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: Neotrops, South America, Gondwana, Andes, Amazonia, geodynamics, paleogeography, Lepidoptera, Morpho, biogeography, phylogeny, diversification

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 multphased 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 & De Vries, 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 & De Vries (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 calibrations. 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 diversifications, 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 correspondence 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
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 Perijá 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 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). 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,
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., 2005; 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 Maranon, the Tambo, Urubamba, etc. Most major valleys open onto the Amazon lowlands through narrow gorges or “pongós”, 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 occurred, 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 (Ituralde-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 et 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 Paleoecene-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 (Fiashc & 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 Gondwana (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 & Mendola-Vargas, 2004). The lowland forests (“selva baja”) reach their upper limit around 800 m. Low mountain forests (“bosque de montaña”) 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 Serrania de Perijá (Thomazs 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,* and *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).
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 & De Vries, 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 & De Vries, 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
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 + deidadia 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...
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

Fig. 3. Geographic variation in species numbers. Maximum numbers occur along the eastern slopes of the Andes.
and Peréné 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 sub-marginal 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 earlier 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. acharles). Morpho helenor is represented in the trans-Andean
region by the *M. 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 across 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. 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. helenor* 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 across 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 Bogotá), 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 dispersions 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.
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)
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.
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. That 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. phokyldises* 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. wernerii* in western Amazonia, *M. h. polyidus* 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 achillaides 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 achillaides 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 Nicaragua (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
3 closely related subspecies in Mexico (\\textit{montezuma}, \textit{octavia} and \textit{guerrerensis}), while it “explodes” into 9 subspecies, some of which are dramatically different (eg. \textit{taboga}, \textit{faustina} and \textit{limpida}), in Panama and Costa Rica (Blandin, 2007b). It is plausible that ancestors of \textit{M. polyphemus} migrated earlier than ancestors of \textit{M. helenor} subspecies, and one may speculate that the Mexican \textit{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 \textit{Morpho} fauna. If this hypothesis was rejected, it would be necessary to admit a recent (< 3 MY) extinction of ancestral \textit{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
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 Centoro-American representatives of Brassolini, Antirrhina 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

Australasian lineages, and that the divergence time between 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

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.
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. theses (Beccaloni et al., 2008, Gullanser 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, rheenor, 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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Table 1. Geological chronology (adapted from the *International Chronostratigraphic Chart, August 2012*) and Nymphalidae evolution (after Wahlberg *et al.*, 2009)

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<th>SERIES</th>
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<td>Paleogene</td>
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<td>~ 55 MY: divergence of the Morphinae clade</td>
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<td>66-56</td>
<td>~ 60 MY: divergence of the clade including Morphinae</td>
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### Appendix 1. Classification of *Morpho* subgenera and species, with subspecies cited in the text

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<th>Subgenus</th>
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<td><strong>Deyrollia</strong></td>
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<td><strong>Morpho</strong></td>
<td>Fabricius, 1807 sensu-stricto (= <em>Pessonia</em> Le Moult &amp; Réal, 1962)</td>
<td><em>Morpho (Morpho) polyphemus</em> Westwood, [1850]</td>
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<td><em>Morpho (Morpho) epistrophus</em> Fabricius, 1796</td>
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<td><em>Morpho (Morpho) deidamia</em> Hübner, [1819]</td>
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<td><em>Morpho (Morpho) neoptolemus</em> Wood, 1863</td>
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<td><em>Morpho (Morpho) pyrrhus</em> Staudinger, 1887</td>
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<td><em>Morpho (Morpho) electra</em> Röber, 1903</td>
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<td><em>Morpho (Morpho) diomedes</em> Weber, 1944</td>
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<td><em>Morpho (Morpho) grambergi</em> Weber, 1944</td>
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<td><em>Morpho (Morpho) annae</em> Duchêne &amp; Blandin, 2004</td>
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<td><em>Morpho (Morpho) jacki</em> Neild, 2008</td>
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<td><strong>Grasseia</strong></td>
<td>Le Moult &amp; Réal, 1962</td>
<td><em>Morpho (Grasseia) menelaus</em> Linnaeus, 1758</td>
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<td><em>Morpho (Grasseia) godartii</em> Guérin-Méneville, [1844]</td>
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<td><em>Morpho (Grasseia) amathonte</em> Deyrolle, 1860</td>
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<td><strong>Cytheritis</strong></td>
<td>Le Moult &amp; Réal, 1962</td>
<td><em>Morpho (Cytheritis) portis</em> Hübner, [1821]</td>
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<td><em>Morpho (Cytheritis) aega</em> Hübner, [1822]</td>
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<td><em>Morpho (Cytheritis) sukowski</em> Kollar, 1850</td>
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<td><em>Morpho (Cytheritis) aurora</em> Westwood, 1851</td>
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<td><em>Morpho (Cytheritis) zephyritis</em> Butler, 1873</td>
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<td><em>Morpho (Cytheritis) rhodopteron</em> Godman &amp; Salvin, 1880</td>
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<td><em>Morpho (Cytheritis) absoloni</em> May, 1924</td>
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