagua-La Bocana (Figs. 1 and 2). This locality was described as being Oligocene, "pre-Deseadan" in age, by Salas et al. (2006). Yet, it may date back to the late Eocene instead (Mustersan SALMA), with new ^{40}Ar/^{39}Ar constraints between 36.47 ± 1.74 Ma and 36.15 ± 0.91 Ma for feldspars from volcanic ashes located 20 m below and 10 m above the vertebrate locality, respectively (see Supplemental Material). The corresponding astrapotheriid fossil is an upper canine with characteristic pear-like cross section, weak curvature, continuous enamel around the crown, and flat shearing surface (Fig. 3a–d). Although of greater dimensions (preserved length = 160 mm; cross section = 36x25 mm), its morphology is similar to that of *Astraponotus* from coeval deposits of Patagonia (e.g., Kramarz et al. 2011). It is also reminiscent of the upper canines of younger large astrapotheriids, such as *Astrapotherium* and *Parastrapotherium* (Kramarz and Bond 2008). Two isolated teeth of a large astrapotheriid were collected in the early 2000s as float specimens on a bank of the Río

Beu, in the Santa Rosa Native Community, less than 2 km away from the Santa Rosa locality; Fig. 2). The first one is interpreted as a third lower incisor (bilobate and low-crowned; Fig. 3m–n); the second is a right P4 with a strong labial cingulum, a long and sagittally elongated protoloph, and a strongly constricted protocone (Fig. 3l). There is no fold on the ectoloph, metaloph, or hypocone. This combination of features points to a taxon of uruguaytheriine affinities, probably distinct from all known taxa (for a review, see Vallejo-Pareja et al. 2015). Other Western Amazonian occurrences consist of middle Miocene uruguaytheriines, such as *Xenastrapotherium amazonense* ("locality 28," Upper Juruá, Brazil; e.g., Ribeiro et al. 2013), *Xenastrapotherium* sp., and *Granastrapotherium* cf. *snorki* (Fitzcarrald; Goillot et al. 2011; Tejada-Lara et al. 2015). The fragmentary canine of a late Miocene uruguaytheriine, described by Frailey (1986: 33) in Acre, was surface-collected on a "sand bar." Accordingly, the persistence of astrapotheriids in the late Miocene of Amazonian lowlands is highly questionable (Fig. 4; Goillot et al. 2011; Ribeiro et al. 2013).

Litopterna occur throughout the middle Eocene–Pleistocene interval in Western Amazonia (Fig. 4). Paleogene remains are not identified accurately (Supplemental Material). Macraucheniids and proterotheriids are documented in the early middle Miocene of Talismã (unidentified proterotheriid; Bergqvist et al. 1998), in the late middle Miocene of Fitzcarrald (dental and postcranial remains of *Theosodon* sp., cf. *Tetramerhinus* sp., and unidentified taxa; Tejada-Lara et al. 2015), in the late Miocene river banks of Acre and Amazonas (cf. *Cullinia* sp.; Ribeiro et al. 2013), and in a Pleistocene terrace from the Upper Madre de Dios (MD-61 Top; *Macrauchenia* sp.: isolated phalanx).

Pyrotheria have a strict Paleogene record in Western Amazonia, as in other South American regions (Fig. 4; Billet et al. 2010). *Griphodon peruvianus* occurs in the Chicoca Red Beds, northeastern Peru, considered middle Eocene in age (Patterson 1977), but without stratigraphic constraint. A close ally of *Griphodon* is documented in the late middle Eocene of Contamana (tooth fragments; Antoine et al. 2016). *Baguatherium jaureguii* is restricted to Bagua-La Bocana (Salas et al. 2006), late Eocene in age (see above). The tip of an unworn anterior tooth was unearthed in 2010 at this locality (Fig. 3e–f). A medium-sized pyrothere, provisionally referred to as ?*Propyrotherium* sp., was described in the Upper Juruá local fauna (Paula Couto 1982), and ascribed to the early Oligocene by Ribeiro et al. (2013). The Deseadan genus *Pyrotherium* (e.g., Shockey and Anaya Daza 2004) is recognized for the first time in Amazonian lowlands, with the small-sized species *P. macfaddeni* in Bellavista, San Martín, Peru (TAR-11 locality, Chambira Fm.; right m1 excavated in-situ [Width = 33 mm; estimated Length = 35–37 mm]: Fig. 3g–i) and *P.* cf. *macfaddeni* in the Alto Río Beu, Ucayali (right m3 [Width = 38 mm; estimated Length = 42 mm]: Fig. 3j–k). Although found as float on a river bank and broken in two pieces, the latter specimen points to the presence of (upper) Oligocene deposits in the close vicinity of Santa Rosa. This is in full contradiction with the hypothesis of a long-ranging unconformity in the concerned area (Eocene–late Miocene "Ucayali Unconformity"; Frailey and Campbell 2004; Bond et al. 2015), and likely to support further a post-Eocene age for this locality (see also Kay 2015).

"Stratum 2" immigrants (rodents, bats, and primates; Simpson 1980) have a fairly contrasted fossil record in Western Amazonia (Fig. 4). With almost 160 species recognized (~98 fossil and 61 living species), Rodentia is the most diversified mammalian order in the region (Supplemental Material). They span the late middle Eocene–Recent interval and include notably the earliest rodents from South America (Contamana, Pozo Fm.; Antoine et al. 2012, 2016). Species-rich communities are documented in both Paleogene and Neogene localities, with up to 17 and 18 co-occurring fossil species, respectively (Santa Rosa and Acre local faunas; Supplemental Material). Early faunas mostly encompass stem caviomorphs (e.g., *Canaanimys* and *Cachiyacuy*; late middle Eocene, Contamana) and stem representatives of Octodontoidea (*Eoespina* in Contamana localities; *Eodelphomys*, *Eosallamys*, and *Eosachacui* in Santa Rosa) and Cavioidea (*Eobranisamys* in CTA-27 and CTA-29; *Eoincamys*, *Eobranisamys*, and *Eopicure* in Santa Rosa; *Eoincamys* in Upper Juruá; Supplemental Material). They also include a chinchilloid (unidentified taxon in CTA-29; Supplemental Material) and an erethizontoid (*Eopululo wigmorei* in Santa Rosa; Frailey and Campbell 2004). The earliest representatives of living families are documented in Santa Rosa (*Eodelphomys*: Echimyidae [spiny rats]; Frailey and Campbell 2004) and in Oligocene localities of Contamana (unidentified adelphomyine echimyids and erethizontids [New World porcupines] in CTA-32 and CTA-61; Antoine et al. 2016). Echimyidae are further represented by an unidentified eumysopine in Acre (Ribeiro et al. 2013). Among cavioids, Caviidae only occur in the middle–late Miocene interval, with *Guiomys* sp. in MD-67 (early middle Miocene; Antoine et al. 2013), *Prodolichotis pridiana* in Fitzcarrald (late middle Miocene; Tejada-Lara et al. 2015), an unidentified caviine in CTA-44 and CTA-43 (earliest late Miocene; Antoine et al. 2016), and an indisputable dolichotine in Acre (late Miocene; Kerber et al. in revision). Hydrochoeridae (capybaras) are represented by the late Miocene cardiomyine *Caviodon* sp. and the hydrochoerine *Cardiatherium* sp. in Acre (Kerber et al. in revision), by *Neochoerus* aff. *sulcidens* in the late Pleistocene of Araras/Periquitos, Brazil (Holanda et al. 2011), and by *Hydrochoerus* sp. in the Pleistocene/Holocene of Fitzcarrald (Río Inuya; Antoine et al. 2007; Supplemental Material). Unidentified dasyproctids (agoutis) and cuniculids (pacas) were recognized in CTA-44 (earliest late Miocene; Antoine et al. 2016) and in Acre deposits

(Ribeiro et al. 2013), respectively. Vucetich and Verzi (2002) recognized a representative of *Dasyprocta* in Upper Juruá deposits, most likely Pleistocene in age. Dinomyids (pacarana and its kin; Chinchilloidea) are a conspicuous element of Neogene Amazonian faunas, as in other regions of South America (e.g., Vucetich et al. 1999). They are mostly represented by small-sized taxa, such as *Scleromys* or close allies in early and early middle Miocene localities (MD-61 and MD-67, Upper Madre de Dios; CTA-63 and CTA-45, Contamana; see discussion in Antoine et al. 2013). Medium- and large-sized dinomyids are prominent in late middle and late Miocene localities, with *Drytomomys* and *Potamarchus* in Fitzcarrald (Tejada-Lara et al. 2015), CTA-44 Top and CTA-43 (Antoine et al. 2016), with *Simplimus*? in CTA-57, and with *Drytomomys* spp., *Potamarchus* spp., *Pseudopotamarchus villanuevai*, *Telicomys amazonensis*, *Tetrastylus* sp., *Gyrabrius* sp., *Simplimus* sp., and *Scleromys* sp. among others in faunas from Acre and Amazonas (Ribeiro et al. 2013; Kerber et al. 2015; in revision). Large-sized neoepiblemids first occur in Fitzcarrald (late middle Miocene: *Neoepiblema* sp.; Tejada-Lara et al. 2015) and span the late Miocene interval in Contamana (CTA-44 Top and CTA-10; Supplemental Material) and Acre (*Neoepiblema horridula* and *N. ambrosettianus*; Negri et al. 2010), where they further co-occur with sheep- to cow-sized representatives of *Phoberomys* (*P. burmeisteri*, *P. bordasi*, and *P. minima*; Ribeiro et al. 2013). Erethizontidae are never abundant in the fossil record of Western Amazonia. In Neogene deposits, they are documented by few isolated teeth and restricted to MD-67 (cf. *Microsteiromys*; early middle Miocene; Antoine et al. 2013), CTA-43 (*Steiromys*? sp.; Antoine et al. 2016), and Acre local fauna (gen. et sp. indet., found float in Upper Juruá; Kerber et al. in revision).

Fossil bats span the middle Eocene–late Miocene interval, with isolated dental remains poorly constrained in terms of infra-familiar assignment (Fig. 4; Supplemental Material). Only Microchiroptera are documented. The earliest representatives are unidentified molossids, phyllostomids, and microbats in the Pozo Fm. (CTA-27 and CTA-66, late middle Eocene; Antoine et al. 2016), and an unidentified microbat in Santa Rosa (Czaplewski and Campbell 2004). The most diversified assemblage occurs in CTA-32 (late Oligocene), with an unidentified emballonurid, a small vespertilionoid, and a probable rhinolophoid (Antoine et al. 2016). Emballonurids are also recognized in CTA-63 and CTA-75 (early and earliest late Miocene, respectively; Supplemental Material). Unidentified late Miocene molossids are mentioned along the Río Purus, Peru (Czaplewski 1996) and in CTA-44 Top (Antoine et al. 2016). Czaplewski (1996) described *Noctilio lacrimaelunaris* in the late Miocene Acre River fauna, as being the first fossil representative of the recent fish-eating noctilionid genus. Today, Chiroptera is the most species-rich order in Western Amazonian, with 118 living species (Fig. 4; Eisenberg and Redford 2000).

Although widely diversified in the Neotropics today (33 species in Western Amazonia; Eisenberg and Redford 2000) and in the La Venta beds (late middle Miocene, Colombia; Kay and Madden 1997; Kay 2015), primates have a scarce fossil record in Amazonian lowlands, strikingly similar to that of bats (Fig. 4; Supplemental Material). The earliest representative is *Perupithecus ucayaliensis* from Santa Rosa (Bond et al. 2015), showing close affinities with the late Eocene oligopithecid *Talahpithecus* from Libya (Jaeger et al. 2010). This taxon is indisputably the earliest and most basal monkey from South America (Bond et al. 2015). Deseadan beds of Contamana have yielded a phalanx of a small primate of uncertain affinities (in CTA-32) and dental remains of a medium-sized soriacebine homunculid (in CTA-61; Antoine et al. 2016). Unquestionable crown platyrrhines occur during the Miocene epoch: the earliest remain is a talus referred to an unidentified callithrichine-sized cebine, from MD-61 (late early Miocene, Upper Madre de Dios; Marivaux et al. 2012). Cebidae are recognized in the late Miocene interval, with the large-sized *Acrecebus fraileyi* in Acre River fauna (Kay and Cozzuol 2006), but also with a capuchin-sized cebine and a marmoset-sized callitrichine in CTA-43 (Antoine et al. 2016). Upper Miocene Acre River deposits yield atelid remains, referred to as *Solimoea acreensis* and cf. *Stirtonia* sp. (Kay and Cozzuol 2006), whereas a talus of an unidentified atelid was recognized in the ?early middle Miocene Talismã locality (Upper Juruá; Bergqvist et al. 1998).

Sirenian fossil remains are also very scarce and poorly diversified (Fig. 4). A brachydont molar referable to an unidentified trichechine was unearthed in the early Miocene locality CTA-63 in Contamana (Antoine et al. 2016). *Ribodon limbatus* was recognized in Acre River deposits (deciduous tooth and fragmentary ribs; Frailey 1986; Negri et al. 2010). Specimens attributed to the extant species *Trichechus inunguis* and *T. manatus* were described from the late Pleistocene of Upper Juruá by Simpson and Paula-Couto (1981) and Rancy (1991). Today, only *T. inunguis* is recorded in Western Amazonia (Eisenberg and Redford 2000).

Fossil Cetacea are represented by odontocetes in the middle–late Miocene interval (Fig. 4). The corresponding cranio-mandibular and dental remains are referable to Recent families, such as Platanistidae (unidentified platanistid in Fitzcarrald: Bianucci et al. 2013; cf. *Pomatodelphis bobengi* in Acre River: Bocquentin et al. 2007) and Iniidae (*Plicodontinia mourai* in Upper Juruá and cf. *Ischyrorhynchus* in Acre; Bocquentin et al. 1990). Another iniid, *Inia* sp., occurs in the late Pleistocene Rio Madeira Fm. at Araras/Periquitos, Brazil (Holanda et al. 2011). A bulla of a delphinidan of uncertain affinities was described by Tejada-Lara et al. (2015) in the late middle Miocene Fitzcarrald fauna. Living Western Amazonian odontocetes are the iniids *Inia geoffrensis* and *I. boliviensis* and the delphinid *Sotalia fluviatilis* (Eisenberg and Redford 2000).

Fossil representatives of most North American migrant orders (i.e., Artiodactyla, Proboscidea, Perissodactyla, or Carnivora) have been described in Western Amazonia for more than one century, with proboscidean remains unearthed near the junction between Ríos Mayo and Huallaga, San Martín, Peru (Raimondi 1898). Except for procyonid carnivorans (late Pliocene of Venezuela and Colombia; Forasiepi et al. 2014), pre-Pleistocene occurrences of 'Stratum 3 migrants' sensu Simpson (1980) in northern South American lowlands are still controversial (e.g., Mothé et al. 2012; Gasparini et al. 2013 regarding proboscideans and tayassuid artiodactyls, respectively). To date, no fossil lagomorph has been mentioned, while *Sylvilagus brasiliensis* roams most of the concerned area today (Eisenberg and Redford 2000).

Among non-cetacean Artiodactyla, Tayassuidae (peccaries), Camelidae (llamas and vicuñas), and Cervidae (deers) have an indisputable fossil record in Western Amazonia. Tayassuid fossilized remains attributed to *Tayassu pecari* (Upper Juruá, Río Ucayali, and Río Napo; Rancy 1991) and *Tayassu* sp. (Río Inuya; Antoine et al. 2007) were found float on river banks and hypothetically referred to the Pleistocene epoch. Mostly based on dental specimens from the Harvey Bassler collection recovered decades ago along the Río Madre de Dios, Frailey and Campbell (2012) erected two new genera and species, *Sylvochoerus woodburnei* and *Waldochoerus bassleri*. The former taxon would be closely related to the recent genus *Tayassu*, and the latter to *Pecari* (Frailey and Campbell 2012). These remains are claimed to be late Miocene in age, which would somehow constrain the timing of the Great American Faunal Interchange (Montellano-Ballesteros et al. 2014; Carrillo et al. 2015), but their stratigraphic context is far from being unquestionable. To our knowledge, the only camelids identified from Western Amazonia are *Vicugna* sp. and *Palaeolama* sp., from late Pleistocene deposits of the Upper Juruá (Simpson and Paula-Couto 1981; Rancy 1991; Latrubesse and Rancy 1998). An unidentified cervid is mentioned in the late Pleistocene Araras/Periquitos assemblage, Rondonia, Brazil (Holanda et al. 2011). Lower jaws of cervids (?*Odocoileus* sp. and *Mazama* sp.), probably Pleistocene–Holocene in age, were found on the banks of the Ríos Inuya and Mapuya in Peru (Antoine et al. 2007). *Surameryx acrensis* was described by Prothero et al. (2014) as a dromomerycine palaeomerycid of North American affinities, late Miocene in age. The exact stratigraphic and geographic location of the holotype (and single specimen) is unknown: the lower jaw was found on a bank of the Acre River "between Cobija and Assis" (which is ~90 km) and its light patina, contrasting with the dark patina of specimens found in situ from Acre River Miocene beds, would point to a Pleistocene–Holocene age instead. Nevertheless, if the referral to dromomerycines is confirmed, it would imply a long ghost lineage for the subfamily in North, Central, or South America in either case.

Following the recent taxonomic revision by Mothé and Avilla (2015), Proboscidea are only represented by the Pleistocene gomphotheriid *Notiomastodon platensis* in Peruvian and Brazilian Amazonia (Supplemental Material). The anatomical features, taxonomic affinities, and stratigraphic age of the alleged late Miocene four-tusked gomphotheriid *Amahuacatherium peruvium* (Campbell et al. 2000) had been strongly challenged (e.g., Mothé and Avilla 2015): this gomphothere was two-tusked and it can be considered as a junior synonym of *Notiomastodon platensis*.

Perissodactyla are only represented by Tapiridae found in Pleistocene–Holocene deposits (Fig. 4; Supplemental Material). Most remains are jaw fragments and isolated teeth found on riverbanks of Peruvian Amazonia and assigned to *Tapirus* sp. (Río Inuya) or to *Tapirus terrestris* (Upper Juruá and Río Ucayali; Simpson and Paula-Couto 1981; Gasparini et al. 2013). Nevertheless, a new species of *Tapirus* (*T. rondoniensis*) was described based on a splendid skull unearthed in the late Pleistocene Araras/Periquitos fauna, Rondonia, Brazil (Holanda et al. 2011). Today, *Tapirus* is represented in Western Amazonia by *T. terrestris* and by *T. kabomani*, the status of which is disputed (see Voss et al. 2014 contra Cozzuol et al. 2013).

To our knowledge, fossil Carnivora from Western Amazonian lowlands include only Mustelidae (Supplemental Material). A mandible with p3 referred to a tayra (*Eira* sp.) was described by Rancy (1991) from the Pleistocene of Upper Juruá. A lutrine of unidentified affinities and age (?Pleistocene–Holocene) collected as float in the Río Inuya was mentioned by Antoine et al. (2007). Around 20 species of living carnivorans are recognized in Western Amazonia (canids, procyonids, mustelids, and felids; Eisenberg and Redford 2000).

Discussion and Conclusion

This work allowed for a synthetic survey of Cenozoic mammalian diversity in Western Amazonian lowlands: 23 orders (one, seven, and 15 among Allotheria, Metatheria, and Eutheria, respectively [i.e., 1/7/15]), 89 families [2/20/67], and 320 species [2/48/270] were recognized in the fossil record (Supplemental Material). Gondwanathere allotherians (of uncertain affinities) are restricted to the middle Eocene-?early Oligocene interval, whereas therian mammals (Metatheria and Eutheria) occur throughout the middle Eocene–Holocene interval in Amazonian lowlands (Fig. 4). For several groups (e.g., didelphimorphian marsupials, toxodontid notoungulates, non-potamarchine dinomyid rodents, octodontoid rodents, or tayassuids; Supplemental Material), a taxonomic revision would probably strongly alter the resulting outline, principally in lowering the related number of genera/species. Nevertheless, taking into account potential gaps in the fossil record (during the late Oligocene–middle Miocene and Pliocene intervals), taxonomic diversity was probably fairly constant at the ordinal level (around 12–14 orders in each interval; Fig. 4) throughout the documented interval. During most time slices, species diversity is also unchanged (40–51 species). The only exceptions are (1) the early Miocene depauperate assemblage (only 21 species), probably due to the existence of the long-lasting Pebas Mega-Wetland System (see Salas-Gismondi et al. (2015) and Antoine et al. (2016) for its influence on coeval vertebrate guilds) and, conversely, (2) the late Miocene climactic guild (85 species within 40 families). In that sense, recent mammalian taxonomic diversity from Western Amazonia (12 orders/37 families/286 species) is at odds with all past intervals, including the Pleistocene–Holocene, as it encompasses only three orders of South American origin (Didelphimorphia, Cingulata, and Pilosa) but four North American immigrant orders (Artiodactyla, Perissodactyla, Carnivora, and Lagomorpha): three orders became extinct during the late Pleistocene–Holocene interval, either native (Notoungulata and Litopterna) or of North American origin (Proboscidea). In terms of taxonomic diversity, recent mammalian guilds are dominated by small-sized taxa (Eisenberg and Redford 2000), such as Stratum-2 migrants (chiropterans, caviomorph rodents, and primates; Fig. 4) and non-caviomorph rodents (muroids and sciuroids) from northern landmasses.

Major gaps in the Western Amazonian fossil record correspond with the pre-Lutetian interval (Paleocene–middle Eocene: one specimen of uncertain affinities), the early Miocene (only 17 families encompassing 21 species), and the entire Pliocene epoch (one cingulate species; Fig. 4). Future field studies might focus on these intervals, in particular in order to unveil early mammals, to evaluate the influence of the Pebas System on mammalian evolutionary dynamics, and to better constrain the pattern and timing of the Great American Biotic Interchange(s), as highlighted by Carrillo et al. (2015).

Croft (2001) highlighted the scarcity of large-sized flesh-eaters in pre-GABI South American mammalian guilds, with the notable exception of La Venta (Colombia, late middle Miocene; Kay and Madden 1997). Middle Eocene–Holocene assemblages from Western Amazonia further support that statement, with (1) a strikingly low number of sparassodont marsupials, and (2) the virtual absence of post-GABI carnivorans (Supplemental Material). Crocodiles and birds were most likely top predators in these communities (e.g., Salas-Gismondi et al. 2015).

The pattern and timing of mammalian dispersals from northern landmasses into Western Amazonia are not elucidated yet, as most claimed pre-Pleistocene records of North American immigrants are not accurately constrained in terms of age (surface collections: tayassuid and "dromomerycine" artiodactyls; Frailey and Campbell 2012; Prothero et al. 2014) and/or highly challenged regarding their taxonomic affinities (e.g., the gomphotheriid proboscidean *Amahuacatherium peruvium*; Mothé and Avilla 2015). New geochemical methods performed on fossil dentine and/or enamel, using rare earth element uptakes as an indicator for quantifying relative diagenesis among mammalian orders (REE Index; MacFadden et al. 2010), could probably help disentangling such enigmas in the forthcoming years, in blueprinting these fossils, and recognizing their potential source levels (upper Miocene formations vs. Pleistocene terraces, likely to display highly distinctive REE indices).

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