Amazonia: landscape and species evolution

A look into the past

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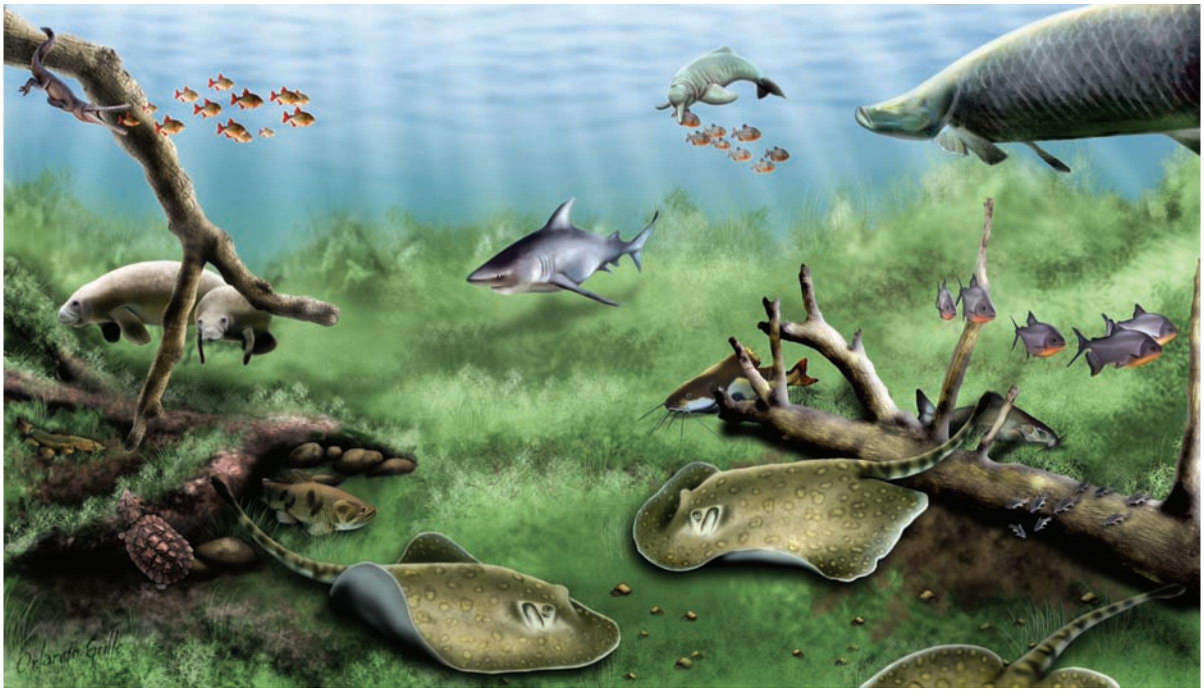
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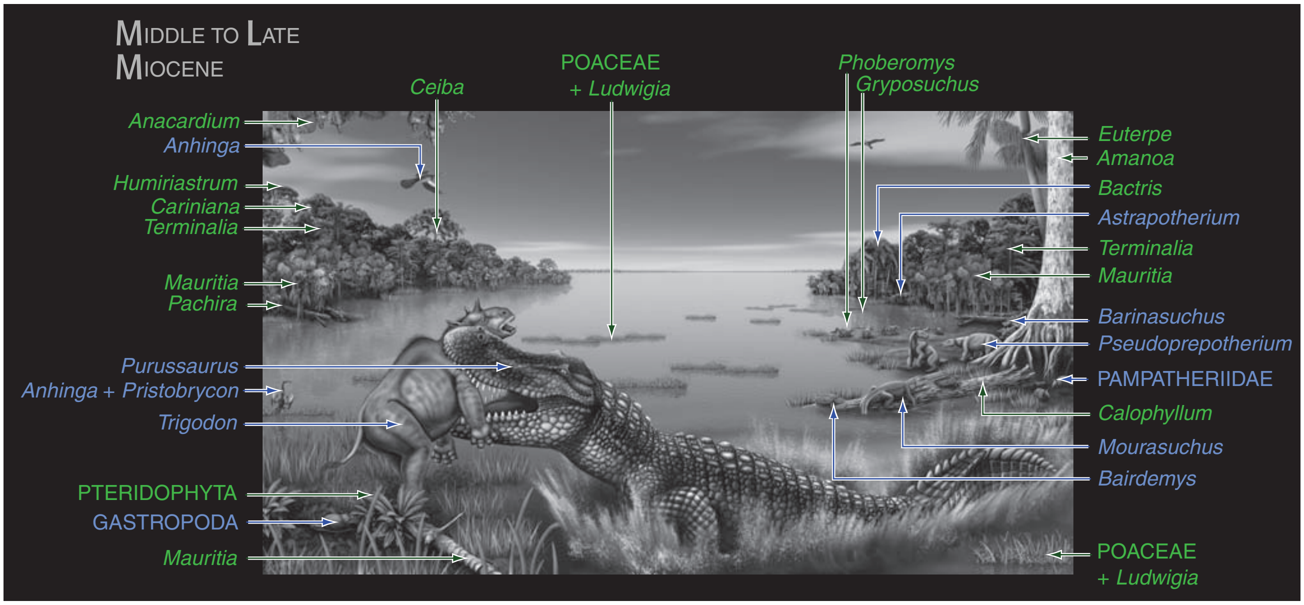

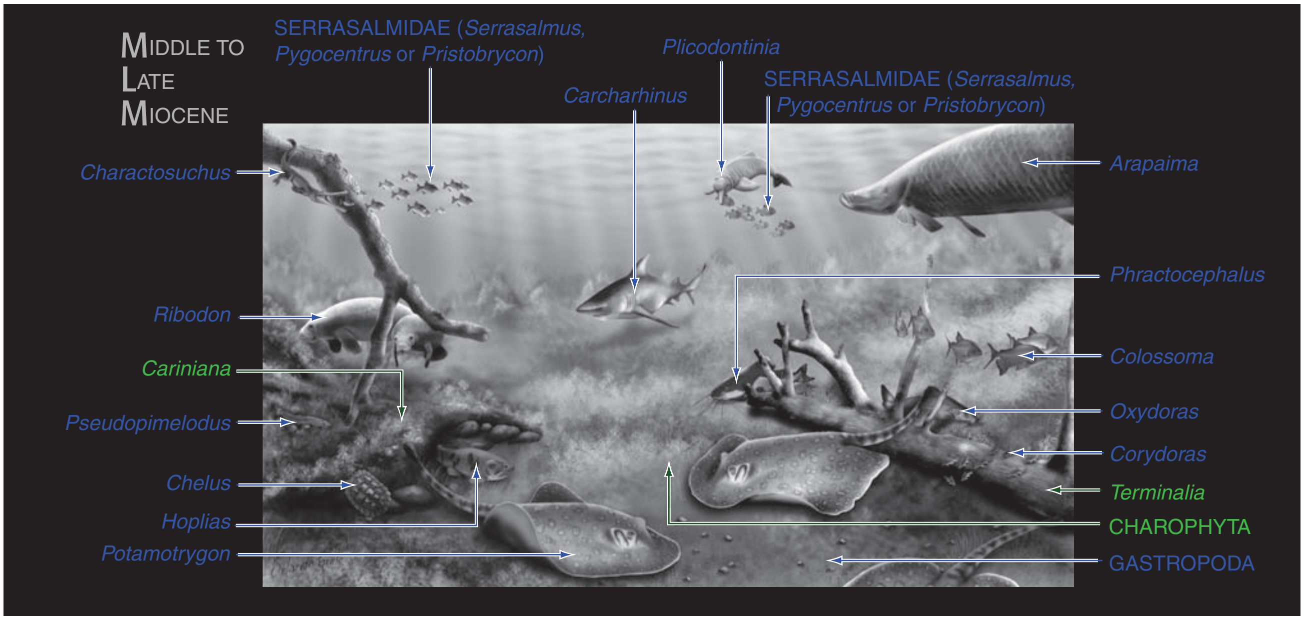

These plates show a reconstruction of the Middle to Late Miocene (16—7 million years ago) terrestrial and underwater landscape in Amazonia. Names for taxa are provided in latin and further explanations on the Miocene flora and fauna can be found in chapters 15 to 19 (Illustrations by Orlando Grillo).

Amazonia: landscape and species evolution

Companion website

A companion website for this book is available at:

www.wiley.com/go/hoorn/amazonia

The website includes:

- Figures from the book for downloading
- Color versions of selected figures
- Additional illustrations.

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Contents

Part I Tectonic processes as driving mechanisms for palaeogeographical and palaeoenvironmental evolution in Amazonia

Part II Cenozoic depositional systems in Amazonia

Part III Amazonian climate, past and present

Part IV Cenozoic development of terrestrial and aquatic biota: insights from the fossil record

Part V Modern perspectives on the origin of Amazonian biota

Part VI Synthesis

Color plate section is found facing p. 210

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Dedication to Thomas van der Hammen

We dedicate this book to the life and work of Professor Thomas van der Hammen who is one of the most prominent Dutch geoscientists, making many links between geology, biology and archaeology. The study of altitudinal vegetation distributions in the northern Andes is a red line through his work and it has served studies of the Neogene uplift history of the northern Andes as well as studies of pollen-based Pleistocene climate change. During more than two decades he lectured at the University of Amsterdam and inspired generations of Dutch students. Since his retirement in 1989 he has lived in Colombia where, with his never-ending enthusiasm, he continues to motivate large numbers of Colombian students.

Carina Hoorn, Frank P. Wesselingh (editors)
Henry Hooghiemstra, Hubert Vonhof, Salomon Kroonenberg
(editorial advisors)

Biography

Thomas van der Hammen was born in The Netherlands in 1924 and had an innate interest and love for nature. After the Second World War he studied geology at Leiden University. He was trained as a palynologist by Professor F. Florschütz but also had regular contact with other founding fathers of this discipline such as J. Iversen and R. Potonié. His PhD dissertation was on '*Late glacial flora and periglacial phenomena in the Netherlands*', a subject that would remain of interest to him for the rest of his life. In 1951 he started working for the Geological Survey in Colombia and did pioneering research on Cretaceous and Cenozoic sediments. Through his trademark multidisciplinary approach he unravelled the stages of tectonic uplift of the Andes. Later, he and his co-workers were able to make a link with the evolution of the montane forest and *páramo* vegetation of the Northern Andes.

In 1959 Thomas returned to The Netherlands and worked at the Department of Geology of Leiden University. He developed a research line in palaeoecology and climate history in the eastern part of The Netherlands while continuing his research in tropical palynology, often in cooperation with the geologist Lex Wijmstra, and focusing on exploratory studies in Guyana, Suriname and the Amazon Basin. In 1966 Thomas moved to the University of Amsterdam where he was appointed as a Professor in Palynology. A suite of both Dutch and Colombian (PhD) students were trained in topics such as geology, archaeology, biostratigraphy, climate history and vegetation analysis, and conducted field work in areas located in Brazilian Amazonia, Colombian Amazonia, the Colombian Andes and Venezuela. During the late 1970s and early 1980s he designed the large 'Ecoandes Project' and the 'Tropenbos Colombia Programme' respectively. The Ecoandes Project focused on integrated palaeo/actuo-ecological research of transects across different sectors of the Colombian Andes. These unprecedented studies resulted in seven volumes in the series *Studies of Tropical Andean Ecosystems*, published at Cramer/Borntraeger in Germany. The Tropenbos Colombia Programme studies focused on a wide variety of subjects, ranging from fishery, plant systematics, floristic inventories, sociogeographical studies, anthropology, palaeoecology, geology and tropical vegetation ecology. These studies resulted in 20 volumes of the series *Studies on Colombian Amazonia*, published at Tropenbos-Colombia office in Bogotá. To promote distribution of scientific results among Colombian institutes and colleagues around the world in 1973 he started the series *El Cuaternario de Colombia* [*The Quaternary of Colombia*], which he edited up to volume 20 (1995).

Perhaps his most valuable contribution to science was to increase our understanding of the history of Pleistocene climate change. His training in the climate history of Western Europe enabled him to show us that the Neotropics also had a dynamic history of climate change. Thomas van der Hammen discovered the immense value of the pollen archives in the deep intra-Andean sedimentary basins. He studied the first deep boreholes in the Bogotá Basin and the Fúquene Basin, and created a basis for later studies on long continental pollen records from Colombia. During the decades that Thomas lectured in The Netherlands he played an active role in Dutch nature conservation and in developing international structures for nature assessment studies. His contributions to the advancement of science were rewarded by her Majesty Queen Beatrix with a knighthood.

After his retirement he implemented his valuable experience in Colombia and, in collaboration with national research institutes such as the Geographical Institute (IGAC), the Geological Institute (Ingeominas), the Archaeological Institute, and the Von Humboldt Biodiversity Institute, he helped to promote many collaborative studies. Thomas van der Hammen was the author of more than 100 international peer-reviewed publications and contributed much to our understanding of tropical ecology and tropical climate history. His contributions to the training of Colombian scientists, and to the development of nature conservation and awareness of infrastructural issues in Colombia are highly valued. For the latter Thomas received the Colombian *Order of San Carlos,* which he received out of the hands of the Colombian President. Thomas's enthusiasm, charisma, vision and ability to make people work together made him a most inspiring person and a true leader.

Henry Hooghiemstra and Carina Hoorn

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Prologue

It is now almost 60 years since I arrived in Colombia for the first time to start investigations for a geological survey. I had one great desire: to work in Amazonia. Very soon afterwards, early in 1952, this desire was fulfilled; for one month I was able to work in one of the most remote and undisturbed areas of Western Amazonia, the middle to lower Apaporis River, to study the flora and the geology. This was possible because of the help of the (ethno)botanist Dick Schultes, who had good relations with the rubber trade company in Soratama. The company had a base there and collected rubber from the local Indian tribe. Once a month this rubber was sent to Bogotá with the Catalina (a small airplane) but – on request – it occasionally also transported researchers.

An assistant, two local Indians and I set off in a tree-canoe equipped with two hammocks, a plant-press, sample bags and some food. We travelled several hundreds of kilometres along the Apaporis and Cananari Rivers to study the rainforest and the outcrops. We climbed the table mountains, measured the cross-bedding in the old *tepui* sandstone formations and established that in early (Palaeozoic) times the rivers ran to the northwest, instead of to the modern southeasterly direction. We also encountered the younger Tertiary sediments, and concluded that the presence of iron oölite and manganite could only indicate one thing: that lacustrine and brackish-water conditions had once ruled in the heart of Amazonia.

After a month of fieldwork in the area I came back to Soratama to wait for the plane; Schultes also arrived from another expedition at the same time, and so we had some days together. We were out of food and lived on what was available in Soratama. One day Schultes said to me: ‘I have still a tin with plum-pudding, let’s go into the forest and eat it together!’ And so we did: Christmas pudding in March, in the jungle. I was 27 years old then and at the beginning of a life lived in pursuit of understanding the composition and evolution of the forests through time in the Andes and in Amazonia.

It was some 25 years after our first Amazonian survey that I again saw samples from this area. This time they came in the form of bagged clays that were collected during an extensive Colombian survey, the Proradam project (1974 to 1979). The question that came with the bags was whether the age and environment could be established through palynology. A Neogene age was soon evident, and the presence of abundant pollen of mangrove trees (*Rhizophora)* for the first time confirmed the presence of saline or brackish waters in ancestral Amazonia.

Around this time two other major geological and geographical surveys were carried out in Brazil: the RadamBrasil survey and the coal exploration project by the Companhia de Pesquisa de Recursos Minerais (CPRM). The latter project drilled close to 50 cores in the subsurface of Brazilian Amazonia, and so far constitutes the best register of Neogene Amazonian history. In addition, the Brazilian oil company Petrobras drilled numerous cores though the Lower to Middle Cretaceous, which permitted the reconstruction of the floral history of that period. There were of course also groups of dedicated researchers who spent most of their life in Amazonia. One of them was Harald Sioli, who recently died but is much remembered through both his research papers and his autobiography.

Another 10 years passed and in the 1980s Tropenbos International, an initiative of the Dutch government, established a large research project with the Amazonian ecosystem as its focal point. Within this project, Carina Hoorn carried out a much more extensive and profound geological, palynological and environmental study of the Miocene of western Amazonia. This coincided with a renewed interest in Amazonia by several other countries, which all greatly increased our knowledge of the Neogene history.

Meanwhile Quaternary geologists and palynologists contributed to the knowledge of the younger Pleistocene-Holocene history of the area, indicating that Amazonia passed through periods of drier climate. Moreover, the first reconstruction by the international CLIMAP project (in 1976) of the Last Glacial Maximum indicated lower temperatures for Amazonia. It was Jürgen Haffer who in 1969 published his theory of speciation of Amazonian forest birds and his theory of glacial forest refugia. For many years his ideas had an enormous influence and caused deep controversies and forthright discussions, which, as more data become available, gradually became less extreme. The time necessary for the formation of subspecies or species may have been much longer than originally was assumed, but still the place and functions of the centres of endemism and their history continue to be a key point in the scientific debate.

The first palynological data that showed the glacial time transition of rainforest to grass-savanna (in Rondondia, Brazil), were published in 1972. These were followed by data showing the more or less continuous presence of forest in other areas (Lake Pata, in the north of Brazilian Amazonia), the drying up of lakes during the Last Glacial Maximum and/or the replacement of forest by open vegetation (Carajas, Brazil). Other areas (Rio Branco) in the northern part of Brazil show a well-dated glacial time and early Holocene extension of dune fields. Vegetation maps of the possible – or probable – situation during the Last Glacial Maximum, based on the available data and the use of present rainfall patterns, have been published, and are open to corrections – if and when more data become available.

Not all problems and discussions on Amazonia's past have been resolved, and the cause of its enormous biodiversity is one of the great mysteries that still need an explanation. Nevertheless, our knowledge has advanced considerably since 60 years ago, and the time seems to be right for a major effort to gather all our present knowledge on Amazonia's history and evaluate the problems and existing controversies, whilst reflecting on the gaps that still exist in our knowledge. Altogether this book will form a solid base to direct future research.

One of the most promising avenues of future research that can resolve some of our current questions is the study of genetics and the use of the molecular clock as an indicator of the separation of subspecies and species. This could enable us not only to compare geological and climatic history with the present climatic pattern, but also to assess the differences within Amazonia and the earlier proposed centres of endemism, as suggested by Haffer, Prance and others. These centres of endemism are, at least in part, related to geographical and climatic patterns that existed since the Late Miocene, Pliocene and the Quaternary. In particular, during the glacial periods the differences may have become much more pronounced because of the resulting changes of vegetation.

It now seems more than probable that new species and subspecies were formed over millions of years; there are even strong indications that biodiversity was greater during the Miocene than at Present. This suggests that the speciation–extinction balance may have become negative during the Pleistocene glaciations, when the lower temperatures and drier climate intervals led to higher extinction rates (but eventually to the appearance of certain new subspecies).

The importance of the Amazonian rainforest and its enormous biodiversity for the conservation of the environmental equilibrium of the earth can only be underestimated. Moreover, the expected negative effect of the disappearance of a major part of the forest on both Amazonia and Earth as a whole, would affect us all. Therefore a better understanding of this sensitive ecosystem and its dynamics over a range of timescales is important to the global scientific and political community. The conservation of Amazonia, and a better understanding of its plant, animal and human life, is doubtlessly related to the future well-being of our planet.

This book may therefore be considered as a very important contribution to the knowledge of Amazonia, but also to science in general. It concludes a period of intensive investigations but also might herald the beginning of a new era of investigations that will hopefully lead us to the answers of many of the questions that for long have remained unanswered, and to more definite guidelines that will ensure the future of our Earth and its living inhabitants.

Thomas van der Hammen
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ONE

Introduction: Amazonia, landscape and species evolution

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Motivation

The Amazon drainage basin covers over 8 million km^2 and has the largest rainforest on earth (Sioli 1984). The Amazon River is 6400 km long, from its source in the Andes to its mouth in the Atlantic, and the drainage basin includes a variety of landscapes such as the enigmatic *tepuis* in the north, the forested slopes at the foot of the Andes in the west, and the wide tracts of rainforest in the central part of the basin.

The region is renowned for its great biodiversity, both aquatic and terrestrial. Exact figures to quantify this diversity do not yet exist, and estimates of species numbers are still increasing. This incomplete understanding of species numbers makes any firm estimate impossible; nevertheless, the region is thought to harbour no less than 7500 butterfly species (possibly about 40% of the world butterfly species), 1500 species of birds (about one-third of the world total) and an estimated 11,200 tree species (Hubbell *et al.* 2008).

The Amazon system plays a significant role in the world's climate as it produces about 20% of the world's oxygen supply. Nutrients delivered by the Amazon River to the Atlantic Ocean help to foster oceanic life that sequesters globally relevant amounts of carbon (Subramaniam 2008), and in the terrestrial realm the Amazon rainforest is responsible for 10% of the net primary productivity of the whole terrestrial biosphere (http://earthobservatory.nasa.gov). Therefore, Amazonia is of the greatest concern to us all.

In spite of Amazonia's importance the number of studies on species composition and their distribution is still limited. Diversity hotspots seemingly coincide with biological field stations and specific large-scale biological expeditions (Nelson *et al.* 1990), and indicate just how much basic research still is required. Even the classification of habitats in Amazonia is far from straightforward (e.g. Kalliola *et al.* 1993) as major parts of the region are hardly accessible and remote sensing techniques cannot grasp the variety without substantial 'ground-truthing'.

If our knowledge of Amazonia's present is limited, this is even more so for its past. When did the Amazonian landscape and jungles arise? What climatic, chemical, geological and other non-biological processes were involved in the development of these ecosystems and sustain them now, and what part did they play in the previous episodic demise of these ecosystems? In order to assess ecosystem resilience it is imperative to understand the historical (i.e. geological) processes that have shaped Amazonian landscapes and their biota.

For decades scientists have speculated about the evolution of species and biodiversity. However, the scientific debate was mostly dominated by biologists and geomorphologists using species and geomorphology as a basis for their theories (Haffer 1969; Ab'Sabr 1982; Absy *et al.* 1991; Colinvaux *et al.* 2000, 2001; Haffer & Prance 2001; see also Chapter 26) and few geologists were involved in this discussion. Scientists are now increasingly aware that the geological substrate in Amazonia, and the relatively young age of the Andes and the Amazon River, were of paramount importance in species evolution and distribution of diversity hotspots (e.g. Salo *et al.* 1986; Hooghiemstra & Van der Hammen 1998; Lundberg *et al.* 1998; Lovejoy *et al.* 1998; Van der Hammen & Hooghiemstra 2000; Nores 2002; Wesselingh and Salo 2006; Tuomisto 2007; Antonelli 2008) yet an undisputed theory about the timing and context of Amazonian diversifications – in the light of geological evidence– still has to materialize.

Geology only recently started playing a role in the debate on the origin of biodiversity as it was hampered by the same obstacles as the biological and geomorphological sciences – the lack of firm evidence due to the difficult access to the terrain. However, in the past two decades geological studies in Amazonia quickly followed one another. The sedimentary environments in Amazonia and their age (e.g. Räsänen *et al.* 1987; Hoorn 1993; Wesselingh *et al.* 2002; Hovikoski 2006), the ancient nature of rainforests (e.g. Morley 2000; Jaramillo *et al.* 2006), the importance of soil heterogeneity and distribution in relation to floristic biodiversity (e.g. Kalliola & Flores-Paitan 1998; Ruokolainen *et al.* 2007), past climate dynamics (Sugden 2000; Bush & Flenley 2006; Bush *et al.* 2007) and the exact age of the establishment of the Amazon River (Dobson *et al.* 2001; Figuereido *et al.* 2009) are but a few of the thrilling insights that were obtained.

Simultaneously, a relatively young branch of science, DNA studies, increasingly suggested that the origin of extant biodiversity dates back well before the Quaternary (Antonelli 2008;

Amazonia, Landscape and Species Evolution: A Look into the Past,
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Rull 2008) and may have coincided with regional geological events (see Chapters 23–25). Consequently, at the turn of the millennium, geology and biology were drawn to each other in a concerted effort to explain the origin of Amazonian biodiversity and landscapes.

A journey through the geological history of Amazonia

The scientific advances of the past two decades, and the newly gained perception that biotic and abiotic evolution might be intimately related, demanded an interdisciplinary, multinational effort to summarize the state of the art in Amazonian geological sciences. This book attempts to fulfil this role. It not only presents an outline of the geological history, but also assesses the implications of the geological past for landscape evolution and biotic diversity. The contributors show that the development of Amazonian diversity is intimately linked to landscape evolution, and that modern Amazonian ecosystems were formed during the geodynamic processes of the Cenozoic. The implication of this work is that before the Quaternary there were periods with even more diverse ecosystems.

The contributions to this book are grouped into five themes, corresponding to the book's five parts. The first of these themes discusses the origin, architecture and stratigraphic and tectonic relationships of the major geological units of the eastern Andes and Amazonia. The second theme focuses on the Amazonian sedimentary record from the Mesozoic era to the Quaternary period. This record is subdivided into cratonic and Andean-driven depositional systems although Neogene and Quaternary systems are a combination of both Andean and cratonic fluvial systems. In addition, megafan depositional systems in western Amazonia are also reviewed. Climatic evolution and the implications for the Amazonian region during the Miocene are assessed in the third part. The Amazonian palaeontological record of the aquatic and terrestrial realms constitutes the fourth part of the book. Despite the uneven concentration of fossiliferous deposits in western Amazonia and the adjacent Andes, the palaeontological chapters provide an in-depth insight into the development of Amazonian floras and faunas. The final, fifth, part of the book is concerned with modern perspectives on the origin of Amazonian biodiversity. The book concludes with a chapter by Wesselingh *et al.*, who summarize the highlights of each chapter and provide a synopsis of the Cenozoic history of Amazonia. The best localities for observing the outcrops and fossils are shown in Fig. 1.1.

Main geological processes shaping Amazonia through time

The geography of Amazonia was shaped during three principal geological phases. The first was a Proterozoic phase (3–1 Ga [gigayears]) of cratonic formation dominated by magmatism, continental accretion and tectonic processes (see Chapter 2 by Kroonenberg & de Roever). The craton forms most of eastern Amazonia and consists of ultrastable basement with landscapes that date back to the Cretaceous and Paleogene. In terms of biodiversity these areas are relatively poor compared to the nutrient-rich, Andean-dominated western part of Amazonia (see Chapters 21 & 22). At the end of the Proterozoic a series of east–west orientated intracratonic sedimentary basins were formed, which acted as fluvial conduits. Throughout geological history basement reactivation formed 'arches' that, at different times, created drainage divides. Seismic data and new stratigraphic charts from the Brazilian oil company Petrobras illustrate the development of these sedimentary basins in Brazilian Amazonia (see Chapter 3 by Wanderley Filho *et al.*).

The second major geological phase was characterized by rifting and break-up of the supercontinent Pangaea. This period also saw the opening of the Atlantic (Jurassic, c. 195 Ma) during which the Americas became fully separated from Europe and Africa. The separation was completed during the Cretaceous after which sedimentation of the intracratonic basins was resumed (c. 120 Ma). The third and final geological phase was determined by changes in plate configuration along the Pacific. This plate activity was an aftermath of the continental break-up and ultimately responsible for the uplift of the Andean Cordilleras that was initiated during the Cretaceous.

Pulses of uplift continued throughout the Cenozoic; however, Andean tectonism only reached a climax during the Late Miocene and Pliocene (c. 10–4 Ma). This resulted in intense denudation, increased subsidence in the sub-Andean zone and progression of the sedimentary wedge into Amazonia, and ultimately connected the inland drainage system with the Atlantic Ocean creating the Amazon River (see Chapters 4 & 5 by Mora *et al.* and Roddaz *et al.*; Figuereido *et al.* 2009).

Andean uplift remained high during the Pliocene while subduction of the Nazca Ridge caused tectonic uplift of the Fitzcarrald Arch (southeastern Peru and adjacent Brazil). As a consequence the western Amazonian lowlands, which during the Miocene formed continuous aquatic habitats, became fragmented and dissected (see Chapter 6 by Espurt *et al.*). A final marker event in the geological history of northern South America was the closure of the Panama isthmus around 3 Ma. Although tectonism is ongoing, this concluded the Present geographical configuration of the South American continent, its landscape and modern drainage systems (see also Chapter 26).

Cratonic and Andean-driven depositional systems

River systems of cratonic descent or local lowland origin have dominated Amazonian landscapes throughout their history. In this book we review the Mesozoic and Cenozoic cratonic fluvial systems by comparing four different fluvial formations that range in age from Cretaceous to Late Neogene (see Chapter 7). From the Oligocene onwards Andean-driven depositional systems dominated the sub-Andean zone and western Amazonia. These systems extended to at least 1.5 million km^2 during the Miocene and were characterized by very large lakes and wetlands and occasional marine influence. During the Early and Middle Miocene a lake- and wetland-dominated system occurs (Pebas phase) whereas in the Late Miocene the newly formed Amazon River introduces a fluvial element into this otherwise wetland-dominated system (Acre phase) (see Chapter 8). Andean drainages are crucial for the soil development and distribution of species-diverse vegetation on nutrient-rich Andean-derived substrate. Instead relatively species-poor vegetation develops on the craton-derived substrate.

The presence and extent of marine influence in the history of Amazonia has been a hotly debated topic. In Chapter 9, Hovikoski

Fig. 1.1 This map represents the principal Amazonian rivers and outcrops of Cretaceous and Cenozoic origin in Amazonia that are referred to in the various chapters of this book. The locations are represented as numbers and either indicate the author or the common name of the locality. (1) Pebas/Solimões outcrops (Hovikoski *et al.*, see Chapter 9). (2) Pebas/Solimões outcrops (Hoorn *et al.*, see Chapter 8). (3) Fossil mammals (Negri *et al.*, see Chapter 15). (4) Localities of both Negri *et al.* and Hovikoski *et al.* (the localities close to the city of Assis Brasil are situated on the margins of the Acre River, which is not represented here. (5) Cretaceous-Paleogene Alter do Chão (source Petrobras, in Hoorn *et al.*, see Chapter 7). (6) Neogene fluvial deposits of cratonic origin (Hoorn *et al.*, see Chapter 7). (7) Fitzcarrald mammal fauna (Negri *et al.*, see Chapter 15). (8) Lower Miocene Castillo Formation – other important Venezuelan localities are placed close to/into the cities of Urumaco (Upper Miocene Urumaco Formation) or Barinas (Middle Miocene Parángula Formation) – see Riff *et al.*, Chapter 16. (9) Middle Miocene Honda Group (La Venta Fauna), Magdalena Valley. (10) Atalaia Beach (Salinópolis city) and Ilha de Fortaleza (Sao João de Pirabas city), Lower Miocene Pirabas Formation (see Riff *et al.,* Chapter 16). Map made by D. Riff and J. van Arkel.

et al. argue that in the past 30 Ma well-documented episodes of marine influence in Amazonia are limited to the Miocene. However, there is no evidence for fully established marine corridors ('seaways') throughout the South American continent in the Cenozoic.

The Cenozoic Andean uplift and increased denudation rates further resulted in megafan systems along the Andean foothills (see Chapter 10 by Wilkinson *et al.*). Megafans are low-gradient river systems choked by sediments, which force them to continuously change their courses. Understanding their dynamic behaviour sheds light on the development and distribution of aquatic biota. The extent of megafan depositional systems in the history of Amazonia is greatly underestimated.

Late Neogene and Quaternary fluvial systems are further explored in Chapter 11, by Irion & Kalliola. They outline the fluvial depositional environments and processes from the foreland basins in the west to the mouth of the Amazon in the east, and consider the resulting landforms, which dominate a major part of the surface of lowland Amazonia. Quaternary fluvial systems along the trunk Amazon River have been dominated by strong eustatic-driven base-level changes.

Amazonian climate

Although palaeoclimatic data are hard to obtain, isotope data from fossil molluscs and cyclicity in the sediment beds indicate that the modern Amazonian hydrological cycle, which ensures the year-round wet conditions that sustain the rainforests, was in place in the Miocene (see Chapter 12). Experimental climate modelling for a low-elevation Andes and the effect on Amazonian climate is explored by Sepulchre *et al.* in Chapter 13. Based on their model, the role of the Andes in maintaining permanent wet conditions in the lowlands is seemingly less prominent than one would expect.

The wet character of the Amazonian climate is mostly the result of the Amazonian hydrological cycle. However, a lower Andes would create different precipitation patterns than at Present, and the removal of the Andes would increase seasonality.

Another climatic controlling mechanism that affects Amazonia is the El Niño Southern Oscillation (ENSO). In Chapter 14 Bookhagen & Strecker explore the influence of the negative ENSO climatic phenomenon (also known as La Niña) on sediment influx and aggradation in the fluvial systems. The extreme high water levels as a result of high precipitation during the negative ENSO years have a disproportionate effect on denudation and are thus extremely important to the Amazonian river dynamics.

The palaeontological record in Amazonia

Amazonia has hosted a highly diverse mammal fauna at least since the Paleogene. Recently discovered Eocene-Oligocene faunas and Middle Miocene faunas from the Peruvian-Brazilian border area provide us with detailed information on the faunal composition. However, most noticeable is the rich Late Miocene fauna from Acre (Brazil), which includes species with remarkably large forms (see Chapter 15 by Negri *et al.*). The demise of the giants coincided with the arrival of North American immigrants associated with the emergence of the Panama land bridge (Stehli & Webb 1995).

The Amazonian crocodile and turtle faunas indicate that during the Cenozoic diversification was slow, but culminated in the Miocene fauna with a diversity and disparity that remains unrivalled (see Chapter 16 by Riff *et al.*). This fauna contains the largest crocodile and turtle that ever lived, as well as a remarkable diversity of gharial species. The Pliocene and Quaternary faunas are clearly less diverse, a feature linked by the authors to global cooling and the disappearance of the large productive aquatic ecosystems of the Miocene.

The diverse Amazonian fish fauna, too, has a long history of gradual diversification, as is shown by Lundberg *et al.* in Chapter 17. Already in the Miocene an essentially modern fauna inhabited the Amazonian aquatic ecosystems. The fishes have provided some of the best indications of the changing outline of Amazonian watersheds throughout their Cenozoic history. Especially well reflected in this fauna is the separation, during the Late Neogene, of northern coastal and Andean drainages from Amazonia.

The Miocene invertebrate fauna developed through a large evolutionary radiation of endemic mollusc and ostracod species in the long-lived lakes of the Pebas megawetland (see Chapter 18 by Wesselingh & Ramos). In addition, species associations characteristic for restricted marine conditions occur in some intervals. Nevertheless, since the Late Miocene the Amazonian rivers and lakes have been the domain of a low-diversity fluvial mollusc fauna and a stunningly diverse decapod fauna.

The palynological and palaeobotanical record of plants shows us that modern angiosperm-dominated rainforests existed in Amazonia throughout the Cenozoic (see Chapter 19 by Jaramillo *et al.*). Diversity culminated during the Eocene, and a major extinction occurred at the Eocene–Oligocene transition. Modern genera were already present during the Miocene, when the current rainforest biome developed and diversities were as high, or even higher, than at Present. In Chapter 20 Behling *et al.* further show that although the Quaternary glaciations affected the distribution of plant species in Amazonia, they did not seem to promote speciation in the Amazonian lowlands. During the Quaternary the fringes of the rainforest were affected at precessional timescales, but the core of lowland Amazonia remained covered by forest. Nevertheless, the composition of forests changed through different parts of the glacial cycle.

Modern perspectives on the origin of Amazonian biota

In Chapter 21 ter Steege *et al.* present the region-wide diversity patterns and explore their relationships with a range of factors, such as edaphic variation and climate. Although the documentation of biodiversity is notoriously incomplete, the addition of niche modelling has substantially improved our insights, and will do so in future. The importance of edaphic heterogeneity for plant diversity is further illustrated by Duivenvoorden & Duque in Chapter 22, which investigates the relationships between the abiotic environment (geology, geomorphology, soils) and biodiversity.

Recently, many important new insights into the origin of Amazonian biodiversity and biogeography have emerged from molecular studies. In Chapter 23 Pennington & Dick review evidence from plants, while Antonelli *et al.* in Chapter 24 review the development of tetrapods, and the fish are treated in Chapter 25 by Lovejoy *et al.* All contributors caution about hasty interpretation of age estimates from so-called molecular clock studies because of the underlying assumptions. Nevertheless, results clearly indicate that the origination of modern biota has been a steady process that mostly played in the Cenozoic.

Outlook

New insights and data about the origin of Amazonian landscapes, ecosystems and biodiversity are accumulating even as we compile this book. Further integration of the various biological, geographical and geological disciplines, as well as further technical and conceptual developments within the different fields, will continue to bring new insights about the Amazonian biological system and its resilience, as well as the importance of Amazonia on global processes on a variety of time scales.

As Amazonia is suffering badly from human activities, new and much more ambitious efforts to assess its biodiversity, mostly by time-consuming field-based taxonomic inventories combined with niche modelling, are paramount to get a better sense of the magnitude of species richness and to identify further priorities for conservation. Molecular studies have become an indispensable tool in identifying real species richness.

Further processing of subsurface data, both seismic as well as borehole data and samples, will add to our knowledge of the development of the region and its landscapes. Study of the reaction of biodiversity to previous natural perturbations will bring more insights about ecosystem resilience, at a time when such insights are so badly needed.

Raising awareness of the unique and amazing diversity of life in Amazonia is needed in order to achieve better protection for the region and its biota. With this book we hope to enhance appreciation of the vast timescales that were needed to create these great ecosystems, which we are challenging so profoundly at this moment in history.

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PART I

Tectonic processes as driving mechanisms for palaeogeographical and palaeoenvironmental evolution in Amazonia

TWO

Geological evolution of the Amazonian Craton

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Dedicated to the memory of Dr D.R. (Rob) de Vletter, deceased 24 May 2008.

Abstract

The Amazonian Craton, the core of the South American continent, consists of: (i) Archean nuclei, including the Carajás-Amapá areas in the southeast and the Imataca area in the northwest (3.0–2.5 Ga); (ii) the 1500-km long Trans-Amazonian greenstone-tonalite belt with associated granulite belts along much of the northern coast of the Guianas and northern Brazil (2.2–2.0 Ga); (iii) a Grenvillian orogenic belt along the westernmost part in southwestern Brazil (1.3–1.0 Ga); and (iv) a vast central part in which Paleoproterozoic and Mesoproterozoic granitoid and low-grade metavolcanic rocks predominate. Granitoid magmatism continued here almost uninterrupted between 2.0 Ga and 1.0 Ga, although cratonization was largely completed by 1.75 Ga. We argue that previous continental accretion models based on progressively younger granite ages westwards have to be revised in view of new geochronological data. Little-deformed sandstone platforms unconformably overlying older basement are widespread, and have been deposited in different episodes of post-orogenic basin formation from the Archean down to the Phanerozoic. Mafic dykes of Proterozoic to Permo-Triassic age testify to various phases of extension, rifting and basin formation, including the formation of the Paleozoic basin system and the later Amazon drainage basin itself. Uplift and denudation since Gondwana break-up greatly increased sediment fluxes towards the surrounding basins from the Mesozoic onwards.

Introduction

The Amazonian Craton forms the oldest nucleus of the South American continent, and is divided by the Amazon drainage basin into two parts, the Guiana Shield in the north, and the Guaporé or Central Brazilian Shield in the south (Fig. 2.1 & Plate 6). In all modern syntheses, the main geological units of the Guiana Shield continue below the Amazon drainage basin into the Guaporé Shield without offset (Tassinari & Macambira 1999, 2004; Almeida *et al.* 2000; Cordani *et al.* 2000; Santos *et al.* 2000; Tassinari *et al.* 2000; Santos 2003; Cordani & Teixeira 2007). The Amazonian Craton also continues westwards below the cover of the sub-Andean basins, as numerous blocks of Precambrian rocks have been incorporated into the cordilleras of the northern Andes during orogeny (Fig. 2.1), and seismic data and drilling by oil companies in the foreland basins invariably show the presence of Precambrian basement below (Kovach *et al.* 1976).

This means that the western Amazon drainage basin, on which this book focuses, is underlain in its entirety by continental crust. As the oldest sediments in the deepest part of the Paleozoic basin system itself are of Ordovician age (Wanderley Filho *et al.* 2005; see also Chapter 3) the geological history of the Amazonian Craton is essentially restricted to the Precambrian. In predrift reconstructions the Amazonian Craton forms part of western Gondwana. It has its counterpart in western Africa, and southwards and eastwards it continues into other cratonic parts of the South American Platform (Fig. 2.1), but we will not consider these correlations further afield.

Knowledge of the geology of the craton is of paramount importance for anyone studying the history of the basins that surround it. The origin and configuration of the basins themselves reflect tectonic patterns and processes, which often can be traced back to the early history of the craton (Brito Neves 2002). The craton is the source of most of the sediments in the intra- and pericratonic

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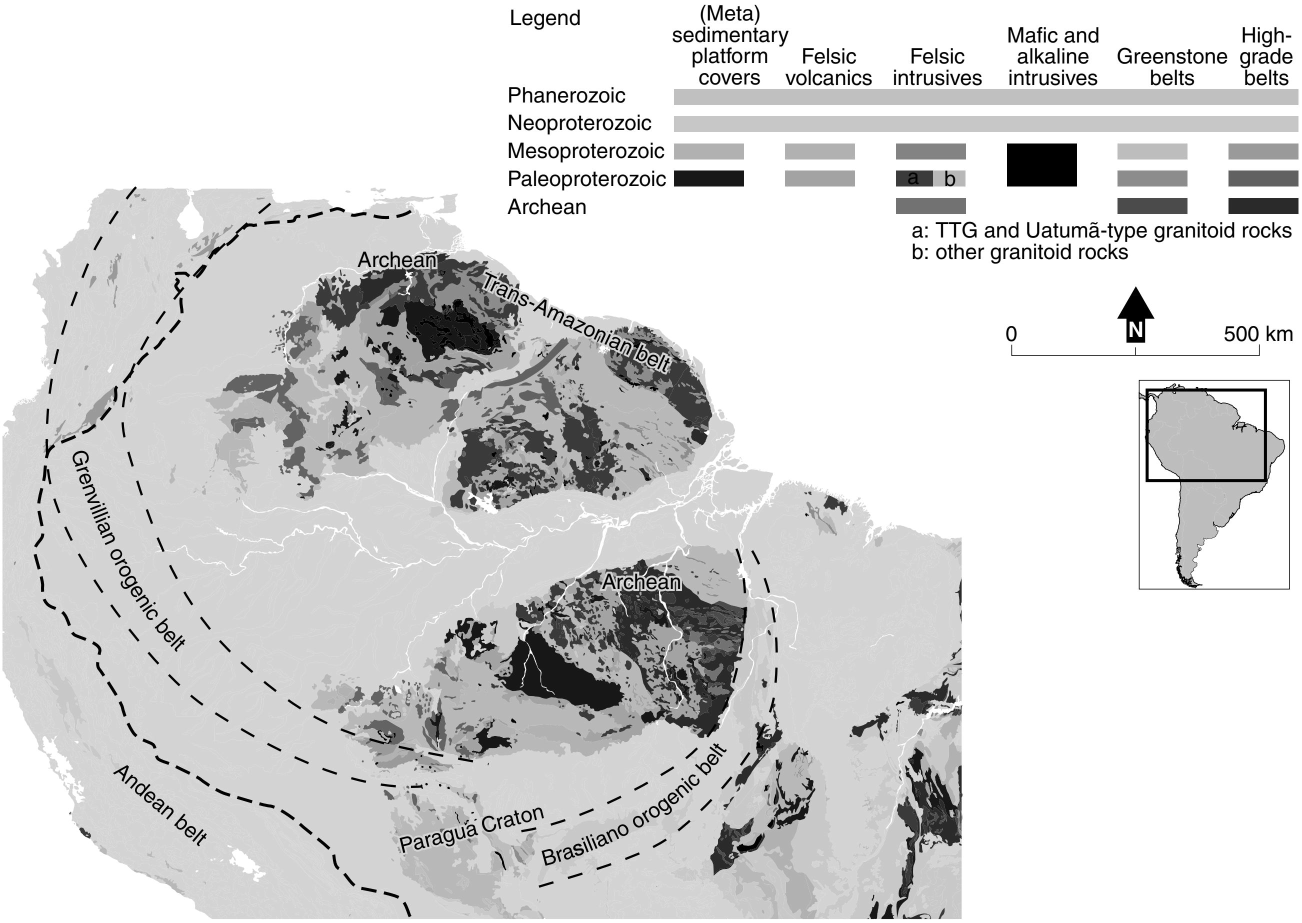

Fig. 2.1 Outline geology of the Amazonian Craton. Map details derived from Schobbenhaus & Bellizzia (2001), Gibbs & Barron (1993) and Tohver *et al.* (2004a). Compiled by S.B. Kroonenberg and E.W.F. de Roever (2009) - Design by GeoMedia (7242). See Plate 7 for a colour version of this figure.

sedimentary basins, and cratonic sediments often have a specific provenance fingerprint when compared with those from the other major source, the Andes (Franzinelli & Potter 1983; Potter 1994; see also Chapter 7). Past and present relief and drainage patterns in the craton not only reflect major uplift and subsidence events, but also minute differences in the susceptibility of specific lithologies to weathering and erosion.

Understanding the history of the Amazonian Craton is hampered by many factors. In the first place, tropical rainforest and deep weathering adversely influence outcrop condition and accessibility. A serious survey of the geological features started only in the 1960s and 1970s, when detailed photogeological studies, such as in Suriname, were carried out, aerogeophysical surveys and extensive radar imagery was obtained through projects like Radambrasil in Brazil, Codesur in Venezuela and Proradam in Colombia; moreover, geochronological, structural and petrological data from numerous field surveys came pouring in. Since then, many excellent reviews of the geology of the craton have been made, including Amaral (1974), Mendoza (1974), Gibbs & Barron (1983, 1993), Teixeira *et al.* (1989), Cordani & Sato (1999), Cordani & Teixeira (2007), Tassinari & Macambira (1999, 2004), Santos *et al.* (2000), Almeida *et al.* (2000), Tassinari *et al.* (2000) and Delor *et al.* (2003). This chapter is based on our own field experiences in the Guiana Shield, especially in Suriname and Colombia, and to a lesser extent in French Guiana, Venezuela and Brazil, and furthermore a large amount of literature in international and local journals and books. It is difficult to do justice to the enormous amount of data and analyses that have been obtained during the last decades, and this review does not pretend to do more than sketch the bare outlines of what we think are the most salient features of the craton.

The Amazonian Craton consists essentially of three major groups of basement terranes: (i) greenstone belts, consisting of intensely folded, low-grade metasedimentary and metavolcanic rocks intruded by tonalitic plutons; (ii) high-grade metamorphic belts, consisting mainly of gneisses and granulites of varying parentage; and (iii) vast expanses of granitic and acid metavolcanic rocks, in which supracrustals are scarce. In several areas flat-lying Precambrian to Ordovician sandstones unconformably overlie the crystalline basement in impressive table mountains. Mafic dykes of greatly varying ages have intruded the basement as well as the sandstone plateaus. There is very little evidence of Precambrian fossil life in the Amazonian Craton, and therefore reconstructing its tectonic history hinges completely on isotope geochronology.

In this chapter we follow the internationally agreed subdivisions of the Precambrian based upon geochronological data (Gradstein *et al.* 2004):

Archean > 2.5 Ga
Paleoproterozoic 2.5–1.6 Ga
Mesoproterozoic 1.6–1.0 Ga
Neoproterozoic 1.0 Ga to 542 Ma

Geochronology has made great technological advances in the past 40 years. On the one hand, this is an advantage, because now we know some parts of the history with much greater accuracy than in the past. On the other hand, it has also a disadvantage in that many earlier models, made on the basis of radiometric dating methods now considered obsolete or at least questionable, have to be reconsidered entirely. In the early years, for instance, 1.2 Ga (= giga annum, 10^9 years) potassium-argon (K-Ar) mica ages in the Colombian Amazonia were considered to reflect the age of the rocks themselves (Pinson *et al.* 1962), while later rubidium-strontium (Rb-Sr) studies (Priem *et al.* 1982) demonstrated this age to represent a later metamorphic overprint over an older rock. Many Rb-Sr isochrons from the 1970s and 1980s, in their turn, now have been superseded by ages obtained by SHRIMP (sensitive high-resolution ion microprobe) uranium-lead (U-Pb) dating on zircons. As a result some rocks are now known to be 100 to 400 million years older than originally thought, as for instance happened to the Roraima sandstones and their intruding mafic dykes (Santos *et al.* 2003b). Moreover, not all geochronological data reflect the same type of event: samarium-neodymium (Sm-Nd) model ages record the first differentiation of granitic rocks from the earth's mantle (Cordani & Sato 1999; Sato & Siga 2000), an age that may considerably predate the date of actual emplacement of a granite pluton in an orogen. Therefore, a review of the history of the Amazonian Craton cannot simply lump together all existing data, but has to make choices in the light of newer insights and dating methods.

A more fundamental problem is what weight to give to geochronological data when confronted with the major lithological and structural units of the Amazonian Craton. Age provinces and geotectonic provinces often do not correspond, and bitter controversies between geochronologists and more geodynamically oriented geologists continue up to the present day. A geochronological province maps all the rocks that show the same age in one province, irrespective of their origin. A geotectonic province, however, maps all the rocks with a common geodynamic origin together, for instance in one mountain belt, even if some radiometric ages in it do not match the general picture. A striking example of this lack of correspondence is given when comparing the geological map of the Guiana Shield by Delor *et al.* (2003) and of the geological sketch map of a large part of the craton by Dall'Agnol *et al.* (1994) with the geochronological maps by Tassinari & Macambira (1999) and Santos *et al.* (2000) and Santos (2003) (compare Plates 6 and 7, and see Fig. 2.4 and discussion below).

This controversy is at the heart of an old question, the subject of the International Geological Correlation Project 204, about whether the Amazonian Craton is a large Archean platform reworked and reactivated during the Proterozoic (Almeida *et al.* 1981), or whether its evolution is punctuated by episodic crustal accretion during the Proterozoic (Tassinari 1981; see discussion by Teixeira *et al.* 1989). In this chapter we will argue that the concept of geochronological provinces is no longer useful, and that many previous subdivisions of the Amazonian Craton based on geochronological provinces will have to be revised. We will also challenge the validity of the continental accretion model for the central granitoid part of the Amazonian Craton that has been in vogue in recent years on the basis of geochronological provinces.

Main subdivisions of the Amazonian Craton

The Amazonian Craton contains three important and well-recognizable orogenic belts of different age:

1. Relatively small Archean cores with ages around 2.8 Ga, encompassing the Carajás range in the easternmost Guaporé Shield, the Amapá block in the easternmost Guiana Shield, and the Imataca Complex in the northwesternmost Guiana Shield;
2. a Trans-Amazonian greenstone belt, stretching along the northern coast of almost the whole Guiana Shield for over 1500 km, with ages around 2.2 to 2.0 Ga
3. a Grenvillian belt, along the southwestern and western margin of the Amazonian Craton, with ages around 1.3–1.0 Ga.

Interestingly, detrital zircons from modern Orinoco and Amazonian sediments also show a predominance of these three age groups (Goldstein *et al.* 1997; Rino *et al.* 2004) (Fig. 2.2). The Amazonian Craton is bordered in the southeast by the Neoproterozoic Tocantins-Araguaia belt (Brasiliano cycle), which will not be discussed in this chapter.

Granitoid and acid metavolcanic rocks occupy vast expanses between these three belts. The main geochronological provinces of the central part of the craton, as defined by Cordani & Sato (1999), Tassinari & Macambira (1999, 2004) and Tassinari *et al.* (2000), refer to these granitoid rocks. However, most of these ages

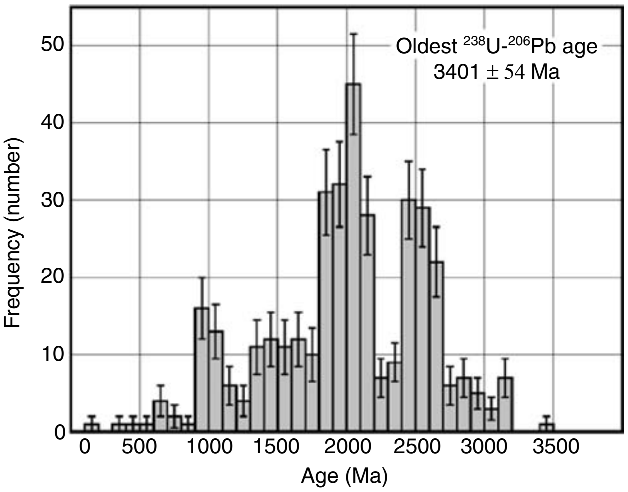

Fig. 2.2 Histograms for U-Pb ages for 369 grains of detrital zircon collected from the mouth of the Amazon River outlet show peaks in the Archean, Trans-Amazonian and Grenvillian intervals. Pb-Pb ages give similar results. The error bars correspond to 1σ. (After Rino *et al.* 2004.)

are based on Rb-Sr isochrons, which are now no longer thought to reflect the age of crystallization. Santos *et al.* (2000), on the basis of new U-Pb zircon ages, make a different subdivision. Dall'Agnol *et al.* (1999) avoid the term geochronological provinces, and refer to them as blocks, using the same boundaries as Tassinari *et al.* (2000).

All these subdivisions cannot hide the facts that there are great overlaps in ages between the different granitoid provinces (see tables 3, 4 and 5 in Tassinari & Macambira, 1999), and that there seems to be a continuum of granitoid magmatism between 2.0 and 1.75 Ga rather than a series of discrete events as suggested by both subdivisions. Furthermore, there is a series of better defined anorogenic Mesoproterozoic granitoid intrusions, concentrated along the northwestern and southwestern parts of the shield. We will therefore stick to a more descriptive subdivision of the craton.

Archean mobile belts

What are the oldest nuclei around which the craton started to grow? There *have* to have been Archean cratons, if only to explain which plates caused the continental collision that gave rise to the 1500-km long Trans-Amazonian orogenic belt that stretches along the northern coast of most of the Guiana Shield and beyond; but where are they?

Unfortunately there is no easy answer to that question. There are numerous Archean ages from restricted areas in the craton, as we will see below, but as Benjamim Bley de Brito Neves (1999) states in one of the seminal papers on the craton: 'none of these Archean terranes/cores appear as autonomous units (*full cratonic areas*); they consist of not-autochthonous, reworked fragments, because they were structured and incorporated in orogenic movements and processes of the Paleoproterozoic (at least)' (translation SBK).

Serra das Carajás terrane

The only unquestionably pure Archean terrane in the Amazonian Craton is the Serra das Carajás area, which occupies a relatively restricted area in the easternmost part of the Guaporé Shield, 900 km south of Belém between the Tocantins and Xingú rivers. It is the most important mineral province of Brazil, hosting the largest iron mine in the world, and containing rich copper, gold, manganese, nickel and other ore deposits (Olszewski *et al.* 1989; Tassinari *et al.* 2000; Tassinari & Macambira 2004; Tallarico *et al.* 2005; Dall'Agnol *et al.* 2008). The area consists of two major tectonic domains: the older Rio Maria and Pau d'Arco or Inajá granite-greenstone terranes in the south, and the younger Carajás Basin proper in the north.

Granulites from the Pium high-grade terranes in the southern part of the Carajás Basin proper show Pb-Pb whole rock protolith ages of around 3 Ga, and a SHRIMP zircon U-Pb age of 2.86 Ga for the granulite-facies metamorphism (Pidgeon *et al.* 2000). They may represent deep slabs caught in the suture zone between the older Rio Maria terrane and the younger Carajás Basin proper (Tallarico *et al.* 2005).

The oldest rocks in the Rio Maria greenstone belt, the Andorinhas supergroup, give ages between 2.98 and 2.90 Ga (Tassinari & Macambira 2004). They were affected by a shear event around 2.87 Ga. The Itacaiúnas Supergroup in the Carajás Basin itself consists of a lower-grade metamorphic greenstone sequence, the Grão Pará Group, and a higher-grade Salobo Group (Tallarico *et al.* 2005). The metavolcanic and metasedimentary sequences of the Grão Pará Group in the greenstone belt, which contain the Banded Iron Formation (BIF) ore bodies, were deposited between 2.75 and 2.74 Ga, according to SHRIMP zircon U-Pb datings (Trendall *et al.* 1998; Tallarico *et al.* 2005), and deformed and metamorphosed between 2.58 and 2.50 Ga. Detrital zircons in these series may be as old as 3.7 Ga. The Grão Pará Group shows the classic greenstone succession of a mainly metabasaltic unit, locally with conspicuous pillow structures, minor meta-andesites and metarhyolites, followed by the BIF and topped by intermediate to acid metavolcanics and metasediments. The greenstone sequences are intruded syntectonically by tonalite-trondhjemite-granodiorite (TTG) bodies dated around 2.87 Ga.

Both domains are intruded by Archean granitic and mafic-ultramafic bodies bodies ranging in age between 2.74 and 2.53 Ga, and Paleoproterozoic granites dated around 1.88 Ga, according to U-Pb data on zircons (Tassinari *et al.* 2000; Tassinari & Macambira 2004). Neodymium isotope data from the Paleoproterozoic granites of the Carajás Basin favour an ensialic evolution (Dall'Agnol *et al.* 2008).

Amapá and Imataca terranes

A large area with predominantly Archean U-Pb zircon ages in high-grade meta-igneous gneisses, intruded by Paleoproterozoic granitoid bodies, is found in the 400-km long Amapá block (Jarí-Guaribas Complex), whereas smaller terranes with such ages are found nearby in Parú, Cupixi and Tartarugal Grande areas in the extreme southeastern corner of the Guiana Shield (see Fig. 2.1) (Santos *et al.* 2000; Delor *et al.* 2003; Avelar *et al.* 2003; Da Rosa-Costa *et al.* 2006).

The Imataca Complex, a 500-km long ENE–WSW-stretching high-grade metamorphic complex in the northwesternmost part of the Guiana Shield in Venezuela consists of granulites, gneisses and amphibolites with important occurrences of BIF, and has long been considered to be of Archean age as well (Montgomery & Hurley 1978). New SHRIMP U-Pb data on oscillatorily zoned zircon cores confirm that the *protoliths*, the parent rocks from which the metamorphic rocks originated, are of Archean age, but the 2.2–2.0-Ga metamorphic overgrowths of the zircons suggest that the high-grade metamorphism is of Trans-Amazonian age, unlike the Carajás granulites (Tassinari *et al.* 2004a,b). The Carajás, Amapá and Imataca terranes are far apart from each other, and there is no physical connection between them; all rocks in the intervening part show Trans-Amazonian or younger ages, although occasionally Archean zircons have been found in some rocks (Delor *et al.* 2003).

Trans-Amazonian orogenic belt

Trans-Amazonian greenstone belts

The term 'Trans-Amazonian Orogenic Cycle' was coined by Hurley *et al.* (1967) to designate an orogenic event around 2.0 Ga