EVOLUTION AND DIVERSIFICATION OF NEOTROPICAL BUTTERFLIES: INSIGHTS FROM THE BIOGEOGRAPHY AND PHYLOGENY OF THE GENUS *MORPHO* FABRICIUS, 1807 (NYMPHALIDAE: MORPHINAE), WITH A REVIEW OF THE GEODYNAMICS OF SOUTH AMERICA

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Abstract – Based on biogeography and phylogeny of the Neotropical genus *Morpho*, and a synthesis of present knowledge on the geodynamics and paleogeography of South America, evolutionary scenarios are proposed to understand the diversification of the genus through time and space.They emphasize the driving role of Andean uplift and subsequent transformations of Amazonia.

Key words: Neotropics, South America, Gondwana, Andes, Amazonia, geodynamics, paleogeography, Lepidoptera, *Morpho*, biogeography, phylogeny, diversification

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INTRODUCTION

Heppner (1991) estimated butterfly diversity of the three richest biogeographic regions in the world as follows: Ethiopian region, 3,267 species; Oriental region, 4,157 species and the Neotropical region 7,927 species. More recently, Lamas (2004) estimated that the number of Neotropical species may range between 8,400 and 8,700. Why is the Neotropical region so rich in butterflies? The Pleistocene Forest Refuges Hypothesis (PFRH) considered that Quaternary climatic changes have been a major driver of the diversification of Neotropical species (Haffer, 1969; Whitmore & Prance, 1987). Historically, Ithomiini and Heliconiini butterflies were utilized to relate distribution patterns to Pleistocene climatic fluctuations (Fox, 1949; Turner, 1965, 1977; Brown *et al*., 1974). However, Hoorn *et al*. (2010) have emphasized that "current biodiversity patterns are rooted deep in the pre-Quaternary". Recent studies of diverse Neotropical butterflies (e.g., Willmott *et al*., 2001; Hall & Harvey, 2002; Willmott, 2003; Hall, 2005; Wahlberg & Freitas, 2007; Peña & Wahlberg, 2008; Elias *et al*., 2009; Mullen *et al*., 2011) have already shown that diversification depended not only on Pleistocene climatic variations, but also on earlier geological events. Certainly, our limited understanding of the causes of butterfly diversification has been due, in part, to the independence of two basic sciences, entomology and geology. But, as Darwin (1859) observed, consideration of "geological time" is necessary to understand species diversification. Obviously, this does not imply that species accumulated during a long period in a stable and ecologically favourable environment, as proposed by the Tropical Conservatism Hypothesis (Wiens & Donoghue, 2004), but that both geological and climatic events affected diversification, positively as well as negatively.

The evolution of Lepidoptera is a long story (Table 1). The earliest fossils have been recorded in different parts of the world from Triassic sediments (Whalley, 1986; Sohn *et al*., 2012), with the earliest butterfly fossils from Early Eocene rocks (*ca*. 50 MY) (Rasnitsyn & Quicke, 2002). Certain Tertiary butterfly fossils resemble modern species; for example, in Oligocene lacustrine sediments from south-eastern France, Nel *et al*., (1993) discovered a Satyrinae attributed to the extant genus *Lethe* Hübner, [1819] with a 25 MY minimum age. Another fossil discovered in southwestern Montana from an Early Oligocene (32 MY) deposit was also attributed to the genus *Lethe* (Miller *et al*., 2012). A riodinid from Dominican amber (Poinar & Poinar, 1999) was described as *Voltinia dramba* Hall, Robbins & Harvey, 2004, its separation from its extant Mexican sister species, *Voltinia danforthi* (Warren & Opler, 1999), being estimated ca. 50-40 MY (Hall *et al*., 2004). All of these fossils imply a substantially pre-Eocene origin for butterflies. However, there is little consensus, some authors arguing for an appearance 120-80 MY ago, others for a more recent, Late Cretaceous-Early Paleogene origin (Hawkins & DeVries, 2009, and references therein). Wahlberg *et al*. (2009) calibrated a phylogeny of the worldwide nymphalids using the minimum age of the *Lethe* species described by Nel *et al*. (1993). Their study indicates that representatives of Nymphalidae existed during the upper Cretaceous (possibly before 95 MY, cf. Table 1), and that the family diversified strongly during the Tertiary, forming the majority of present lineages.

The Morphinae, a Nymphalidae lineage endemic to the Neotropics, originated *ca*. 55 MY ago (Wahlberg *et al*. 2009). Therefore, its evolution coincided with a period of multiple geodynamic events, including the multiphased uplift of the Andes and the formation of Amazonian lowlands (Sempere *et al*., 2008; Hoorn & Wesselingh, 2010). Morphinae includes the genus *Morpho*, which, according to Wahlberg *et al*. (2009), originated about 33 MY, i.e. by the middle Tertiary (Tab. 1). *Morpho* is distributed from northern Argentina to northern Mexico, predominantly in tropical rainforests, and it is one of the few butterfly groups that has been reviewed throughout the entire Neotropical Region (Blandin, 1988, 1993, 2007a, b; Neild, 2008). It is therefore an interesting and suitable subject for biogeographic study.

Where and when did the *Morpho* lineages originate and initially diversify? Where and when did the species existing west of the Andes and in Central America originate? Why do the Central Andes have a higher number of species than the Northern Andes? How and when was the Amazonian fauna established? Why does the *Morpho* fauna of the Guiana Shield differ from that of the Brazilian Shield? Combining phylogenetic hypotheses provided by recent studies (Penz & DeVries, 2002; Cassildé *et al*., 2010, 2012; Penz *et al*., 2012) with a review of the geological evolution of the Neotropics, this paper attempts to identify links between *Morpho* diversification and the history of South America. In so doing, we present a case study which may improve our understanding of the evolution and diversification of butterflies in the Neotropical region.

METHODS

Geology and paleogeography. Many disciplines are involved in the study of the geology and paleogeography of South America, and publications are dispersed in numerous specialized journals. During recent decades research has accelerated, notably with the development of sophisticated dating methods and models. Based on extensive literature, we synthesize information concerning the formation of the South American continent and current knowledge relative to the origin and development of its tropical rainforests, with an emphasis on information which may be relevant to understanding butterfly evolution.

Nomenclature. The genus *Morpho* was divided into 9 subgenera, including 29 species, by Blandin (2007a). In this paper, we adopt a classification taking into account changes resulting from recent phylogenetic studies (Cassildé *et al*., 2010, 2012; Penz *et al*., 2012). The list of subgenera and species, including also subspecies cited in the text, is given in Appendix 1.

Geographical and altitudinal distribution. Our analyses are based on data compiled by Blandin (2007a), and new published or unpublished data. On our maps, points indicate areas where the species have been collected, rather than precise localities.

Phylogeny and times of divergence. Phylogenetic studies based on morphological characters were published by Penz & DeVries (2002) and Cassildé *et al*. (2010). Subsequently, Cassildé *et al*. (2012) published a phylogeny based on the analysis of sequences of two mitochondrial genes in all species, except *M. hercules* (for which DNA extraction was unsuccessful). Revising morphological characters and including the analysis of several mitochondrial and nuclear genes, Penz *et al*. (2012) proposed an improved phylogeny. Despite the fact that they studied only 20 species (not 21, because the specimen (NW134-5) they considered as *M. achilles* is, without doubt, a *M. helenor*; NGS DNA sequences Data Bank, accessed 6 September 2013), these authors clarified some major points. We propose a manually constructed tree, based on the most reliable results of previous studies. However, in these studies, too few subspecies have been sampled to provide useful information concerning diversification at the subspecies level.

Penz *et al*. (2012) estimated divergence times within the *Morpho* clade using the program BEAST v1.6.1, the calibration being based only on the age of the root, taken from Wahlberg *et al*. (2009). We consider that these ages are likely to represent a minimum age of divergence, and that true ages could be older. For example, Sauquet *et al*. (2012), using as a model the fossil-rich plant genus *Nothofagus* (Fagales), checked different calibration scenarios. They demonstrated that the mean estimation of the crown group age of *Nothofagus* ranged from 23.5 MY to 100.3 MY, younger ages being obtained when only secondary calibration points (i.e. not obtained directly from fossil ages, but from previously dated phylogenies) were used, and the youngest being obtained when only a minimum estimate of the age of the origin of the clade was used for calibration.

Relating biogeography, phylogeny and geodynamics. The present distribution of species and subspecies results from divergence and extinction events, which occurred within an evolving paleogeographic context. Our general hypothesis is that these events may have been driven by geodynamic events, provoking vicariant divergences, favouring dispersal or, on the contrary, creating barriers. Therefore, we have compared distribution patterns and evolutionary steps with geodynamic events. However, the driving role of geodynamic events should be accepted only if there is a satisfying correspondance with dated divergence events. Generally, we propose alternative hypotheses, based either on ages estimated by Penz *et al*. (2012), or on older ages. Consistency with geodynamic events should help select the more credible hypotheses, but clearly in many cases more research is needed with more complete taxon sampling and revised divergence time estimates, if possible.

RESULTS

1. GEODYNAMICS OF SOUTH AMERICA

1.1. Formation of the early South American protocontinent

South America, originally part of Gondwana, broke away during the early Cretaceous (135 MY) (Jacques, 2004), the separation from Africa becoming complete *ca*. 100 MY. The proto-continent drifted across the paleo-Pacific during the Cretaceous and approached its present position during the Tertiary, about 75 MY after its initial separation (Jacques, 2004). It consisted of two geological units, the Amazonian and Patagonian platforms; on the Amazonian platform we distinguish the Guiana Shield and the Brazilian Shield, separated by the Amazon structural trough, these units having formed initially on Gondwana (Jacques, 2004).

1.2. Formation and structural evolution of the Andes

The Central Andes (Bolivia and Peru) are essentially a 4000 m high plateau, the *altiplano*, bordered on each side by higher cordilleras. Large valleys are limited mainly to the eastern slopes. However, from Cusco to the north, the *altiplano* gives way to a system of deep valleys, each separated by NW-SE oriented ridges. The more easterly ridge decreases in altitude toward the north-west before disappearing below the western periphery of the Amazon basin. Thus, the Andean system narrows from about 500 km in north-western Bolivia to less than 200 km in Ecuador (Fig. 1). The Northern Andes, a system of two parallel cordilleras (occidental and oriental), oriented

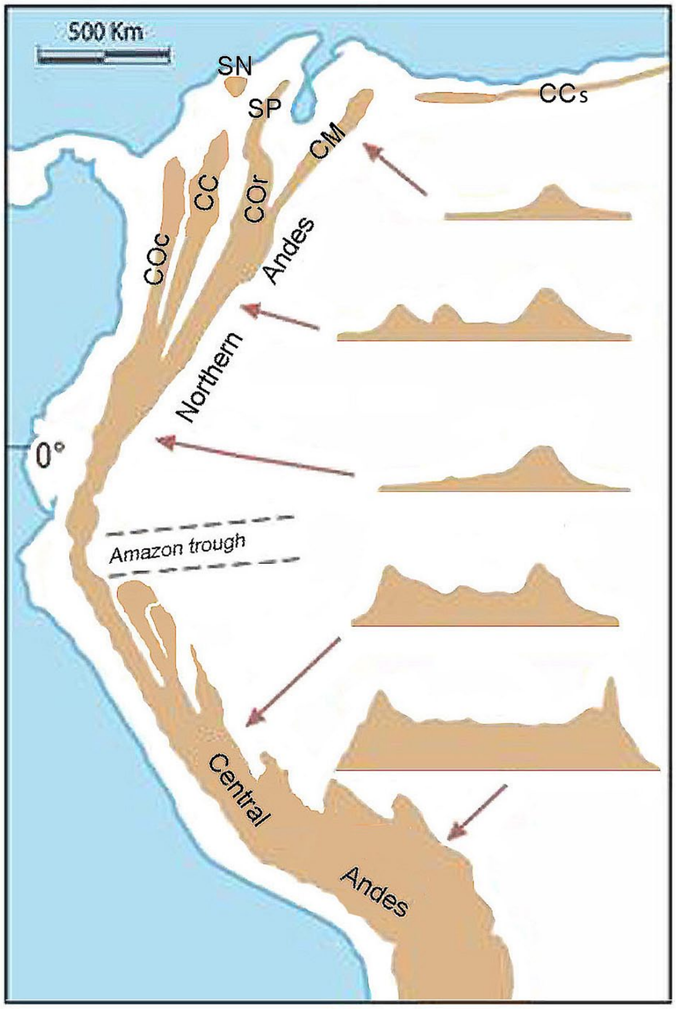


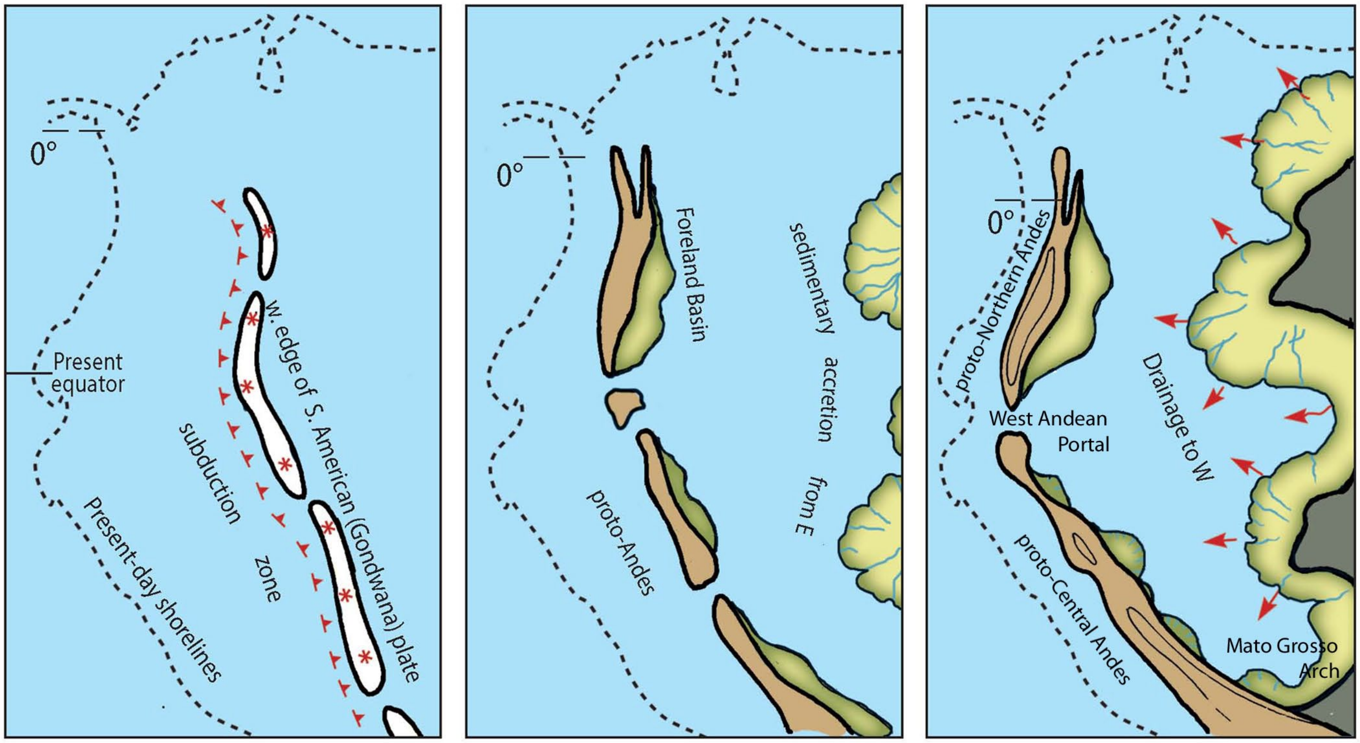
Fig. 1. Schematic representation of the Andes, showing their important North-South morphological variations. CC: Colombian Cordillera Central. CCs: Cordillera de la Costa. CM: Cordillera de Mérida. COc: Colombian Cordillera Occidental. COr: Colombian Cordillera Oriental. SN: Sierra Nevada de Santa Marta. SP: Serranía de Perijá.

S-N in Ecuador, become more complex in Colombia, with the W-E succession of three cordilleras (Cordilleras Occidental, Central and Oriental), plus northern elements: the isolated Sierra Nevada de Santa Marta, and the Serranía de Périjá, connected to the Cordillera Oriental. In Venezuela, the Andes swing to a N-E and then to a W-E direction, with the Cordillera de Mérida connected to the Colombian Cordillera Oriental, and the Cordillera de la Costa (Fig. 1). The absence of plateau and the disposition of these multiple cordilleras and intervening valleys have been conditioned by a geodynamic regime related to the NW progression of the South American plate and its collision with the Pacific and Caribbean plates (eg. Cediel *et al.*, 2003; Jacques, 2004).

The western edge of the Gondwanan South American plate was marked by the development of the future Andean cordillera (the "proto-Andes"), a chain of volcanic islands extending from the Antarctic to the Caribbean (Fig. 2A). Volcanic activity and sedimentation progressively increased the relief and width of islands that evolved into a discontinuous ridge (Gregory-Wodzicki, 2000; Jacques, 2004). The future cordillera emerged above sea-level around 60 MY (Gregory-Wodzicki, 2000) (Fig. 2B). In the Peruvian and Bolivian Andes, conglomerates of Eocene (*ca*. 45 MY) age indicate important uplift and erosion during the Eocene (Lecarros *et al.*, 2000). This early uprise, affecting first the Bolivian Andes, progressed northward during the Miocene. A rapid rise of ~2.5 km, *ca*. 10-6 MY, has been supported by several authors (references in Sempere *et al.*, 2008; Mamani *et al.*, 2010), but other authors suggested that a slow and steady rise since ~40 MY is more likely (Barnes & Ehlers, 2009). The eastern cordilleras of the Central Andes attained 2000 m probably during the Early-Middle Miocene (23-12 MY) (Sempere *et al.*, 2008; Barnes & Ehlers, 2009, and references therein).

The three major Colombian cordilleras differ in age. The Cordillera Occidental is the oldest, being initiated during the late Cretaceous (Jaillard *et al.*, 1995; Branquet *et al.*, 2002), uplift continuing during the Tertiary (Roddaz *et al.*, 2010), with an important ultimate phase during the Middle Miocene (16-11 MY). Uplift of the Cordillera Central, above sea level, was active from the Cretaceous-Paleocene to the Oligocene, its northward development being indicated by the progressive appearance of terrestrial detritus deposited in the Magdalena basin (Gomez *et al.*, 2005; Roddaz *et al.*, 2010). Initially part of the Cordillera Central, the isolated Sierra Nevada de Santa Marta (Fig. 1) has a complex history (Montes *et al.*, 2010). That it emerged during the Early Tertiary (58 MY) is indicated by plant debris and mineralogy (Wing *et al.*, 2009). Its elevation increased progressively, while it became separated from the Cordillera Central and was displaced some 100 km to the north via lateral fault movements. It is possible that the separation initiated during the Late Eocene, allowing a marine ingression to occur through the widening corridor today forming the lower Magdalena valley (Santos *et al.*, 2008). Emergence of the Cordillera Oriental started about 13-12 MY (Albert *et al.,* 2006) and accelerated during the Pliocene and early Pleistocene (5-2 MY) (Dengo & Covey, 1993; McCourt *et al.*, 1984; Gregory-Wodzicki, 2000). This W-E evolution of the Colombian Andes implies that the eastern parts of the Cordillera Central graded directly into the Foreland Basin (see below) until the exhumation of the Cordillera Oriental and the formation of the Magdalena valley (Bayona *et al.*, 2007; Roddaz *et al.*, 2010). Initial uplift differed between the structural blocks forming the Cordillera de Mérida (Bermúdez *et al.*, 2010), but its emergence began about 8 MY, separating the Maracaibo and Orinoco hydrographic basins (Albert *et al.*, 2006). Most of the uplift could be as late as 5 MY, being simultaneous with that of the Serranía de Péríjá whose present altitudes were attained only by 2 MY (Duque-Caro, 1979; Cooper *et al.*, 1995; Higgs, 2008). Further to the east, the relatively low (2000-2700 m) Cordillera de la Costa rose during the Pliocene (~ 3.5 MY). These late movements of the Cordillera de Mérida and Cordillera de la Costa caused the eastward displacement of the proto-Orinoco which flowed initially into the Caribbean near the future Lake Maracaibo (Hoorn & Wesselingh, 2010).

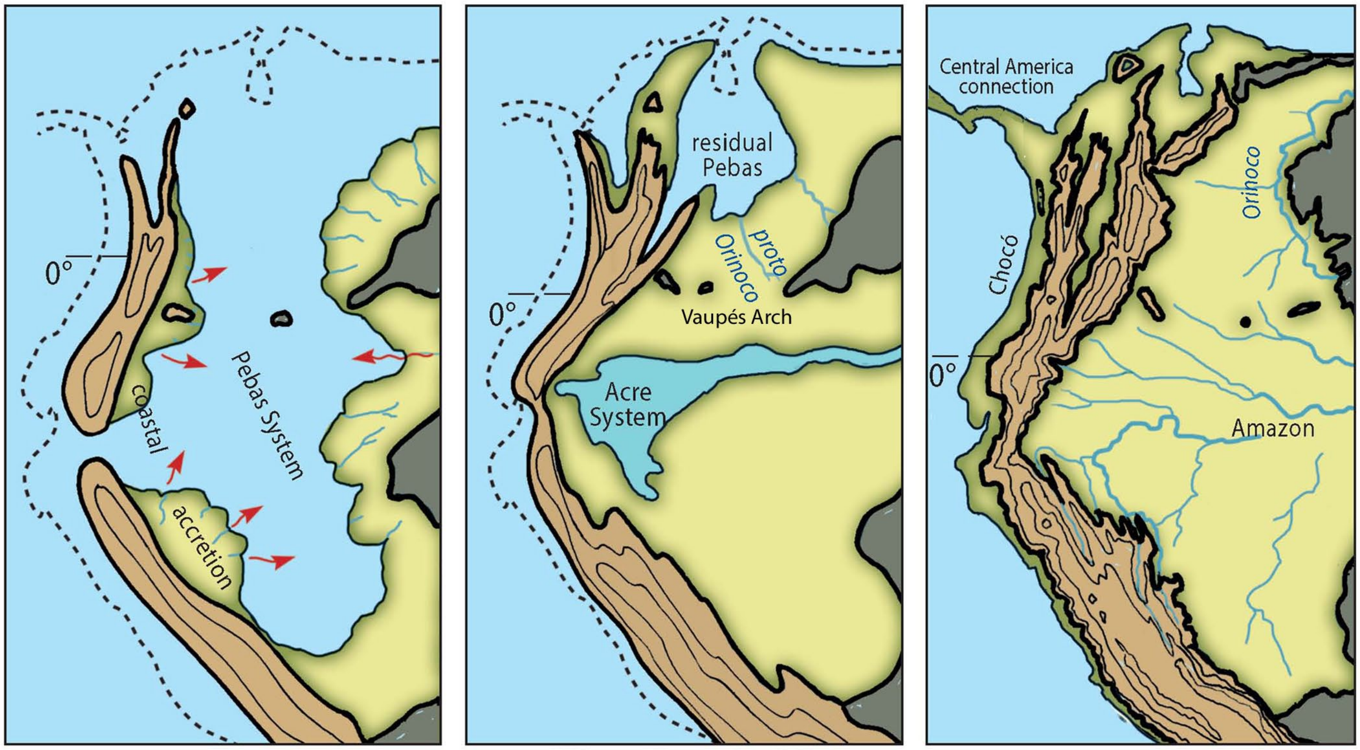
The dominant NW-SE structural grain of the Central Andes is intersected locally by a series of oblique, NE-SW oriented topographic anomalies. The most important is a major morphological change in northern Peru and southern Ecuador,



A. Late Cretaceous (ca **80 MY**)
Volcanic ridge

B. Paleocene (ca **60 MY**)
chain of low islands

C. Late Eocene (ca **35 MY**)
Low hills, proto-Andes highest in S



D. Middle Miocene (ca **14 MY**)
alluvial discharges from Andes

E. Upper Miocene (ca 8 **MY**)
uprise of the E Andes

F. Pliocene-Present (5.3 - 0 MY)

▨ Andes ▨ proto-continent ▨ sedimentary accretion ▨ aquatic

Fig. 2. Paleogeographic evolution of the north-western part of South America. The successive figures illustrate the westward migration of the Gondwanan proto-continent, the formation of the Andes and the evolution of the Foreland Basin. The precise configuration and extent of the Foreland Basin, the Pebas and Acre Systems are uncertain (cf. figures in Roddaz *et al*., 2010, and plates in Hoorn & Wesselingh, 2010).

where the Andes decrease in altitude to less than 2000 m. This saddle formed a corridor, designated as the "West Andean Portal" ("WAP", Antonelli *et. al*., 2009), which initially separated the proto-Central and Northern Andes. From the Eocene to the Middle Miocene (approximately 40-12 MY), this corridor, probably a mosaic of lowlands and wetlands, may have favoured intermittent marine connections between the Pacific and the Foreland Basin, and thus, most importantly, isolated the proto-Northern and proto-Central Andes, until 13-11 MY, when uplift of the Ecuadorian eastern cordilleras began (Hoorn, 1993; Räsänen *et al*., 1995; Steinmann *et al*., 1999; Coltorti & Ollier, 2000; Hungerbühler *et al*., 2002; Santos *et al*., 2008; Antonelli *et. al*., 2009) (Fig. 2C). It is plausible that these cordilleras did not attain 1500-2000 m before 5-2 MY, similarly to the Colombian Cordillera Oriental.

Thus, from the Paleocene to early Miocene (60-22 MY), i.e. during most of its history, the proto-Andes consisted of relatively low hills, the proto-Northern Andes being represented only by the proto-Cordillera Occidental and Central (Duque-Caro, 1979; Cediel *et al*., 2003; Sempere *et al.,* 2008).

1.3. Formation of Andean valleys

The morphological complexity of Andean valleys results from the combined effects of multiphased structural movements, plus variable rates of erosion. In the Central Andes, rejuvenation of old NE-SW fractures influenced the orientation of certain valleys which cut across the predominant SE-NW grain of the Andes, eg. the lower Marañon, the Tambo, Urubamba, etc. Most major valleys open onto the Amazon lowlands through narrow gorges or "*pongos*", where they cut through the more recent eastern cordilleras. Their floors remain at low altitudes (less than 800 m), extending far into the mountains. In the Northern Andes, the parallel Colombian cordilleras determine the S-N orientation of the Cauca and Magdalena valleys. Combined with their variable distance with respect to the major source of humidity (Amazonia), the disposition of valleys in general determines climatic conditions and forest development along their floors and slopes.

Andean valleys have variable ages. In the Northern Andes, the Cauca valley, between the Cordillera Occidental and the Cordillera Central, may have existed long before the middle Miocene, while the Magdalena valley was formed much later, due to upper Miocene uplift of the Cordillera Oriental. When the proto-Central Andes reached a significant elevation (about 2000 m) during the Early-Middle Miocene (23-12 MY), multiple N-S ridges blocked the westward flow of Amazonian humidity, modifying atmospheric convection that increased rainfall and erosion on the eastern side of the Andes since *ca*. 12 MY; however, an earlier important incision of valleys is not excluded (Ehlers & Poulsen, 2009, and references therein).

1.4. The Foreland Basin, Pebas System, and the formation of the Amazon and Orinoco plains

Initially, the proto-Andes were low volcanic islands separated from the Gondwanan shields by an extensive inland sea, the Foreland Basin, extending from Bolivia to the Caribbean Sea at the end of the Cretaceous (Gayet et al., 1993) (Fig. 2B). Late Cretaceous sedimentation indicates that the basin was developed long before the South American plate attained its present position, erosion of the Gondwanan shields generating detritus transported to the basin via important river systems (Hoorn & Wesselingh, 2010). The precise history of the Foreland Basin is complex, with inter-regional differences. For example, in southern Peru, there is evidence that an important change occured, from marine to continental conditions, *ca*. 91-90 MY (Callot *et al*., 2008), while Late Cretaceous sediments, in Bolivia, contain assemblages of marine fossils (Gayet *et al*., 1993). It is likely that marine transgression and regression phases alternated, in relation with variations of sea level and eustatic movements (Thierry Sempere, pers. comm.). During the Eocene, a transgression probably created an embayment parallel to the proto-Andes from the proto-Caribbean Sea to Peru (Roddaz et al., 2010), possibly reaching the Madre de Dios region (Martin Roddaz, pers. comm.). The definite closure of the southern end of the Foreland Basin by the Mato Grosso Arch possibly occurred at the Late Eocene (43-34 MY) (Hoorn & Wesselingh, 2010) (Fig. 2C). The increasing erosion of the rising proto-Andes led to its progressive, centripetal filling. Subsequently, a complex aquatic system, named "Pebas System", developed in western Amazonia from about 25-23 MY, from Peru to the Caribbean Sea, attaining a maximum extent by 14-10 MY of an estimated 1.1 million km² (Wesselingh *et al.,* 2002; Hoorn & Wesselingh, 2010) (Fig. 2D). It was probably not a continuous shallow marine system, but a mosaic of shallow lakes, mangroves, swamps, grasslands, gallery forests and rivers (Latrubesse *et al*., 2010). *Terra firme* lowlands fringing the proto-Andes accreted progressively eastward due to the lateral discharge of Andean detritus (Roddaz *et al*., 2010). Around 10-7 MY, the Pebas System evolved into the Acre System (Fig. 2E), extending from north-eastern Peru and eastern Ecuador to eastern Amazonia, thus forming a very wide proto-Amazon flowing towards the Atlantic Ocean following its reversal to the east during the Late Miocene-Pliocene (8-5 MY) (Wesselingh & Salo, 2006; Hoorn & Wesselingh, 2010). To the north, there is evidence that a large lake existed *ca*. 18-14 MY in the current Venezuelan Llanos, in which marine transgressions occurred, probably isolating emerged parts of the future Cordillera de Mérida (Gomez *et al*., 2009). The proto-Orinoco basin was filled around 5 MY, forming the Colombian-Venezuelan Llanos (Dengo & Covey, 1993; Hoorn, 1993; Cooper *et al*., 1995) (Fig. 2F).

The Foreland Basin probably acted as an ecological barrier between the Andes and the Gondwanan shields for strictly terrestrial species (Wesselingh & Salo, 2006). However, to the south, the Mato Grosso Arch, having linked the Brazilian Shield to the proto-Central Andes possibly from late Eocene (43-34 MY) (Hoorn and Wesselingh, 2010) or at least during the Oligocene (30 MY) (DeCelles and Horton, 2003), may have facilitated early dispersion. Nevertheless, Late Miocene sediments in the Beni-Mamore basin (Bolivia) indicate that an open connection probably existed either with the Acre System, or the Atlantic Ocean, or both (Roddaz *et al*., 2006). Latrubesse *et al*. (2010) proposed a second structural ridge, the Vaupés Arch, linking the Colombian Cordillera Oriental and the Guiana Shield (see also Mora *et al*., 2010) (Fig. 2F). The existence of such a connection was indicated by oil exploration along the northern edge of the Amazon Basin (cf. Hoorn, 1993). Although discontinuous, the Vaupés Arch may have favoured Late Miocene dispersal of certain species between the Eastern Andes and the Guiana Shield (Mora *et al*., 2010).

1.5. The Central American connection

Closure of the Panama Isthmus is frequently considered to be a recent event which occurred around ~3 MY (Iturralde-Vincent & MacPhee, 1999; Webb, 2006). However, several hypotheses propose much earlier geological connections between North and South America. For example, Shields & Dvorak (1979) suggested a contact between Mexico and Venezuela during the Cretaceous (100 MY), while Gayet *et al*. (1992), suggested a connection during the Late Cretaceous and Paleocene via the Greater Antilles and a uplifting ridge named "Aves Ridge". Ituralde-Vincent & MacPhee (1999) also proposed this connection, that they named "GAARlandia", at *ca*. 35-33 MY. Based on recent geological studies in Panama, the possibility of connections prior to 3 MY has been reconsidered (Farris *et al.*, 2011; Montes *et al*., 2012a, b). These studies support a collision between central Panama and South America beginning to narrow the seaway between the Pacific and Atlantic oceans *ca*. 25 MY, and resulting in the disappearance of a deep-water seaway by around 15 MY. Therefore, the timing of the "Great American Biotic Interchange", generally considered to have been initiated around 3 MY (Webb, 2006) and favored by the final closure of the isthmus, could be disputed (Cody *et al.,* 2010).

2. ORIGINS AND DEVELOPMENT OF NEOTROPICAL FORESTS

2.1. The age of rainforests, their early existence in South America, and their controversial origin

Davis *et al.* (2005) suggested a mid-Cretaceous (112-94 MY) origin of Malpighiales*,* a group of plants adapted to the understory of tropical rainforests, and provided arguments from the literature for the existence at that time of tropical rainforests in low-latitude regions. Although this work has been disputed (Wing e*t al*., 2009), a calibrated phylogeny of the palm family, also associated with tropical rainforests, supports the hypothesis of tropical rainforest expansion around 100 MY (Couvreur *et al*., 2011a). Annonaceae, another tropical rainforest family, originated at least 110-102 MY ago (Couvreur *et al*., 2011b). Piperaceae, which includes a majority of tropical rainforest species, is considered as one of the oldest lineages of flowering plants, and the genus *Piper* seems to have originated in the Neotropics by ~91 MY (Smith *et al*., 2008, and references therein). These studies indicate that "proto-tropical rainforests" existed before the separation of South America and Gondwana. Moreover, tropical ecosystems probably existed prior to 110-100 MY on western Laurasia, the future North American continent (references in Couvreur *et al*., 2011a, b).

Fossils typical of a tropical rainforest have been described from the late Paleocene (58 MY) in northern Colombia, this flora exhibiting strong similarities with modern lowland rainforests (Wing *et al*., 2009). Moreover, sediments from the Maracaibo Basin revealed a change from pantropical to more obviously Neotropical flora at the Paleocene-Eocene boundary (55 MY) (Rull, 1999). During this period, characterized by high temperatures, Neotropical paleoflora extended southward beyond 37°S (Gayo *et al*., 2005; Hinojosa, 2005). On the Brazilian Shield (Minas Gerais State), the flora of an Eocene formation included 17 extant families (references in Burnham & Johnson, 2004). In a recent review, Graham (2011) concluded that tropical lowland rainforests existed in the Neotropics around 64 MY, and were well developed by 58-55 MY.

Because the South American proto-continent has been isolated since its separation from Africa, it has been suggested (Raven & Axelrod, 1974; Burnham & Johnson, 2004) that South American tropical rainforests could have resulted from *in situ* evolution. However, this hypothesis is being reevaluated. The presence of early angiosperm lineages within the South American Atlantic forests supports the possible dispersion of African ancestors via putative island routes, directly between Africa and South America (Fiaschi & Pirani, 2009, and references therein) or, alternatively, from Laurasia through Caribbean routes (Pennington & Dick, 2004, and references therein; Antonelli *et al.*, 2009; Herrera *et al*., 2011). Finally, an Australasian origin has been considered for certain lineages. For example, a southern Gondwanan (Australasia-Antarctica-South America) origin has been proposed for major monocot groups (Bremer & Janssen, 2006). During the Paleocene, a paleoflora termed "Paleoflora Gondwanica" (Hinojosa, 2005) composed of Australasian, Neotropical and Pantropical elements existed in South America and Antarctica. However, following a thermal maximum at the Paleocene-Eocene boundary, southern biomes changed from tropical forest to steppes (Ortiz-Jaureguizar & Cladera, 2006). Therefore, it is unlikely that species continued to migrate toward ancestral Neotropical rainforests via the "Antarctica Route" (Pennington & Dick, 2004). This route was open until 54-51 MY (as indicated notably by mammal fossils; references in Crame, 1999), later more or less interrupted by shallow waters between islands, and definitely closed by the opening of the inter-oceanic Drake passage by 28-23 MY (Beu *et al.*, 1997; Le Roux, 2012).

2.2. The role of Andean uplift

Progressive uplift of cordilleras favoured forest ecosystems adapted to increasing altitudes. Today, the vegetation is altitudinally stratified (eg. Brack Egg & Mendiola-Vargas, 2004). The lowland forests ("*selva baja*") reach their upper limit around 800 m. Low mountain forests ("*bosque de montana*") are distributed between 800 and 1500 m. Above this altitude, the cloud forests ("*bosque de neblina*") are subdivided into a low zone (1500-2000 m) and a high zone (2000-3500/3800 m). Limits between zones are gradual and change with latitude, slope orientation, and geomorphology. According to Sempere *et al.* (2005) who referred to a dated phylogeny of tanager birds living between 2000 and 3500 m (Burns, 1997), cloud forests began to differentiate in the Central Andes around 20-18 MY. Picard *et al*. (2008), via a molecular phylogeographic and phylochronologic analysis of a potato parasite nematode, confirmed that altitudes of 2000-2500 m were attained during Early Miocene in southern Peru, and Late Miocene in central and northern Peru. It is interesting to note that Chusqueinae bamboos, host-plants of the cloud forest *Morpho sulkowskyi*, diverged from woody bamboos by 17 MY (Fisher, 2011). The WAP , which was closed around 13-11 MY, may have continued to act as a barrier for cloud forest species as long as the connection between Peruvian and Ecuadorian Andes remained low (Antonelli *et al.*, 2009). In Colombia, it is likely that cloud forests existed in the Cordilleras Occidental and Central long before their appearance in the geologically recent Cordillera Oriental, where the vegetation changed from low mountain conditions (< 1000 m) to upper mountain forest (2500 m) between 5 and 3 MY (Hooghiemstra *et al.*, 2002).

2.3. Development of lowland Amazonian rainforests and their relations to Atlantic forests

In the Middle Miocene, already complex tropical rainforests existed in western Amazonia (Antoine *et al.*, 2006). The progressive reduction of the Pebas System from the Middle Miocene favoured eastward dispersals, driven by the transformation of landscapes. Thus, the establishment of *terra firme* rainforests linking western Amazonia and the Guiana Shield is relatively recent. Southward, however, *terra firme* rainforests probably existed around the southern and eastern banks of the Foreland Basin due to the Mato Grosso Arch connection. The southern part of the Atlantic forests has floristic affinities with Amazonia, but also with Andean-centered taxa, a fact consistent with the Mato Grosso connection (Fiaschi & Pirani, 2009). This is important, as this connection was probably established before the initial diversification of *Morpho*. However, the south-eastern extension of Amazonian rainforests was limited by the development of the Cerrado dry forests and savannas, associated with the onset of Middle Oligocene (29-28 MY) aridity (Safford, 1999, and references therein).

3. GEOGRAPHY OF THE GENUS *MORPHO*: AN OVERVIEW

Morpho may be divided geographically into 4 groups: i) - an Atlantic group, corresponding to the Atlantic forests; ii) - a Cis-Andean-Amazonian group, corresponding to the Amazon and Orinoco basins, and the Guianas; iii) - a Cis-Andean-mountain group, in the eastern Andean slopes; iv) - a Trans-Andean group, in western Colombia, western Ecuador and/or Central America (Fig. 3). The same groups were recognized in Brassoline butterflies (Blandin, 1977), and correspond to biological regions that were recognized for example by J. Haffer for birds and K.S. Brown Jr for various butterfly groups (references in Whitmore & Prance, 1987; see also Tyler *et. al.*, 1994), Each group includes species unique to the region, which we term "macro-endemic" species. There are 24 macro-endemic species. Six species have broader distributions, overlapping two or more regions (Fig. 4).

Morpho species are distributed from sea-level up to about 3000 m in Andean cloudforests and appear to be approximately altitudinally stratified. Lowland species (i.e. *M. marcus*, *M. cisseis*, *M. rhetenor*, *M. deidamia*, etc.) exist up to around 800 m, while cloud forest species (i.e. *M. lympharis*, *M. sulkowskyi*) are common above 1600-2000 m. A few species fly between low and high altitudes, i.e. around 1000-1500 m, or even 2000 m, for example *M. aurora*. Locally, altitudinal limits may depend on the latitude and the orientation of slopes. In Atlantic forests, only *M. portis* attains *ca*. 1700 m; (Olaf Mielke pers. comm). Some trans-Andean species fly only at low altitudes (0-800 m, eg. *M. cypris*), while others (eg. *M. theseus*) exist from sea level to *ca*. 1800 m (DeVries, 1987). *Morpho helenor* also has a wide altitudinal range, flying from sea level to more than 1500 m, as observed in Bolivia (Gareca & Blandin, 2011), or to *ca*. 1900 m in the Serranía de Perijá (Thomasz Pyrcz pers. comm.).

On mountain slopes it can be difficult to define precise altitudinal assemblages because of overlapping distributions. At the local scale, the richest assemblages attain a maximum of 10 coexisting species, for example *M. marcus*, *M. eugenia*, *M. telemachus*, *M. hecuba*, *M. cisseis*, *M. rhetenor*, *M. menelaus*, *M. deidamia*, *M. helenor*, and *M. achilles* in the lowland rainforests near Iquitos in western Amazonia, at an altitude of *ca*. 100 m, or *M. marcus*, *M. telemachus*, *M. cisseis*, *M. rhetenor*, *M. zephyritis*, *M. absoloni*, *M. godartii*, *M. deidamia*, *M. helenor*, and *M. achilles* in the Alto Madre de Dios valley near Salvación, ca. 500-700 m (Madre de Dios department, Peru). In order to present a general pattern of the geographical variation of species richness, we have established a map indicating the number of species within limited regions covering, when necessary, the whole range of altitudes (Fig. 5). The richest regions occur along the Andes, with a maximum of 16 species in northern Peru (lowland species: *M. marcus*, *M. eugenia*, *M. telemachus*, *M. hecuba*, *M. cisseis*, *M. rhetenor*, *M. menelaus*, *M. deidamia*, *M. helenor*, *M. achilles*; low mountain species: *M. theseus*, *M. aurora*, *M. godartii*; cloud forest species: *M. amphitryon*, *M. lympharis*, *M. sulkowskyi*). The number decreases markedly towards the north, attaining 5 species (*M. theseus*, *M. rhetenor*, *M. menelaus*, *M. helenor*, *M. achilles*) in the Cordillera de Mérida (6 if the presence of *M. sulkowskyi*, indicated by Blandin & Deroche (2011), is confirmed). Along the Pacific slopes there are no more than 7 species (*M. theseus*, *M. niepelti*, *M. cypris*, *M. sulkowskyi*, *M. amathonte*, *M. granadensis* and *M. helenor*). In the Atlantic domain, the maximum regional richness is observed in Rio de Janeiro state, where 8 species exist (*M. hercules*, *M. anaxibia*, *M. portis*, *M. aega*, *M. menelaus*, *M. epistrophus*, *M. iphitus*, *M. helenor*). Species diversity decreases towards the latitudinal limits of the genus, in Central America and eastern Brazil. On the whole, the distribution of the genus *Morpho* is obviously related to the distribution of tropical rainforests, a few species existing, however, in areas where wet forest gives way to dry forest, such as western Ecuador and north-western Peru, and central Bolivia (Blandin, 2007a; Nakahara & Blandin, 2010; Gareca & Blandin, 2011).

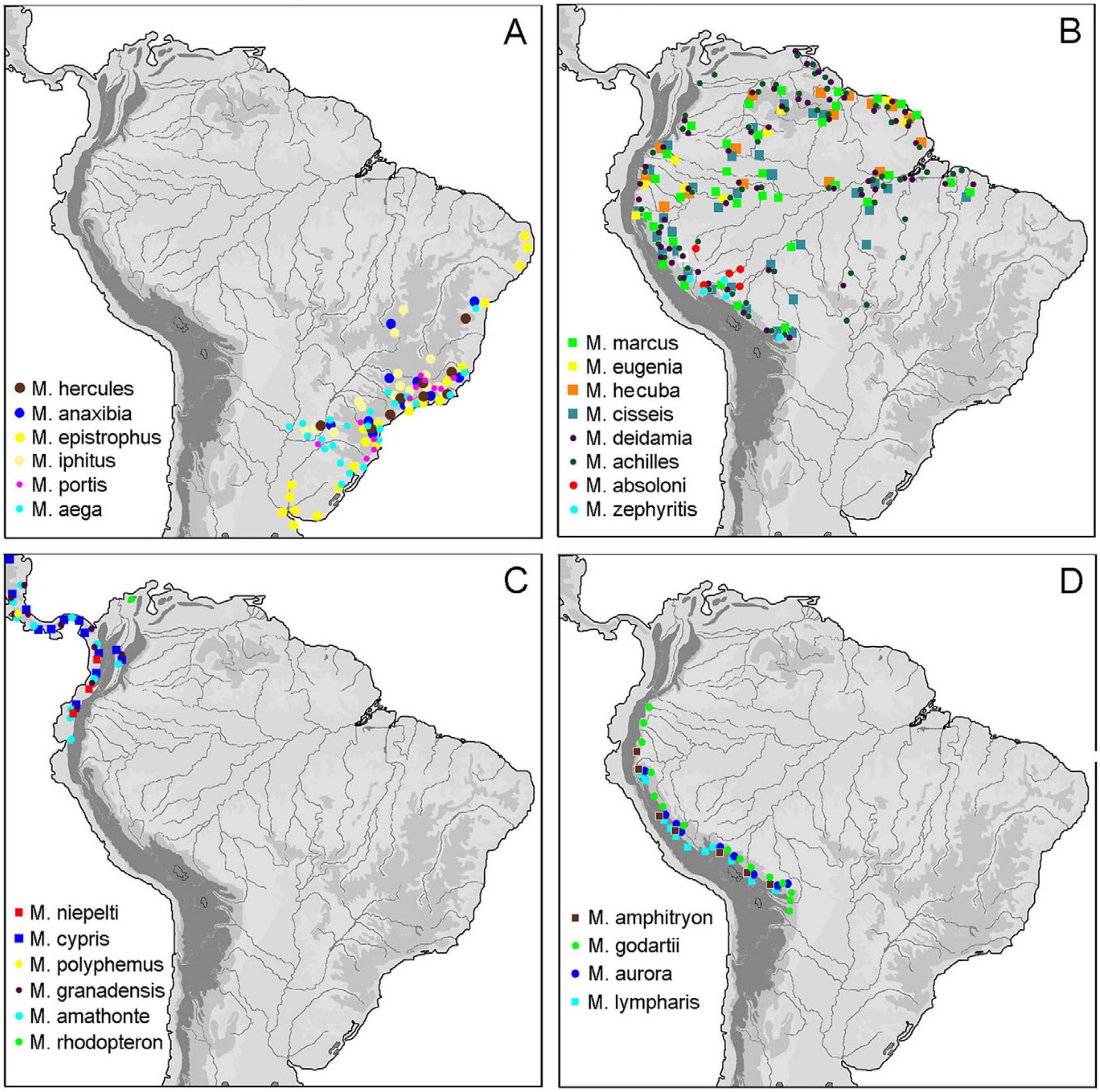


Fig. 3. Geographic distribution of *Morpho* species. A: Atlantic group. B: Cis-Andean group. C: Trans-Andean group. D: Cis-Andean mountain group. After Blandin (2007a), modified.

4. THE DIVERSIFICATION OF *MORPHO* THROUGH TIME AND SPACE

4.1. Phylogeny of *Morpho*

Phylogenetic studies have established that the genus *Morpho* is monophyletic (Penz & DeVries, 2002; Wahlberg *et al*., 2009; Cassildé *et al*., 2010, 2012; Penz *et al*., 2012). The first event is the initial divergence between the *marcus* clade and a clade that includes all other lineages (Fig. 6). One major difference between these two clades is that, in *M. marcus* and *M. eugenia*, the brilliant blue color is produced by superposition of scales, while in all other iridescent *Morpho* species, it is produced by highly specialised microstructures on the dorsal surface of scales (Cassildé *et al*., 2010). The sister clade of the *marcus* clade underwent an important diversification, first with the divergence of the "canopy clade" (Penz & DeVries, 2002), in which males fly high above streams or tracks, or even above the canopy. This clade diversified into the *telemachus* and *hecuba* clades, and into the *anaxibia* and *rhetenor* clades. As proposed by Penz *et al*. (2012), the *helenor* clade includes not only *M. deidamia*, *M. granadensis*, *M. helenor* and *M. achilles*, but also the three "white *Morpho*" (*M. epistrophus* and *M. iphitus*, endemic to the Brazilian Shield, and *M. polyphemus*, endemic to Central America). DNA analyses failed to clarify the relationships within the "white *Morpho*", the placement of

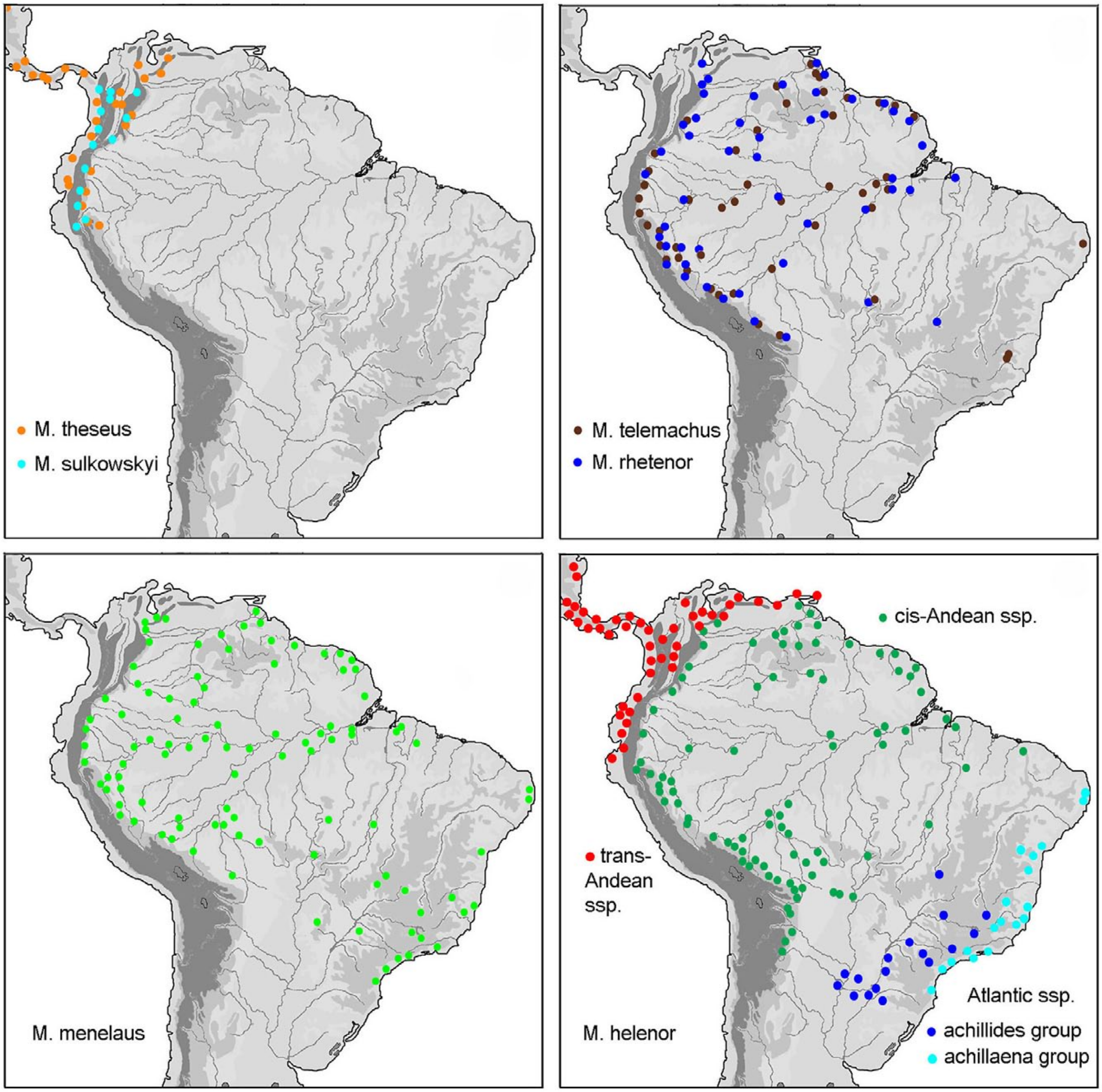
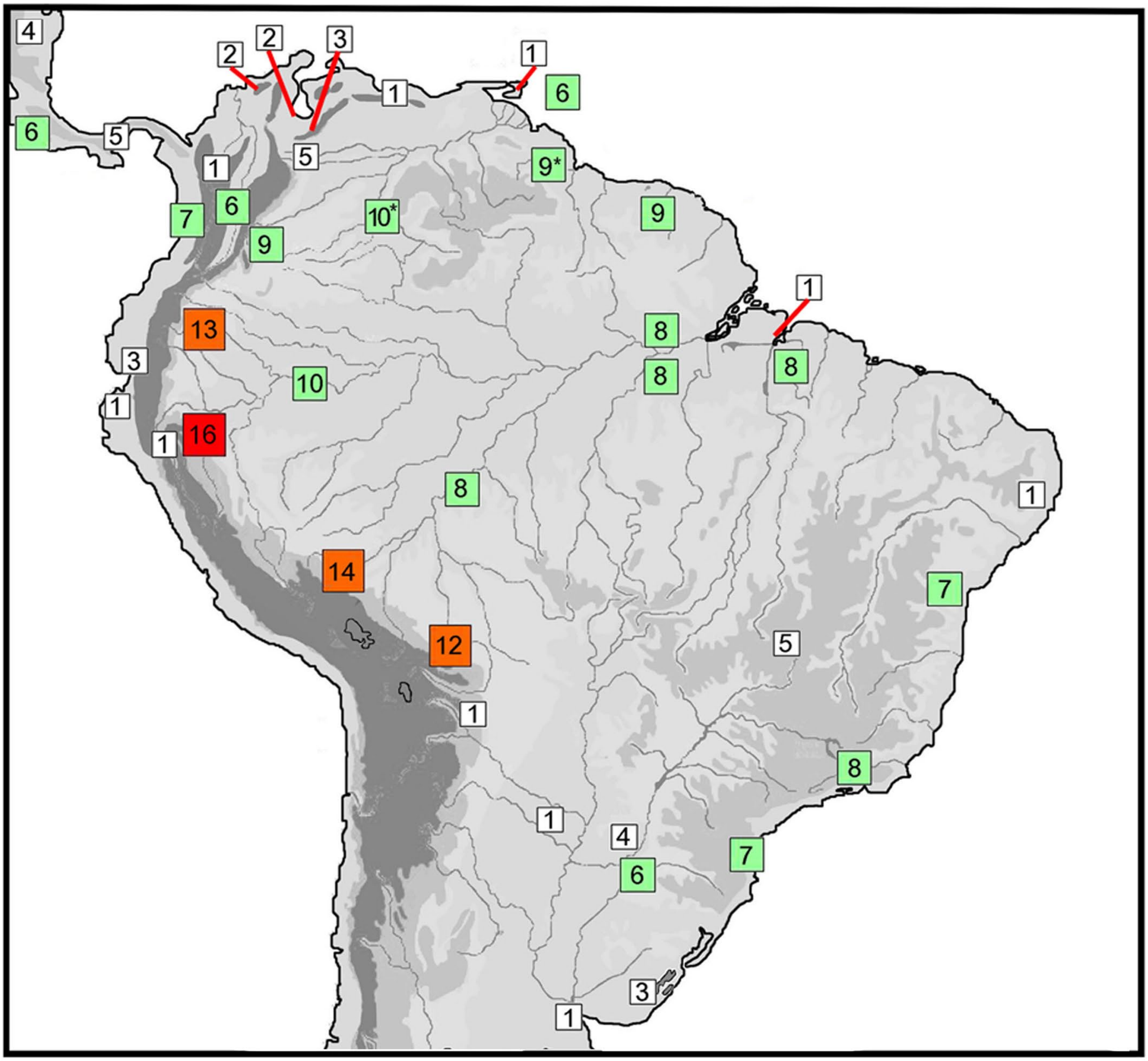


Fig. 4. Geographic distribution of the *Morpho* species overlapping cis-Andean and trans-Andean regions, and/or the Atlantic region. After Blandin (2007a), modified.

M. polyphemus in trees being unstable (Cassildé *et al*., 2012; Penz *et al*., 2012). However, from a morphological point of view, these three species form a clade, supported notably by wing-scale microstructures (Cassildé *et al*., 2010). Therefore, we agree that *M. polyphemus* belongs to the *epistrophus* + *iphitus* + *deidamia* lineage within the the *helenor* clade (Fig. 6). The sister clade of the *helenor* clade diverged into the *menelaus* clade and the *portis* clade. Within the latter, relationships were not definitely established, as Penz *et al*. (2012) did not study *M. zephyritis*, *M. rhodopteron* and *M. absoloni.* Therefore, our arrangement of branches is hypothetical. Considering the amazing morphological similarities between the Atlantic *M. portis* and the north-Andean *M. rhodopteron*, both obviously differing from *M. sulkowskyi* (Fig.10), we propose that *M. rhodopteron* belongs to same clade as *M. portis*, while we suggest that *sulkowskyi* + *lympharis* and *aurora* + *absoloni* are sister lineages.

4.2. Diversification of lowland and low mountain *Morpho* in the north-west part of South America

In the region situated north-west of a line joining the department of Tumbes (Peru) to eastern Venezuela south of the Orinoco Delta, cordilleras separate lowlands and valleys into several "compartments", each having distinct species assemblages (Fig. 7). Because geodynamic studies provide reliable estimations of the ages of these cordilleras, this region presents ideal conditions to attempt to link geological events



Fig; 5. Geographic variation in species numbers. Maximum numbers occur along the eastern slopes of the Andes.

with diversification of *Morpho* lineages.

Several clades have separated into trans-Andean and cis-Andean branches. As the Colombian Cordillera Oriental and the Cordillera de Mérida today separate trans-Andean and cis-Andean species, the simplest hypothesis is that these mountains separated previously widespread populations when they attained a sufficient height to prevent gene flow, i.e. ca. 5-2 MY.

The *rhetenor* clade (or subgenus *Megamede*), which diverged from the *anaxibia* clade *ca*. 10 MY according to Penz *et al*. (2012), includes two lowland species: *M. cypris*, a trans-Andean species (Fig. 3D), and its sister species *M. rhetenor*, which exists throughout Andean slopes, Amazonian lowlands and the Guiana Shield (Fig. 4). *M. rhetenor* also exists in the swamp forests of the south-western shores of Lake Maracaibo and of the Orinoco Delta (*M. r. hightoni* and *M. r. augustinae* respectively), and in some Llanos gallery forests (*M. r. colombianus*). In the Peruvian Central Andes, the very distinct *M. r. helena* inhabits the Huallaga valley, whose males exhibit dorsal white bands comparable to those of *M. cypris* (Fig. 8). However, there exists in the middle Huallaga valley a significant proportion of males having narrow white bands that may be discontinuous or virtually absent (Fig. 8). In some respects, this variability is similar to that observed in *M. r. augustinae* and *M. r. hightoni*: in both subspecies, certain specimens have dorsal surfaces evoking that of *M. cypris,* with whitish areas reminiscent of the white bands, and sub-marginal white patches; other specimens, on the contrary, have only reduced sub-marginal patches (Neild, 2008). In the basins of Ucayali and Perené rivers, rare males of *M. r. mariajosianae* and *M. r. cacica* have more or less developed dorsal white bands. In Amazonian populations (*M. r. rhetenor*), white bands may be lacking, except in very uncommon specimens where there exist reduced patches of white scales. These data suggest the phylogenetic relationships represented on Fig. 8. We speculate that the *Megamede* male ancestor had white bands and submarginal patches, which were subsequently reduced or lost in certain lineages.

Penz *et al*. (2012) estimated the age of the *cypris-rhetenor* divergence *ca*. 5 MY. At that time, the proto-Central Andes and the proto-Northern Andes were already connected (closure of the WAP after 13-11 MY), the western Amazonian lowlands were continuous along the Andes following the regression of the Acre System (after 10-7 MY), while the Llanos were almost filled, and the Cordillera de Mérida was very low. A simple evolutionary scenario (*Megamede* scenario 1), based on this geographic setting, should be as follows. Event 1: *ca*. 10 MY, divergence of *Iphixibia* and *Megamede* ancestors somewhere, the former dispersing towards the Atlantic forests. Event 2: *ca*. 5 MY, widespread populations of *cypris* + *rhetenor* ancestor are separated into the proto-*cypris* and proto-*rhetenor* populations by the rise of the Colombian Cordillera Oriental. Event 3: a *rhetenor* lineage adapts to gallery and swamp forests throughout the proto-Orinoco basin, while other(s) lineage(s) remain adapted to *terra firme* forests. Event 4: perhaps in the last 2 MY, the gallery/swamp forests lineage is fragmented into Lake Maracaibo, gallery forests and Orinoco Delta populations, in relation to climate and landscape transformations subsequent to the rise of the Venezuelan cordilleras. Event 5: in the meantime, the *terra firme* populations along the Central Andes evolved into various populations, some retaining more or less developed white markings, others, notably in Amazonian lowlands and along the Northern Andes, having lost those markings.

However, if Penz *et al*. (2012) estimates of divergence times are too young (as we discussed above under Methods), the separation between proto-*cypris* and proto-*rhetenor* populations may have occurred ealier than 5 MY, possibly *ca*. 10 MY. At that time, it is unlikely that the Cordillera Oriental was sufficiently high to form a definite barrier. Consequently, an alternative scenario could be explored. We recall that swamp forests existed in western Amazonia, around the Pebas System, which flowed into the Caribbean in the vicinity of the present Lake Maracaibo. The separation of Lake Maracaibo and Orinoco hydrographic basins, dated at *ca*. 8 MY (Albert *et al.*, 2006), could explain the divergence of *M. r. hightoni* and *M. r. augustinae*, if a swamp forest ancestor already existed. This hypothesis is compatible with a 10 MY age for the formation of the *rhetenor* lineage. Consequently, one must explain how the divergence of proto-*cypris* and proto-*rhetenor* occurred, prior to 8 MY, either by vicariance or by dispersal processes.

The proto-Northern Andes were separated from the proto-Central Andes by the WAP**,** at least from the Eocene until 13-11 MY, and they were isolated from the Guiana Shield at least until around 14-10 MY, when the Pebas System evolved into the Acre System, or even later, until the filling of the Llanos (*ca*. 5 MY). Moreover, the Magdalena basin continued to isolate the Colombian Cordillera Central from the low Cordillera Oriental until the latter was connected to the proto-Northern Andes. Given this information, two alternative hypotheses must be considered: either the *Megamede* ancestor existed in the proto-Northern Andes, where it was isolated, or it existed elsewhere, in the Guiana Shield or in the proto-Central Andes. The first hypothesis implies that *rhetenor* ancestors resulted from a dispersal outside of the proto-Northern Andes, the second that *cypris* ancestors resulted from a dispersal into the proto-Northern Andes, either from the Guiana Shield or from the proto-Central Andes.

To select the simplest hypothesis, the following arguments should be considered. If one supposes that *cypris* + *rhetenor* ancestors existed first on the Guiana Shield, or in the proto-Northern Andes, one must envisage an initial dispersal of *M. anaxibia* ancestors toward the Brazilian Shield through the Amazonian lowlands, and the subsequent extinction of their descendants everywhere except on the Brazilian Shield. It is simpler to suppose that the divergence between the *anaxibia* and *rhetenor* clades occurred in the proto-Central Andes rather than thousands of kilometres to the north. On the other hand, the presence in Peru of populations sharing developed white markings with *M. cypris* is consistent with the hypothesis that *cypris* ancestors dispersed from the north of the proto-Central Andes towards the proto-Northern Andes across the WAP ecological mosaic that probably acted more as an intermittent filter than a permanent barrier. This scenario (*Megamede* scenario 2) should be summarized as follows: Event 1: divergence of the *anaxibia* and *rhetenor* clades in the proto-Central Andes. Event 2: dispersal of *cypris* ancestors, through the WAP, towards the proto-Northern Andes. Event 3: within the *rhetenor* clade, divergence between a *terra firme* lineage and a gallery/swamp forest lineage. Event 4: fragmentation of the latter, following the evolution of the proto-Orinoco basin. Event 5: after the closure of the WAP, and in relation with the development of western Amazonian lowlands, northwards dispersal of *rhetenor* populations reaching the Colombian Cordillera Oriental after it was sufficiently high to form a barrier, and subsequently the Cordillera de Mérida that they failed to cross.

The scenarios 1 and 2 do not imply different phylogenetic hypotheses, both being consistent with the tree presented on figure 8. Scenario 1 is the simplest. However, the crucial point is the estimate of divergence times. If ages were much older than those estimated by Penz *et al*. (2012), then scenario 2 would be preferred. But the dispersal route of *cypris* ancestors remains a problem, as there are two possibilities, along either the western or the eastern slopes of Ecuadorian Andes. The western route supposes that lowland rainforests existed in SW Ecuador, where, today**,** ecosystems are adapted to a relatively dry climate. The eastern route supposes that the *cypris* ancestors attained the eastern slopes of the Colombian Cordillera Central before the uplift of the Cordillera Oriental, their descendants suffering widespread extinction east of the Northern Andes. Currently, there is no convincing argument supporting one or other route.

Another interesting case concerns the *helenor* clade. It includes 2 trans-Andean species (*M. polyphemus* and *M. granadensis*) and 2 cis-Andean species (*M. deidamia* and *M. achilles*). *Morpho helenor* is represented in the trans-Andean

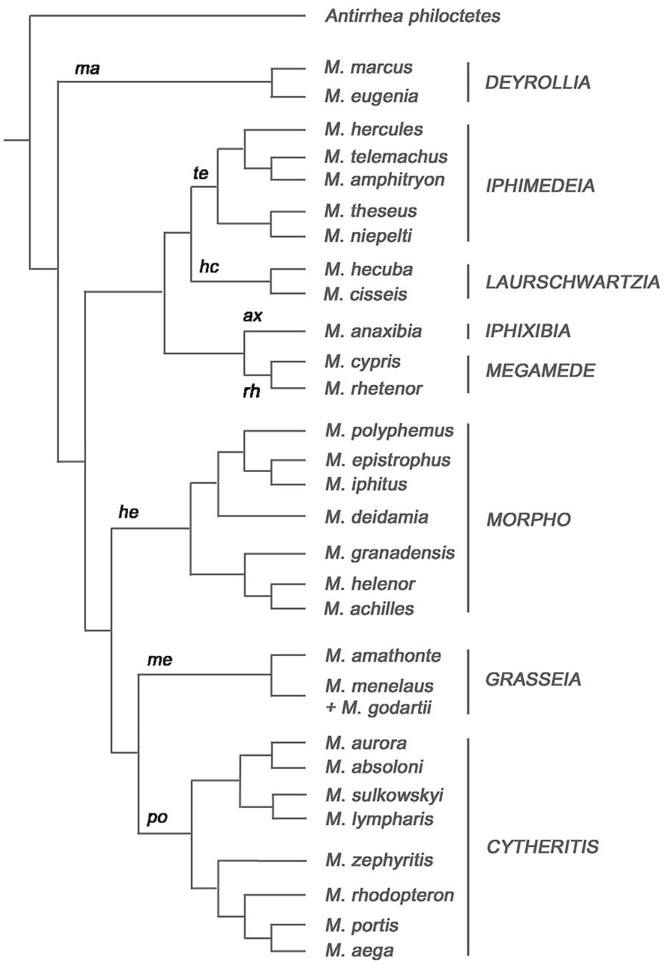


Fig. 6. Hand-constructed phylogenetic tree of the genus *Morpho* (after Cassildé *et al*., 2012, and Penz *et al*., 2012). Major clades, corresponding to subgenera: ma: *marcus* clade – te: *telemachus* clade – hc: *hecuba* clade – ax: *anaxibia* clade – rh: *rhetenor* clade – he: *helenor* clade – me: *menelaus* clade – po: *portis* clade.

region by the *M. h. peleides* group (Fig. 4), with includes subspecies clearly different from the cis-Andean subspecies (Blandin, 2007a, b). Penz *et al*. (2012) suggested that *M. polyphemus* originated on eastern Andean slopes at around 10 MY, subsequently undergoing a range contraction. Given its relationships with the Atlantic forest *M. epistrophus* and *M. iphitus* and with the cis-Andean *M. deidamia* (cf. Fig. 6), this seems to be the only credible hypothesis. Thus, *M. polyphemus* ancestors should have dispersed from the proto-Central Andes toward the proto-Northern Andes accross the WAP.

Penz *et al*. (2012) estimated the divergence between *granadensis* and *helenor+achilles* ancestors at around 5 MY. Thus, the divergence of the *M. h. peleides* group should be more recent. Let us assume that the divergence between *granadensis* and *helenor+achilles* ancestors effectively resulted from the uplift of the Colombian Cordillera Oriental. Thus, the ancestors of *M. helenor* had a cis-Andean distribution, and were unable to cross the Cordillera Oriental. Consequently, the separation of the *peleides* group should be explained by events having occurred after the Cordillera Oriental became a barrier. Cis-Andean populations may have spread towards the proto-Cordillera de Mérida and the periphery of Lake Maracaibo. The recent uplift of the Cordillera de Mérida may have isolated *M. h. peleides* ancestors which subsequently passed over the Serranía de Perijá, dispersing towards the Magdalena valley, the Pacific slopes (attaining north-western Peru), and throughout Central America, where they split into more than 10 subspecies (Blandin, 2007a). Today, however, the Cordillera de Mérida does not form a complete barrier: the cis-Andean *M. h. peleus* hybridizes directly with the trans-Andean *M. h. peleides*, due to the low altitude pass in Táchira state. Moreover, *M. h. peleides* is distributed around the north-eastern extremity of the cordillera, and along the SE slopes as far as Barinas state, where it also hybridizes with *M. h. peleus* (Blandin, 2007a; Neild, 2008). Therefore, if today the Cordillera de Mérida is not a complete barrier between the cis-Andean and trans-Andean lineages of *M. helenor*, it is unlikely that it previously formed a definite barrier favouring their vicariant divergence. Consequently, a scenario similar to the *Megamede* scenario 1 could be more credible, i.e. a separation by the uplift of the Colombian Cordillera Oriental, around 5-2 MY. However, such a scenario implies an older divergence between *granadensis* and *helenor+achilles* ancestors. Therefore, this earlier divergence could be better explained by a dispersal from the north of the proto-Central Andes to the proto-Northern Andes, as in the *Megamede* scenario 2. On the whole, the evolution of the *helenor* clade should have been marked at least by two dispersals towards the proto-Northern Andes and Central America, before the major uplift of the Colombian Cordillera Oriental, (*M. polyphemus* and *M. granadensis* ancestors), and possibly by a vicariant event having produced the trans-Andean *peleides* group, that resulted of this uplift, *ca*. 5-2 MY ago, unless this group also resulted from dispersal accross the WAP, a hypothesis that we do not exclude (Fig. 9).

4.3. Does the south-to-north variation of the number of lowland species reflect a south-to-north dispersal?

The number of lowland species along the eastern slopes of the Northern Andes decreases northwards, from 10 in Ecuador to 4 in the Cordillera de Mérida. Three species (*M. eugenia*, *M. hecuba*, *M. cisseis*) have their northern limits between Mocoa and Villavicencio, three others (*M. marcus*, *M. telemachus*, *M. deidamia*) in the area of Villavicencio (approximately at the latitude of Bogotà), while *M. rhetenor*, *M. menelaus*, *M. achilles* and *M. helenor* exist along the Cordillera de Mérida, the latter being represented by the cis-Andean *M. h. peleus* on the south-eastern side. These data suggest a progressive south-to-north dispersal, consistent with an initial diversification of the genus in the proto-Central Andes. Northward dispersals should have been favoured once the WAP was closed and the Acre System had regressed, i.e. by 10-7 MY. According to this scenario, dispersing populations could not have attained the eastern slopes of the Colombian Cordillera Oriental before 5-2 MY, when it formed a barrier; otherwise, populations of all species should exist on both sides of this cordillera. Furthermore, it is necessary to suppose that at least populations of *M. marcus*, *M. eugenia*, *M. hecuba*, *M. cisseis* and *M. deidamia* became extinct

Fig. 7. *Morpho* assemblages in north-western South America

on the western slopes of the Cordillera Oriental (if one admits that *telemachus*, *menelaus*, and *helenor* populations diverged at that time into *M. theseus*, *M. amathonte* and *M. peleides* respectively). A relatively recent south-to-north dispersal seems to be simpler. The northward diminution in the number of species may be explained either by differences in dispersal capacity, or by the extinction of some species subsequently to the recent regression of rainforests in the Orinoco basin.

4.4. Diversification of mountain species in relation to tectonic uplift

The *telemachus* clade provides a rather simple example: its cis-Andean branch initially diverged into an Atlantic clade (*M. hercules*) and a branch which diverged subsequently into a lowland branch (*M. telemachus*, which flies from sea level up to ca. 1200 m) and a cloud forest branch (*M. amphitryon*, which generally flies between *ca*.1500 m and *ca*. 2500 m) (Fig. 6). *Morpho amphitryon* exists in Bolivia (1 subspecies), in Peru (5 subspecies) and southern Ecuador (1 subspecies). Therefore, it is credible that its ancestors diverged from *M. telemachus* ancestors somewhere in the proto-Central Andes. This event could not have occurred before the mountains attained sufficient altitudes, i.e. Early Miocene (*ca*. 20-17 MY) in northern Bolivia or southern Peru, and Late Miocene (10-5 MY) in central and northern Peru (Sempere *et al*. 2005; Picard *et al*., 2008). Therefore, two alternative hypotheses should be explored.

The first hypothesis is based on Penz *et al*.'s (2012) estimate of 2.5 MY as the date of the divergence between the *hercules* lineage and the *telemachus* + *amphitryon* lineage (they presented this result as an estimate of the divergence between *M. hercules* and *M. theseus*; unfortunately, their "*theseus*" specimen labelled CP 07-01 proved not to be *M. theseus*, being instead a male of the cloud forest *M. amphitryon* from central Peru; NGS Data Bank, accessed 6 September 2013). According to their estimate, the divergence of ancestral *M. amphitryon* resulted from a very recent shift from lowland or low mountain populations into cloud forests, this event being followed by a rapid dispersal of populations throughout the Central Andes and southern Ecuador, and their diversification into 7 subspecies. The second hypothesis supposes that the divergence between ancestral *M. amphitryon* and *M. telemachus* was associated with tectonic uplift-driven differentiation of cloud forests, during Late Miocene in central or northern Peru, possibly earlier if it occurred in southern Peru or Bolivia. However, this hypothesis implies a much earlier divergence of the *hercules* and *telemachus* + *amphitryon* lineages than estimated by Penz *et al*. (2012).

Like the *telemachus* clade, the *portis* clade includes: i)- an

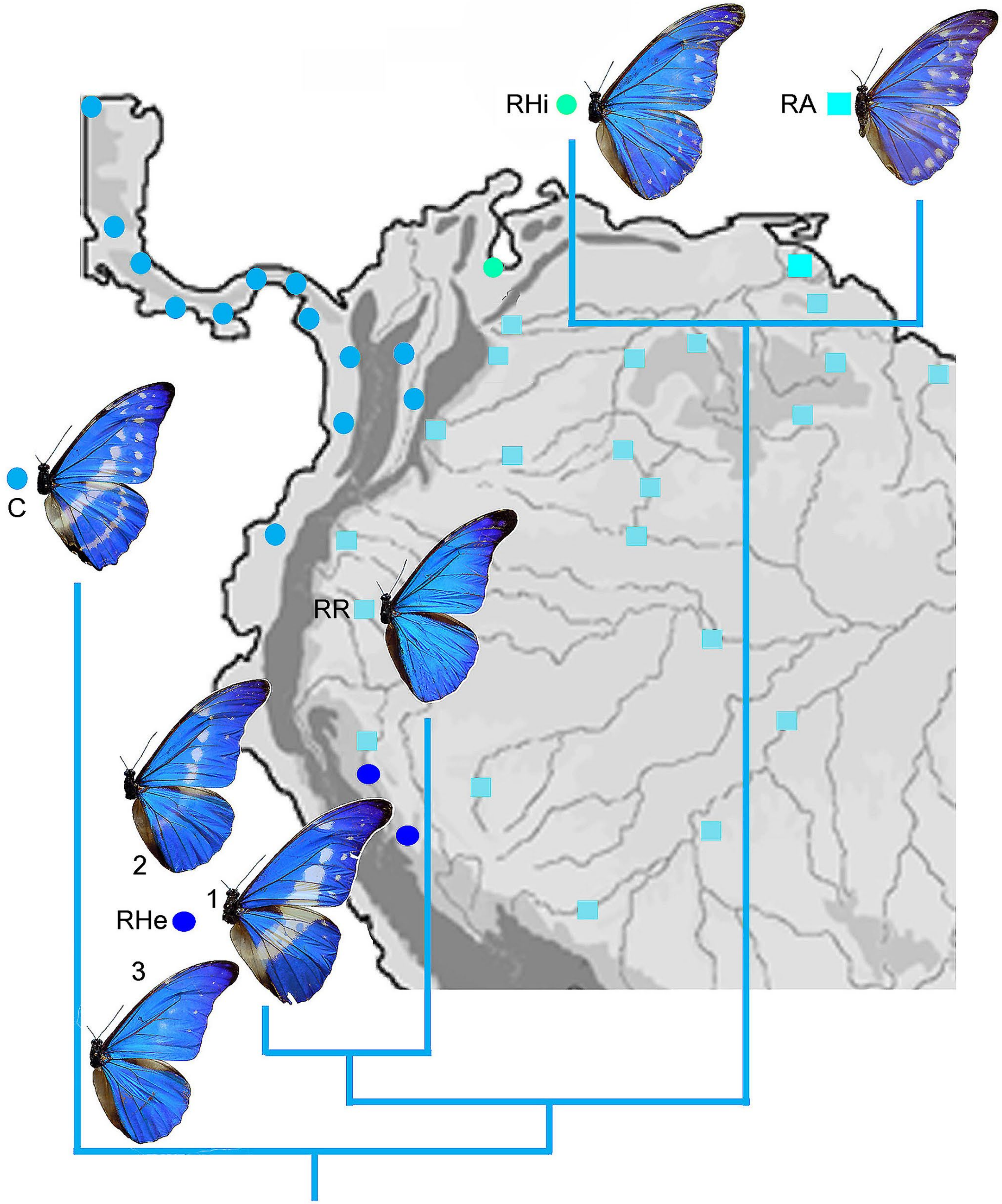


Fig. 8. Hypothetical cladogram of the subgenus *Megamede*. C: *M. cypris*. RHe: *M. rhetenor helena* (1, 2, 3: three specimens from the middle Huallaga Valley illustrating the variations of the white markings). RR: *M. r. rhetenor* (including *M. r. equatenor*, distributed along the eastern slopes of the Northern Andes). RHi: *M. r. hightoni* (Lake Maracaibo). RA: *M. r. augustinae* (Orinoco delta). *M. r. columbianus*, from Llanos gallery forests, is not illustrated.

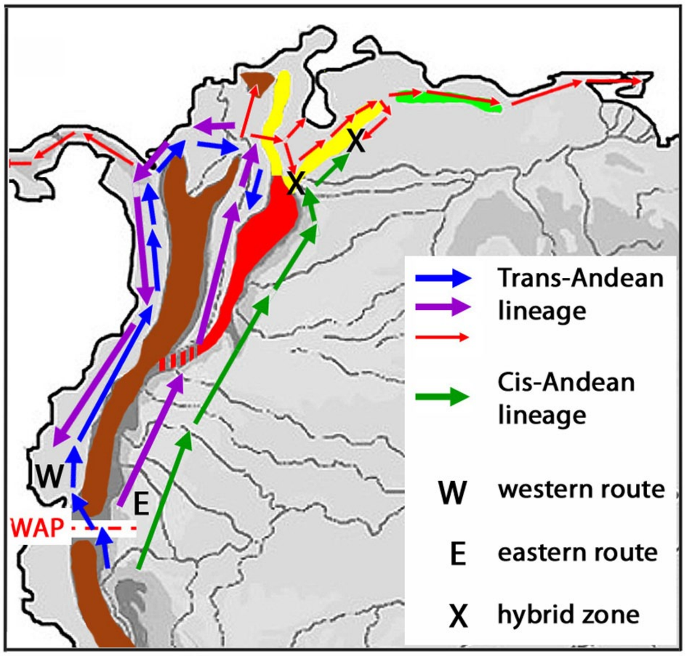


Fig. 9. Hypothetical dispersal scenario of the *M. helenor* lineage from the north of Central Andes to Northern Andes and Central America. Ancestors of the trans-Andean populations could have crossed the WAP, and followed either the western route or the eastern route.Subsequently, they dispersed towards Central America, and towards Venezuelan cordilleras, and Trinidad and Tobago. Dispersal of the cis-Andean populations probably occurred after the closure of the WAP. They reached the Cordillera de Mérida, where the cis-Andean *M. h. peleus* today hybridizes with the trans-Andean *M. h. peleides* in two zones.

Atlantic branch (*M. portis* and *M. aega*); ii)- a cis-Andean branch, with 2 lowland and foothill species in SW Amazonia (*M. zephyritis* and *M. absoloni*), a low mountain/cloud forest species (*M. aurora*, living mainly between 1000 m and 2000 m, and 2 cloud forest species (*M. lympharis* in Central Andes, and *M. sulkowskyi*, which extends from northern Peru to Northern Andes). Moreover, the *portis* clade includes *M. rhodopteron*, endemic to the Sierra Nevada de Santa Marta (Colombia). Penz *et al*. (2012) did not analyze *M. zephyritis*, *M. absoloni* and *M. rhodopteron*, and studied only a very limited sample of the *lympharis* + *sulkowskyi* lineage. Therefore, we propose a plausible phylogeny (Fig. 6) which takes into account morphological similarities, notably in the structure of ventral ornamentation, between *M. zephyritis*, *M. portis*, *M. aega* and *M. rhodopteron* (Fig. 10). As we discussed for the *telemachus* clade, two hypotheses should be considered.

Penz *et al*. (2012) concluded that *M. sulkowskyi* and its relatives originated somewhere in the Eastern Andes. According to their estimates, the *menelaus* clade and the *portis* clade diverged *ca*. 10 MY, the *sulkowskyi* branch and the *portis* branch between 10 and 5 MY. This is consistent with a differentiation of the *lympharis* + *sulkowskyi* lineage in the north of Central Andes. However, this hypothesis implies that the origin of *M. rhodopteron* is very recent, and that its ancestors were able to reach the Sierra Nevada de Santa Marta despite the fact this sierra was completely isolated (perhaps since Late Eocene, as suggested by Santos *et al*., 2008). A second hypothesis supposes an earlier differentiation of the *lympharis* + *sulkowskyi* lineage, *ca*. 20 MY, which is consistent with the beginning of cloud forests formation. This supposes that ancestors of the *portis* clade dispersed progressively upward, and that different species subsequently adapted to the different ecological belts. That these ancestors had a wide altitudinal range is in agreement with the ranges of extant species, notably *M. rhodopteron* (600-2400 m; Montero Abril & Ortiz Perez, 2010), and the two Atlantic species (*M. aega* from sea level to *ca*. 1200 m, *M. portis* from 800 to 1700 m; Olaf Mielke and Tomasz Pyrcz pers. comm.). On the other hand, the dispersal of ancestral *M. rhodopteron* towards the Sierra Nevada de Santa Marta via the Northern Andes is more credible, as it may have occurred before the Sierra Nevada was widely separated from the Colombian Cordillera Central. Both hypotheses imply that the dispersals of the Andean ancestors of the *portis* + *aega* and *rhodopteron* lineages were followed by their extinction in the Andes. There is no obvious explanation. However, we speculate that this extinction was favoured by competition with *M. aurora*, *M. lympharis* and *M. sulkowskyi* ancestors, which dispersed within the same ecological belts.

4.5. The role of Andean valleys in diversification of *Morpho*

Morpho assemblages vary between Andean valleys, sometimes at species level. For example, in the Northern Andes, all trans-Andean species are represented in the Magdalena valley (except *M. niepelti*), while only *M. helenor* is present in the drier Cauca valley. Similarly, in the Central Andes, only *M. helenor* exists in the dry middle Marañon valley, while in other major valleys there are rainforests inhabited by several lowland and low-mountain species, most often represented by markedly different subspecies (Fig. 11).

At least two hypotheses may explain the formation and diversification of tropical rainforest assemblages in Central Andean valleys: i)- a progressive isolation of Andean slope populations, as the valleys deepened, ridges becoming geographic barriers favouring vicariant divergence; ii)- a dispersal of lowland populations into the deepening valleys, followed, in certain cases, by a differentiation into subspecies that may differ from one valley to another. A combination of the two hypotheses may explain situations where a transition exists between upper valley subspecies and corresponding lowland subspecies. For example, in the Satipo area, between the upper and lower courses of the Perené river, there exist intermediate specimens between upper and lower valley subspecies of *M. deidamia* (*M. d. pyrrhus* and *M. d. grambergi*), *M. helenor* (*M. h. papirius* and *M. h. theodorus*), and *M. achilles* (*M. a. agamedes* and *M. a. phokylides*) (Blandin, 2007a).

4.6. The conquest of the east: origin and diversification of *Morpho* in the Amazonian lowlands and the Gondwanan Shields

Ten *Morpho* species inhabit the western Amazonian lowlands, of which 8 exist to the south of the lower Amazon, while 9 exist in the Guianas (Fig. 5). The *Morpho* fauna of the Guiana Shield is characterized by a W-E change: along the Orinoco and the Rio Negro, the different species are represented by subspecies very similar to the western Amazonian subspecies, while several species are represented in the Guianas by subspecies differing from western subspecies. Moreover, in some cases, western and eastern subspecies are separated by different subspecies existing in the Tepuis region. For example, *M. achilles glaisi* separates the western *M. a. phokylides* from the eastern *M. a. aguiro*, while *M. deidamia jacki* separates the western *M. d. neoptolemus* from the eastern *M. d. annae* (Blandin, 2007a; Neild, 2008). These data suggest a complex dispersal from western Amazonia towards the Guiana Shield, probably related to the progressive development of lowlands between the Northern Andes and the Guiana Shield, from 10 to 5 MY approximately. Possibly, the Vaupés Arch may have facilitated migration before the complete filling of the Orinoco basin.

There are important differences between regions north and south of the middle and lower Amazon. Several species that exist on both sides are represented by distinct subspecies. For example, north of the Amazon, *M. t. telemachus* is a dimorphic subspecies, with a blue ("*telemachus*") and an ochre-yellow ("*metellus*") morphs; on the contrary, south of the Rio Amazon, *M. t. foucheri* is highly polymorphic, with blue, yellow, greenish, and brown morphs (Blandin, 1988). The more remarkable situation is that of *M. hecuba* and *M. cisseis*, which are sister-species separated by the middle and lower Amazon, *M. hecuba* to the north, *M. cisseis* to the south, while they overlap in western Amazonia (Fig. 3B). If their ancestors were sympatric in western Amazonia before they dispersed eastward, both should have dispersed to the north and the south of the proto-Amazon, and both should exist on either side, unless *cisseis* ancestors became extinct to the north, and *hecuba* ancestors to the south. It is simpler to suppose that a northern *hecuba* ancestor and a southern *cisseis* ancestor resulted from a vicariant event. The more recent W-E barrier that may have separated them is the Acre System, developed *ca*. 10-7 MY (Fig. 12). The subsequent filling of western Amazonia allowed the eastward dispersal of *M. hecuba* to the north, and of *M. cisseis* to the south of the paleo-Amazon. Subsequently, *M. cisseis* was able to disperse towards north-western Amazonia and then towards the Guiana Shield, becoming sympatric with various subspecies of *M. hecuba* (*M. h. werneri* in western Amazonia, *M. h. polyidos* and *M. h. obidonus* on the Guiana Shield). This scenario implies that the *hecuba* clade diverged from the *telemachus* clade before 10 MY; in that way it is not consistent with Penz *et al*. (2012) who estimated this divergence between 10 and 5 MY, and the *cisseis-hecuba* divergence around 2.5 MY. Considering the geodynamic of the Amazonian basin, these estimates are doubtful. That the Acre System acted as a temporary barrier may also explain the present distributions of *M. eugenia* and *M. marcus* (cf. Fig. 3B), and possibly the fact that several species have different subspecies to the north and the south of the Amazon.

The *Morpho* fauna of the Brazilian Shield differs dramatically from the Amazonian fauna (Fig. 3A-B). The 6 species endemic to the Atlantic forests are centered in an area covering Rio de Janeiro, São Paulo, Paraná and Santa Catarina states (Fig. 3A). Among the species existing in Amazonia, only *M. menelaus* and *M. helenor* are distributed throughout most of the Brazilian Shield (Fig. 4). In the present state of knowledge, *M. telemachus* has a more limited distribution (Pernambuco, Minas Gerais). *M. rhetenor* exists in the area of Brasilia, where it is probably uncommon (we know only one male in the Federal University of Paraná collection), and possibly in northern São Paulo state (K. Brown Jr., pers. comm; field observation not confirmed).

Considering the diversification and distribution of the different lineages, it is likely that the present situation results from several historical events, as suggested by Penz *et al*. (2012), and illustrated by the *helenor* clade. The latter is represented by the white *Morpho*, *M. epistrophus* and *M. iphitus*, and 10 subspecies of *M. helenor*, which form two groups, distinguished by their geographical distribution (Fig. 4). The western *achillides* group, extending from Chaco and Paraguay to Misiones, eastern Paraná and São Paulo, Goias and central Minas Gerais, includes subspecies with a blue band crossing the wings, while the eastern *achillaena* group, distributed from Santa Catarina to Paraíba, includes subspecies in which the metallic blue extends to the base of the wings (Blandin, 2007b). We previously hypothesized that the ancestors white *Morpho* existed in the proto-Central Andes, and that the *epistrophus* + *iphitus* ancestor dispersed towards the Brazilian Shield. We speculate that the ancestors of the *achillaena* group and that of the *achillides* group migrated towards the Atlantic forests subsequently, the former before the latter. In the *telemachus* clade, at least two dispersal events may also be envisaged, the first producing the ancestors of *M. hercules*, the second corresponding to migrations of *M. telemachus* populations. On the contrary, single events are sufficient to explain the migration of the *anaxibia* and (*portis* + *aega*) ancestors. It is likely that migrating populations followed the Mato Grosso connection, and attained the Atlantic forests in the southern part of the shield. As the connection was established perhaps as early as the Late Eocene (43 – 34 MY), and certainly during the Oligocene, dispersion from proto-Central Andes towards the Brazilian Shield was possible much earlier than dispersion towards the Guiana Shield.

4.7. Origin and evolution of Centro-American *Morpho*: what was the role of the Panama Isthmus?

The Centro-American *Morpho* fauna includes the endemic *M. polyphemus* (Costa Rica to Mexico) and 5 species existing in Colombia, the number of which decreases from Nicargua (5 species) to Honduras (3 species), and Mexico (2 species). At first glance, this pattern suggests that Colombian populations dispersed towards Central America. Penz *et al*. (2012) have suggested that this colonization resulted from repeated dispersal events after the closure of the Panama Isthmus (~3 MY). However, as already noted, the possibility of earlier migrations should be considered (Cody *et al*., 2010, and references therein) because they may explain certain aspects of the distribution of *Morpho* species and subspecies. For example, within the *helenor* clade, there are two strongly contrasting cases. On the one hand, the endemic *M. polyphemus* is distributed from NW Costa Rica to the Atlantic and Pacific sides of Mexico, forming 3 markedly different subspecies (*catalina*, *luna* and *polyphemus*). On the other, the widespread *M. helenor* is represented by only

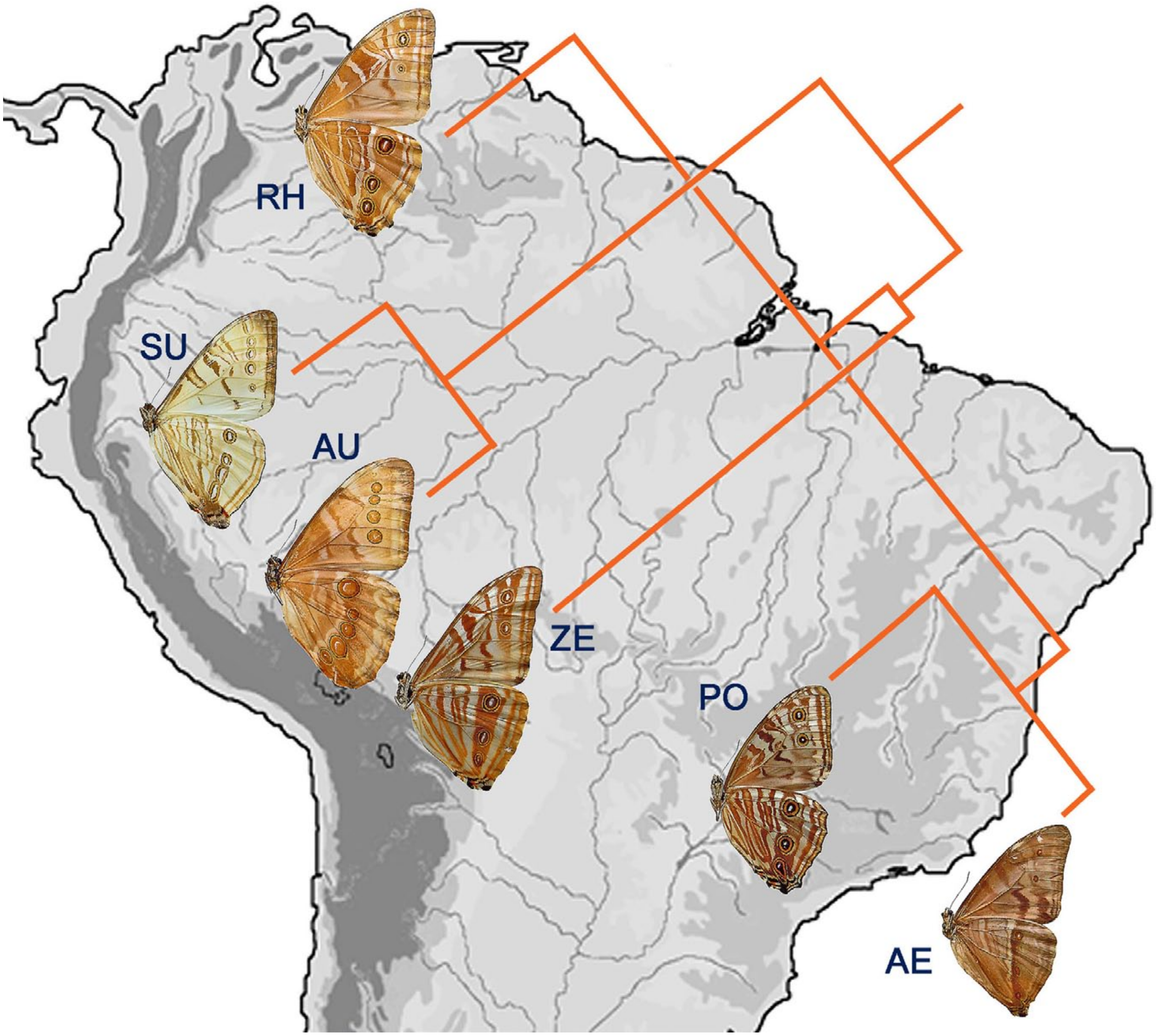


Fig. 10. Hypothetical cladogram of the subgenus *Cytheritis*. RH: *M. rhodopteron* (endemic to the Sierra Nevada de Santa Marta). SU: *sulkowskyi* lineage (*M. lympharis* in the Central Andes; *M. sulkowskyi* from the north of Central Andes to Colombian cordilleras). AU: *aurora* lineage (*M. aurora* along the Central Andes; *M. absoloni* in SW Amazonia). ZE: *M. zephyritis* (SW Amazonia). PO: *M. portis* (Atlantic forests). AE: *M. aega* (Atlantic forests).

3 closely related subspecies in Mexico (*montezuma*, *octavia* and *guerrerensis*), while it "explodes" into 9 subspecies, some of which are dramatically different (eg. *taboga*, *faustina* and *limpida*), in Panama and Costa Rica (Blandin, 2007b). It is plausible that ancestors of *M. polyphemus* migrated earlier than ancestors of *M. helenor* subspecies, and one may speculate that the Mexican *helenor* subspecies resulted from a first dispersal event, while the Costa Rican and Panamean subspecies dispersed later, and diverged within a region which was completely transformed during the Miocene (Farris *et al.*, 2011; Montes *et al.*, 2012a, b). Reliable dated phylogenies would enable one to check this hypothesis. If confirmed, the Pleistocene closure of the Panama Isthmus should have played only a partial role in the formation of the Centro-American *Morpho* fauna. If this hypothesis was rejected, it would be necessary to admit a recent (< 3 MY) extinction of ancestral *M. polyphemus* at least in Colombia and Panama.

DISCUSSION

5.1. Early times

Ancestral Morphinae probably originated between 65 and 50 MY (Wahlberg *et al.*, 2009) when the proto-Andes were discontinuous lowlands separated from the Gondwanan shields by an important Foreland Basin. Proto-tropical rainforests already existed in several regions. Where did the ancestral Morphinae appear? Three hypotheses can be considered: HYP 1- Morphinae resulted from a southward dispersal of Laurasian (proto-North America) ancestors, as it has been suggested for

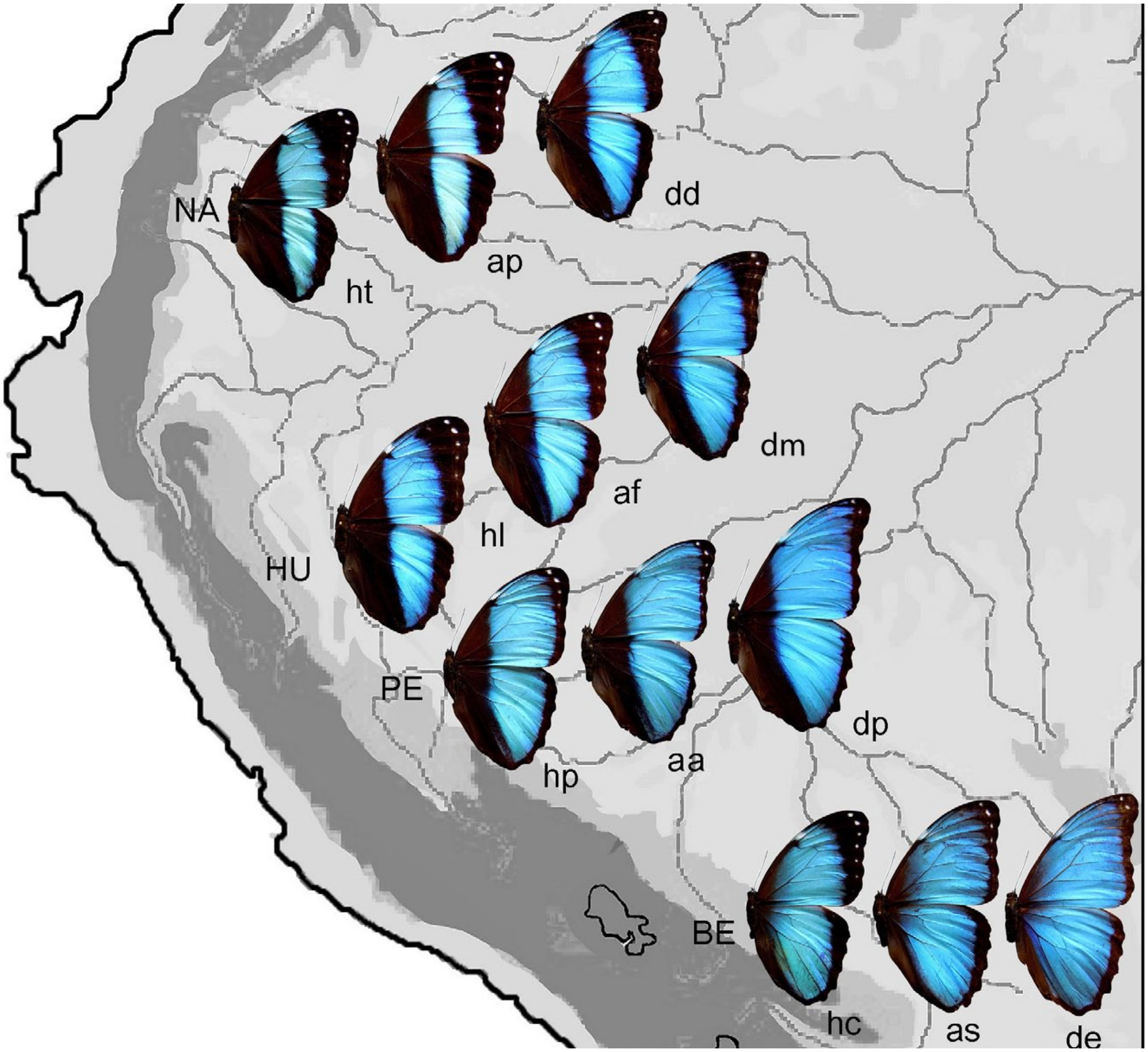


Fig. 11. Variations of *M. deidamia*, *M. achilles*, and *M. helenor* in major valleys of the Central Andes (NA: upper Napo valley, Ecuador. HU: upper Huallaga valley, Peru. PE: upper Perené valley, Peru. BE: upper Beni valley, Bolivia).ht: *M. h. theodorus*. ap: *M. a. phokylides*. dd: *M. d. diomedes*. hl: *M. h. lacommei*. af: *M. a. fagardi*. dm: *M. d. mariae*. hp: *M. h. papirius*. aa: *M. a. agamedes*. dp: *M. d. pyrrhus*. hc: *M. helenor coelestis*. as: *M. achilles songo*. de: *M. deidamia electra*.

several butterfly lineages; HYP 2- they differentiated on the Gondwanan proto-continent following its separation from Africa; HYP 3- they resulted from the dispersal of Australasian ancestors via the Antarctic continent.

HYP 1 involves a process considered as the more probable for various plants (Antonelli *et al*., 2009; Couvreur *et al*., 2011a), and for certain butterflies. For example, Willmott (2003) and Mullen *et al*. (2011) suggested that the ancestor of the genus *Adelpha* Hübner, [1819] arrived in South America within the last 15 MY, thus before the final closure of the Isthmus of Panama. Wahlberg & Freitas (2007), Peña *et al*. (2011), and Condamine *et al*. (2012a) have suggested that the ancestors of various groups migrated into South America around 32 MY, via the hypothetical GAARlandia route. One could suppose that ancestral Morphinae differentiated in tropical rainforests that existed in Laurasia, and later migrated into the New World, while the lineage became extinct in proto-North America. Therefore, it would be important to know whether the Centro-American representatives of Brassolini, Antirrhaeina and *Morpho* clades correspond to very basal branches of each of the three clades: it is obviously not the case for the *Morpho* clade, the earliest divergence event having produced the strictly cis-Andean *marcus* clade, while all the extant Centro-American lineages resulted from more recent divergence events.

That Morphinae are endemic to the Neotropics seems to be more simply explained by HYP 2. However, this implies that the divergence of the Morphinae clade occurred somewhere on the Gondwanan Shields after the separation of the South American proto-continent, *ca*. 100MY. This supposition is not consistent with the fact that the sister clade of Morphinae includes notably

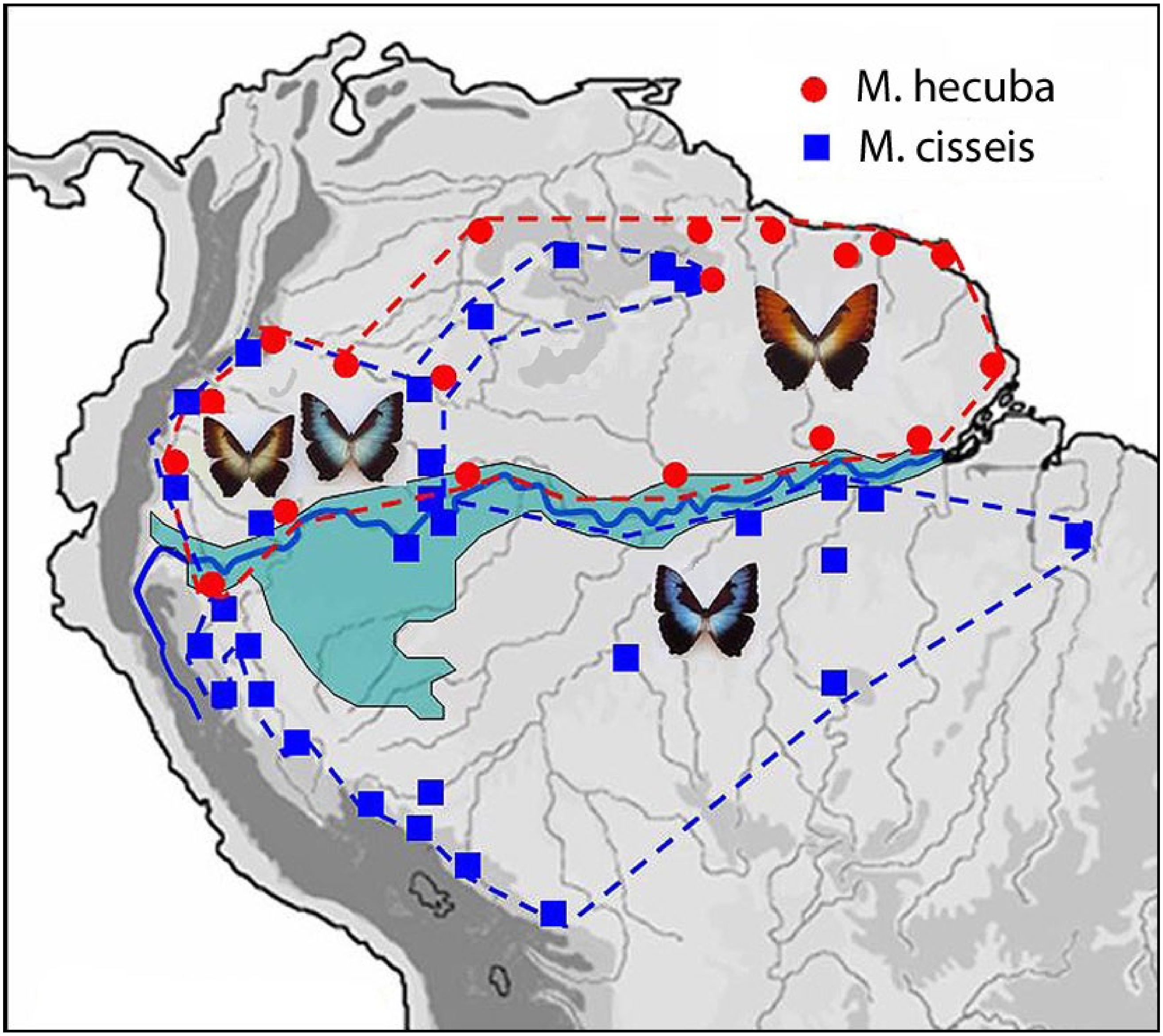


Fig. 12. Present geographical ranges of *M. cisseis* and *M. hecuba*, in relation to the Acre System, a possible barrier (10-7 MY). The illustrated subspecies are *M. c. phanodemus* and *M. h. werneri* in Western Amazonia, *M. c. cisseis* to the south of the Amazon river, *M. h. hecuba* in the Guianas.

Australasian lineages, and that the divergence time beween the two clades is estimated at *ca*. 55 MY (Wahlberg *et al*., 2009).

Terrestrial dispersal through Antarctica via ecosystems having tropical affinities was possible at least until the thermal maximum at the Paleocene-Eocene boundary, around 56 MY. By 54-51 MY, the opening of the Drake Passage was followed by lower Eocene (~50 MY) cooling of Antarctica. HYP 3 is consistent with the divergence time of the Morphinae clade and the fact that its sister-clade includes Australasian, African (notably South African) and other South-American endemic lineages (Wahlberg *et al*., 2009).

According to Wahlberg *et al*. (2009), the *Morpho* clade originated *ca*. 33 MY, and Brassolini, the sister-clade of Morphini, diversified into several lineages corresponding to extant genera between 39 and 20 MY. Surprisingly, Penz *et al*. (2012) estimated that the first divergence event within the *Morpho* clade (separation of the *marcus* clade) occurred only *ca*. 20 MY, and that all other extant major lineages were initiated between 15 and 5 MY. We suggest that these age estimates may be too young, and that a first diversification of the *Morpho* clade occurred earlier, in the proto-Central Andes. Unfortunately, there exists no precise information on the geodynamic transformation of the proto-Central Andes during the Oligocene (34-23 MY), which may have permitted reliable interpretation of this diversification. Allopatric speciation in different mountain ranges may have played a role, but limited datation of geologic events precludes evaluation of this hypothesis. Furthermore, geodynamic events are not the only evolution stimulants to be considered. Adaptation to different ecological niches may have played an early role, for example in the divergence between canopy and understorey species (Penz & DeVries, 2002). Moreover, adaptation to new hostplants may explain the divergence of some clades, such as the *portis* clade, which specialized on woody bamboo species, that probably existed since the late Eocene or Oligocene (Fisher, 2011). Similarly, it is possible that the ancestor of the *telemachus* clade shifted to Menispermaceae. This family that includes the known hostplants of *M. telemachus*, *M. hercules* and *M. theseus* (Beccaloni *et al*., 2008, Gallusser *et al*., 2010), is represented by various Paleocene and Eocene fossils in South America (Burnham & Johnson, 2004; Herrera *et al*., 2011).

5.2. From South to North?

The initial diversification of the *Morpho* clade plausibly occurred in the proto-Andes. But where? Depending on whether it occurred in the proto-Northern Andes or the proto-Central Andes, evolution scenarios could be different. As we have demonstrated, alternative hypotheses for the formation of trans-Andean lineages imply different spatio-temporal processes, depending on the supposed geographical origin. Therefore, the estimate of divergence times is crucial. Either most divergence events occurred during the Late Miocene-Pliocene times (Penz *et al*., 2012), or they occurred during the Oligocene-Early Miocene times, a plausible hypothesis considering that the estimation method used by Penz *et al*. (2012) is likely to produces young estimates of ages (Sauquet *et al*., 2012). This is of major importance, as the geography of South America dramatically changed throughout all the north-western part of the continent, from the end of the Oligocene to the Pleistocene, notably during the 13-7 MY period.

We have presented different hypotheses for the evolution of the trans-Andean as well as that of mountain lineages. Many arguments support an initial diversification of the genus *Morpho* in the proto-Central Andes, but this implies older ages than those proposed by Penz *et al*. (2012). If this was confirmed, then a general south-to-north scenario would be credible, implying: i)- the existence of representatives of the *telemachus*, *rhetenor*, *helenor*, *menelaus*, and *portis* clades in the proto-Central Andes; ii)- the subsequent formation of trans-Andean lineages by dispersal from the north of the proto-Central to the proto-Northern Andes across the WAP, their subsequent geographic organization being driven by the W-E sequence of uplift events in the Colombian and Venezuelan Andes; iii)- the dispersal of lowland cis-Andean lineages along the eastern slopes of the proto-Northern Andes once the WAP was closed; iv)- the subsequent dispersal of certain mountain species from the proto-Central to the proto-Northern Andes. This scenario stresses the importance of the WAP, the possible role of which was emphasized by other authors (Antonelli *et al*., 2009). However, a precise paleogeographical history of the WAP is required, notably to evaluate the relative credibility of the western or eastern dispersal routes along the proto-Ecuadorian Andes.

5.3. Out of the Andes

Paleogeographic reconstructions along the eastern slopes of the proto-Andes suggest a general W-E model for landscape evolution, from an aquatic dominated landscape, with lakes and temporary or long-lasting, shallow marine embayments, mangroves and swamp forests, to emerged land, with *terra firme* rainforests, dissected by channelized, meandering and braided fluvial systems. Elias *et al*. (2009) discussed the importance of colonization from the Andes towards adjacent lowlands, and concluded that “new areas were apparently promptly colonized as they became available (...), sometimes enabling further diversification”. Our analyses support this view, and emphasize the role of the Pebas System, and subsequently of the Acre System, as barriers to dispersal probably until Late Miocene. Thus, certain dispersal events towards the Guiana Shield may be recent. However, the formation of the Guianan assemblages may have resulted from different events, among which the late Miocene exhumation of the Vaupés Arch may have played a role. Conversely, SW-NE dispersal was possible along the west-northern fringes of the Brazilian Shield long before the Amazonian lowlands were formed, while successive dispersal events probably occurred through the Mato Grosso Arch towards southern Atlantic forests. Thus “Out of the Andes” processes may have occurred at different times, along various routes, contributing to the present complexity and diversity of *Morpho* assemblages to the east of the Andean Cordillera.

CONCLUSION

Several recent discussions concerning the high biodiversity of tropical rainforests have been based on the study of Neotropical butterflies. For example, Mullen *et al*. (2011) hypothesized a Laurasian origin for the genus *Adelpha*, and suggested that the high number of *Adelpha* species resulted from a rapid diversification, within South America, in the last 15-10 MY. Similarly, Condamine *et al*. (2012b) provided evidence for a North American origin of Troidini butterflies, dispersal towards South America having occurred *ca*. 35-32 MY, and they suggested subsequent diversification in the middle of Amazonia at *ca*. 23-16 MY, on the Brazilian Shield at *ca*. 16-7 MY, and again in Amazonia from *ca*. 7 MY to Present. That different lineages dispersed to South America at different times via different routes is probably part of the response to the question “Why is the Neotropical Region so rich in butterflies?”. However, diversification processes subsequent to immigration would explain better this remarkable richness.

Information concerning the exceptionally active geodynamics of South America has increased considerably during the last two decades, revealing the complex nature of the continent: it now provides an improved framework for the elaboration of butterfly diversification scenarios, as illustrated by the present study. The geographical origin of Morphinae remains uncertain, but it is clear that the genus *Morpho* originated within the proto-South American continent, in the context of the initial diversification of the Morphinae clade, *ca*. 55-30 MY, according to Wahlberg *et al*. (2009). In agreement with Penz *et al*. (2012), we consider that the *Morpho* clade diversified first in the proto-Andes. More precisely, it is likely that its initial diversification occurred in the proto-Central Andes, perhaps as early as the Oligocene (34-23 MY). Subsequently, diversification followed different stories. Within the Central Andes, the Northern Andes, the Amazonian lowlands, the Gondwanan Shields and Central

America, evolutionary trajectories resulted in different *Morpho* assemblages.

The majority of *Morpho* species occurs within the shadows of the Andes, and our analyses suggest that Andean geodynamics played a major driving role in the diversification of the genus. Had this mountain chain not existed it is highly probable that diversity of Neotropical butterflies, and other groups, would have been considerably lower. Obviously, the history of the genus *Morpho* demonstrates that various dispersal events occurring at different times within the Neotropics were an important factor in diversification, a result that supports simulations by Arita & Vázquez-Domínguez (2008). Additionally, adaptation to new host plants, to ecosystems as different as swamp forests, lowland, low mountain and cloud forests, to drier contexts, to different ecological niches within the rainforest ecosystem, have certainly contributed in the diversification of the genus. Thus, the Neotropics can not be interpreted as a single evolutionary unit fitting one of the diversification models proposed by Stebbins (1974): the "museum model" (extinction rates being low, species exist for long periods), or the "cradle model" (active generation of new taxa in relation with geographical and/or ecological changes). Several authors have argued (eg. Mittelbach *et al*., 2007; Arita & Vázquez-Domínguez, 2008; Antonelli & Sanmartín, 2011) that tropical rainforests can be both "museums" and "cradles". Precise studies of the diversification of *Morpho* lineages – including the subspecies level – in regions having different geodynamic histories, will no doubt improve this debate, and we have provided a number of hypotheses which we hope to see tested.

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