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# The scarcity of fossils in the African rainforest. Archaeo-paleontological surveys and actualistic taphonomy in Equatorial Guinea

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## ABSTRACT

The African rainforest is considered a 'palaeontological desert', exemplified with the virtual absence of ape fossils from the last 10 Ma. To overcome this deficiency of the fossil record, archaeo-palaeontological surveys have been undertaken in the rainforest of Equatorial Guinea. We have inventoried 225 outcrops and eluvial materials and the formation of 'stone lines' (of diverse genesis) predominate. Close to the Atlantic estuaries, there are short fluvial sedimentary sequences (sands and gravels), where remains of lithic industry and charcoal appear, but in no case macro vertebrate fossils. Given the intensity of the survey, the scarcity of sampling is ruled out as the cause of this 'palaeontological desert'. Besides, biogenic, biostratigraphic and fossil diagenetic factors have been explored by means of an actualistic approach. The rainforest ecosystem produces very low density taphocenosis. Simultaneously, there is a low rate of sedimentation/erosion and the action of scavengers has not been detected, although the action of ants and termites may be determinant. Two fossil diagenetic factors can be inferred: lixiviation as a destructive cause and the existence of periods of intensive erosion. The search for palaeontological record should focus on protected sedimentary environments (rockshelters) or more confined ones (maars and small endorheic basins).

## ARTICLE HISTORY

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Taphonomy; African rainforest; Monte Alén; fossil apes

## Introduction

The scarcity or total absence of the mammalian fossil record from Central Africa, an area currently covered by dense rainforests, is a well-known but not well understood fact (Cote 2004; Almécija et al. 2021). The absence of a fossil record concerning the evolution of the African great apes, gorillas and chimpanzees, stands out as an illustrative example. By contrast, an increasing number of Upper Miocene hominin remains are being recovered from different parts of East Africa (genera *Orrorin* and *Ardipithecus*) and Chad (genus *Sahelanthropus*). In this sense, the equatorial forests of central and West Africa hold a special palaeoanthropological attraction, being the preponderant habitat of the current African apes, and possible origin of the group (Darwin 1871; Wrangham and Pilbeam 2001). At present, we still know almost nothing of their African ancestors from the Middle and Upper Miocene, the fossil record of apes in Eurasia being much more abundant. In fact, we only know of three chimpanzee molar teeth of about 0.5 Ma from the Kapthurin Formation, Kenya, associated with semi-arid environments (McBrearty and Jablonski 2005). We have to go back to the Miocene with *Samburupithecus* (Ishida and Pickford 1997) to find the remains of hominoids hypothetically related to present-day apes. That is, therefore, more than ten million years

with a very scarce palaeontological record (d'Oliveira Coelho et al. 2021). The same is true for other groups of mammals that are practically absent in the regions currently covered by rainforest (see Lihoreau et al. 2021).

Such a mammalian palaeontological gap raises questions about the possible causes of the non-preservation of skeletal remains in these ecosystems. Historically, the absence of a mammalian fossil record has been associated with social factors such as political instability, which has led to a still reduced prospecting effort, made difficult by the inaccessibility of some regions, as well as by the dense vegetation cover in these ecosystems that prevents the appearance of outcrops (Cote 2004; Taylor 2014, 2016; Almécija et al. 2021). In order to overcome these drawbacks, since 2014 an intensive project of archaeo-palaeontological surveys has been carried out in the insular and continental territories of the Republic of Equatorial Guinea (EG), a country that is home to dense rainforests but has developed an abundance of public works that has uncovered many outcrops, where the sediments are exposed, susceptible to observation (Terrazas and Rosas 2016; Rosas et al. 2019a, b, 2021a).

In parallel, the assumption is that in the rain forest soils are acidic and destroy skeletons quickly (Peterhans et al. 1993; Roberts et al. 2016). In a broader sense, it is maintained that high soil biological activity leads to rapid decomposition of organic remains. However, previous studies carried out in Ituri (Democratic Republic of Congo) (Tappen 1994) and Kibale (Uganda)

(Peterhans et al. 1993) forests suggest that other factors must also be affecting (such as vertical segregation of small bones, biological activity of some organisms: plants, termites, mosses, algae, rodents). To this end, we explore an actualistic taphonomic approach consisting of direct observation in natural rainforest ecosystems in the Monte Alén National Park of the different generally accepted phases of fossilisation processes: 1) biogenic production phase (ecological stage), 2) tanatocenosis formation phase (biostratigraphic), and 3) burial phase and formation of taphocenosis and subsequent fossilisation. Most of the physico-chemical fossilisation processes (leaching, lateritisation) are outside the scope of observation. However, erosional phenomena responsible for the dismantling of the sedimentary record are considered.

If we want to know what happened to the remains of organisms from the past, it is informative to know what happens to the remains of organisms that inhabit these ecosystems today (Brain 1983; Behrensmeyer et al. 2000; Domingo et al. 2020). If we could find a pattern of the factors that impede conservation, we could design better survey strategies and predict potential sites suitable for the preservation of the palaeontological record.

## Material and methods

### Archaeo-palaeontological surveys

Within the framework of the palaeoanthropological research programme in Equatorial Guinea undertaken since 2014 (Rosas 2015), seven field campaigns have been undertaken. The scope of action includes both the insular region (Bioko Island) and the continental region (Muni River). The prospecting methodology is based firstly on the location on a geological map of potential areas of interest for the discovery of fossils (sedimentary deposits, areas of favourable Mio-Plio-Pleistocene age and conditions, etc.). In these areas, exhaustive surveys were carried out by sampling and documenting specific points where sediments are exposed. Given the intense vegetation cover of EG, this access to sediments is possible in natural or artificial

clearings, quarries, earthworks, etc., most of them of anthropogenic origin. A more detailed description of this methodology can be found in Rosas et al. (2021b).

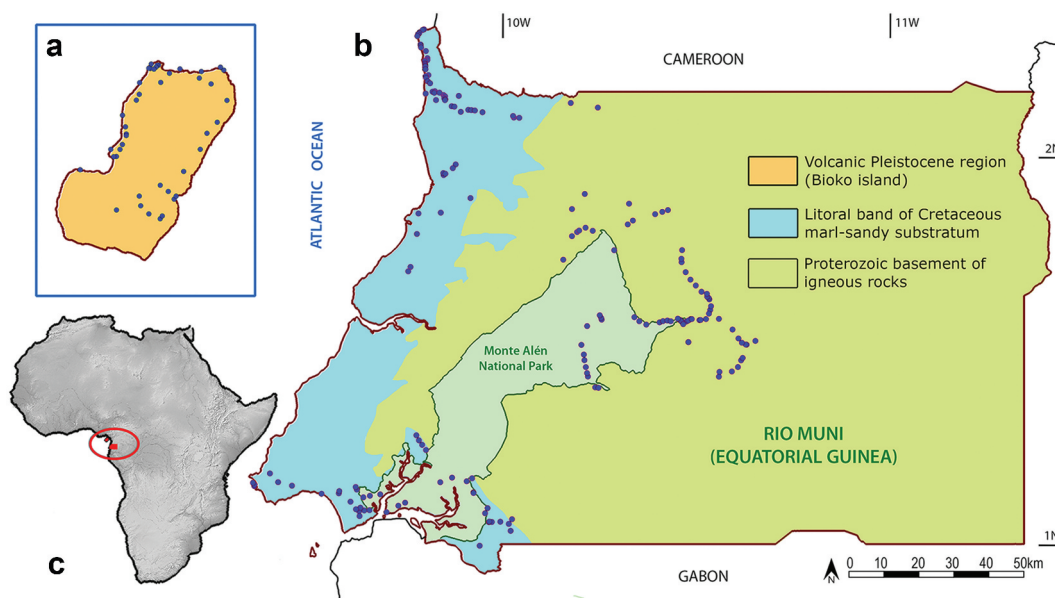
In the 7 campaigns carried out between 2014 and 2021, a total of 225 outcrops have been prospected and documented on roads, quarries and forest clearings located on three different rock substrates (Martínez-Torres and Ríaza 1996) (Figure 1). For ease of analysis and better understanding, we distinguish: 1) Island region, Bioko Island, formed by Pleistocene volcanic edifices (43 points); 2) continental region (Muni River), where a coastal strip of Cretaceous marl-sandy substrate is differentiated (101 points); and 3) the interior of the country with a Proterozoic basement of igneous and other strongly metamorphosed rocks (81 points).

### Actualistic taphonomic approach

In order to document the taphonomic phenomenology of the presence and/or preservation of skeletal remains in a tropical rainforest environment, this study focuses on the interior of the continental part of EG (Rio Muni), in the Monte Alén National Park (Figure 1). This protected area of high ecological value has allowed a high degree of conservation due to its difficult access, with large extensions of primary tropical rainforest.

Several areas of Monte Alén have been explored in the course of four campaigns (years 2019 to 2021), covering a total of 206 km, with 156 hours of recording and documentation. In order to exhaustively cover as much land as possible, the transect methodology was used as a basis, organised on the basis of square cells of  $1 \times 1$  km, and adapted when necessary to the characteristics of the environment (vegetation, watercourses, natural obstacles, etc.). At the same time, our direct observations were supplemented by an extensive network of information provided by locals and forest guides.

From a biogeographical point of view, Rio Muni is entirely included in the African lowland or plain rainforest belt, with scarce mountainous areas that in any case do not exceed 1200 m in altitude, currently covered by dense equatorial rainforests of the Guineo-Congolese domain (regional centre of endemisms), in its



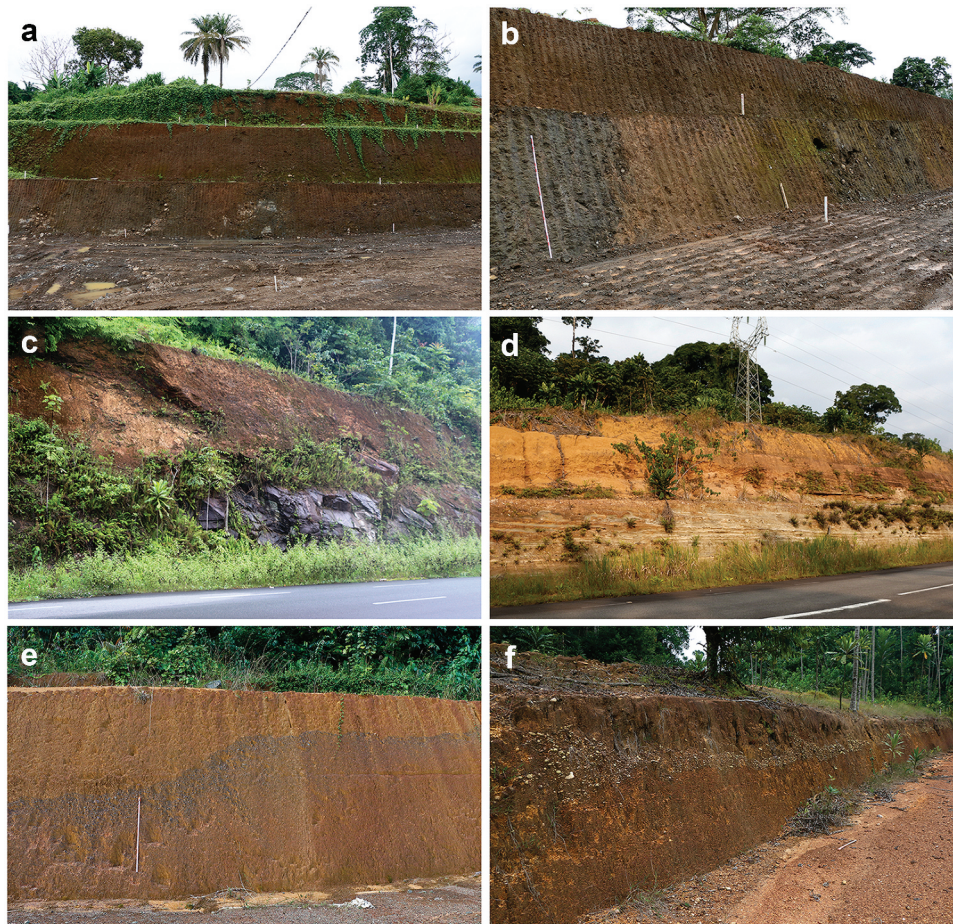
**Figure 1.** Map of Equatorial Guinea with the location of the surveyed points. Note the presence of three distinct geological basements. A) Pleistocene Volcanic in the Bioko Island. B) Continental part of EG (Rio Muni), with two differentiated prospection areas: cretaceous sandy-marls in the littoral fringe and proterozoic basement at the interior region. C) location of EG in Africa.

variety of hygrophilous coastal evergreen rainforest (White 1983). Only on Mount Mitra does African montane forest develop. According to Lerebours-Pigeonnière and Ovono (2001), unsaturated yellow ferrallitic soils predominate throughout the continental region. They are composed mostly of quartz sands and clays (kaolinite) and characterised by a strong acidity (pH between 4.5 and 5). In other African rain forest environments, due to the presence of humic components, the pH is even lower (between 3.5 and 4.5) (Lecomte 1988), while Mercader et al. (2002) report average values of 4.63 for the Mosumo area (Equatorial Guinea). These soils are very poor in phosphorus, potassium, calcium, magnesium and trace elements, all of which are concentrated near the soil surface in humus and organic matter from plant decomposition, which feeds a high diversity of invertebrates (dipodops, termites, ants) and fungi. The climate is of the warm humid equatorial type, with two short, mild dry seasons (from December to mid-February and from July to September, more pronounced) separating two rainy seasons, more intense between September and December, ranging from 1,800 to 3,800 mm. Although high, rainfall is relatively low compared to other rainforest areas on other continents. Even so, rainfall generates a dense river network with fast-flowing rivers rich in osteichthyes. Relative humidity is very high at around 90%, dropping to 85% in the dry season. The daily

and inter-monthly thermal amplitude is very limited, with average values close to 25° (20–23° in higher areas). These conditions are conducive to the formation of dense rainforests in the African forest belt, the ecosystem that is the subject of our study.

## Results

From a stratigraphic point of view, alteration profiles with eluvial materials and the formation of the so-called ‘stone lines’ (of diverse genesis) are predominant among the Quaternary sediments (see Mercader et al. 2002) in the three geological areas (Figure 2). Sedimentary sequences are very scarce, except in alluvial plains where stratigraphic sequences of low power, sandy floodplain materials and channel-bottom gravels are observed. In none of these contexts have we found macroscopic faunal remains, with the exception of Cretaceous-age ichnofossils (*Thalasinoides* and *Ophiomorpha*), which are beyond the scope of this study. Neither are plant macrofossils or remains of gastropods, which are very abundant in the ecosystem, preserved. This confirms the difficulty of finding macroscopic palaeontological records in environments currently covered by rainforest. On the other hand, several sites with in situ lithic industry and untransported charcoal remains have been located (Table 1 and Figure 3, Mercader and Marti 2002; Terrazas and Rosas 2016; Rosas et al. 2019a, b), which implies

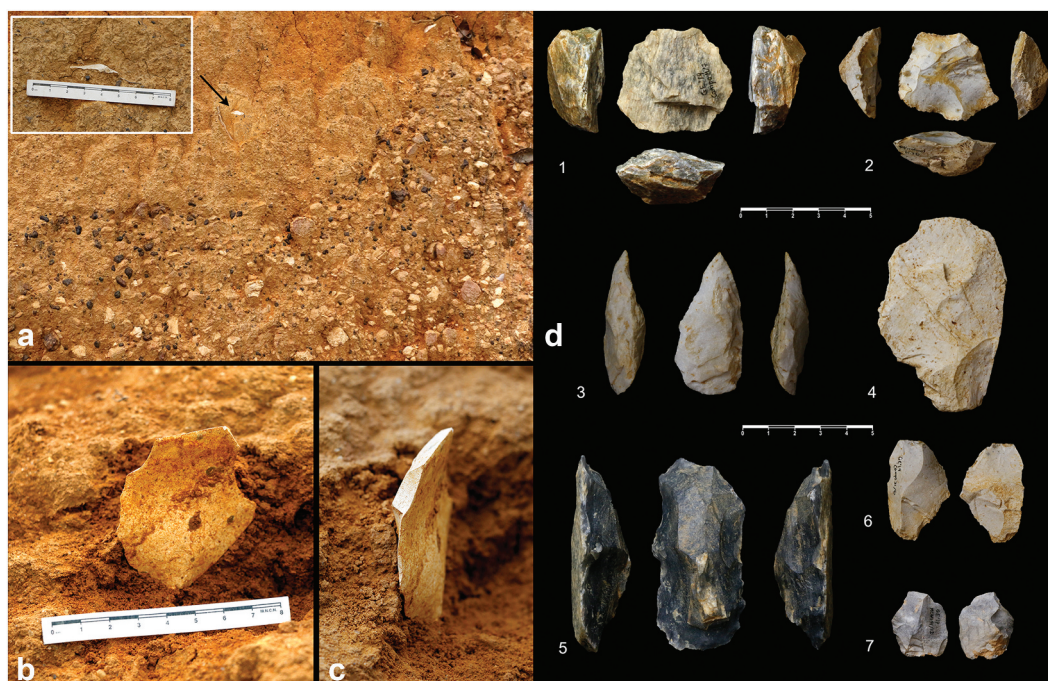


**Figure 2.** Some examples of outcrops analysed in the Equatorial Guinea territories, mostly uncovered by road construction and other public works. Figure 2 A and B show, respectively, a general view of eluvial sediments on basaltic substrate and detail of eluvial sediments on Bioko Island, western Basakato area. Figure 2C shows eluvial materials on granitoid saprolite in the Monte Alén region and Figure 2D on Cretaceous near-shore Cretaceous saprolite in the Rio Campo region. Figure 2E shows the typical ferrolitic nodule estone line (Alen point 8). Figure 2F shows detrital sediments (gravels) from the channel bottom in the Rio Campo area.

**Table 1.** Table of the lithic industry found in the continental part of Equatorial Guinea sorted by areas, where relevant data related to materials, density and techniques used are shown.

Area	Localities	Lithics	Raw materials (%)			Localities by lithics density				Reduction techniques	Bifacial tools	Heavy-duty tools
			Quartzite	Quartz	Chert	<10*	11–50*	51–150*	>151*			
Bata	1	17	17,6	0	82,4	-	1	-	-	Centripetal	-	-
Evinayong	4	19	0	94,7	5,3	4	-	-	-	Bipolar	-	-
Monte Alen	1	2	100	0	0	1	-	-	-	Centripetal	-	-
Mosumu	8	122	19,7	13,1	67,2	6	1	1	-	Centripetal Bipolar Levallois	Yes	Yes
Rio Muni	5	67	7,5	7,5	85,1	2	3	-	-	Bipolar Centripetal	No	No
Rio Campo	16	415	34,2	7,0	58,8	13	1	1	1 (n = 288)	Centripetal Bipolar Levallois Laminar	Yes	Yes

\*Intervals of number of lithics.



**Figure 3.** A. Flint flake *in situ* found in Campo 31 location, just above a stone line. Within the frame, a detail view of the stone tool. B and C. Two views of a flint flake *in situ* from in Campo 11 site. D. Plate showing some pieces of lithic industry: 1 and 2 – Levallois cores (Campo 4, Campo 11); 3 – bifacial point (Campo 11); 4 – preferential Levallois flake (Campo 11); 5 – Core-axe (Mosumu); 6-7 – splintered tools/bipolar cores (Campo 31, Muni 14).

the potential association with bone remains (from human food) in these sites, a circumstance that has not been confirmed. On the contrary, a multitude of skeletal remains of wild vertebrates (bushmeat) have been collected around the present-day human settlements, revealing the present-day human being to be a powerful taphonomic accumulating agent (Rosas et al. 2021a). Therefore, given the intensity of the surveys, the scarcity of sampling (sulleptic factors) can be ruled out as a cause for the absence of records in the rainforest environment, which raises the question of other explanations for this ‘palaeontological desert’.

#### Biogenic production (Ecological factors)

The rainforest ecosystem generates abundant biogenic production, especially plant production. Species of gastropods and hard-cut cuticle arthropods (myriapods, coleoptera) are abundant. In contrast, mammal species have low population densities and a dispersed spatial distribution (White 1994 and cites therein; Zhu et al. 2018). In

rainforest areas, most species of rain forest mammals are solitary (Happold 1996) and there are no gregarious large herbivores and catastrophic die-offs are rare (Tappen 1994). Although there are large animals, most of the mammals inhabiting the rainforest are smaller than 10 kg (Andrews and Humphrey, 1999; Rosas et al. 2021a). Most rain forest mammals are frugivores (36%) and insectivores (37%) (White 1994; Happold 1996), and there are more insectivores than carnivores (Rosas et al. 2021a). There are no potential biotic accumulators such as carnivorous predators or scavengers, nor are there bone breakers such as hyenas. The behaviour of jungle leopards is very dispersed, in addition to a secular human hunting pressure that possibly also conditions the ethology of this species.

#### Biostratinomic processes

In deforested environments, the biostratinomic triad of 1) gastropod shells (on average 12 specimens every 7.8 km/6 hours of browsing), 2) myriapods and beetles, and 3) isolated bones from

human food and chewed by dogs are frequently found on the surface. Exoskeletons of gastropods, myriapods and beetles are also found in the forest interior, where leaf litter and wood remains (necron) are abundant. Soft fruits eaten by primates and other small mammals, as well as woody endocarps gnawed by squirrels and other rodents, are also very frequent. The clayey substrate with abundant mud favours the preservation of elephant and buffalo footprints and other smaller organisms, as well as traces of their activity (burrows, baths) and excrement. Occasionally feathers are found. In situ or dismantled termite mounds are very frequent. However, we confirm the shortage of vertebrate skeletal remains on the Monte Alén rainforest ground, except those occasionally derived from prey hunted by humans. This is the case even in areas where the forest canopy is very dense and the herbaceous substrate is very sparse and open (little light reaches it), allowing the ground surface to be clearly observed. Local informants claim never to have seen chimpanzee remains in the forest. Remains of cercopithecines (e.g., *Cercopithecus cephus*, *C. nictitans*) preyed upon by crowned eagles (*Stephanoaetus coronatus*) are sporadically observed.

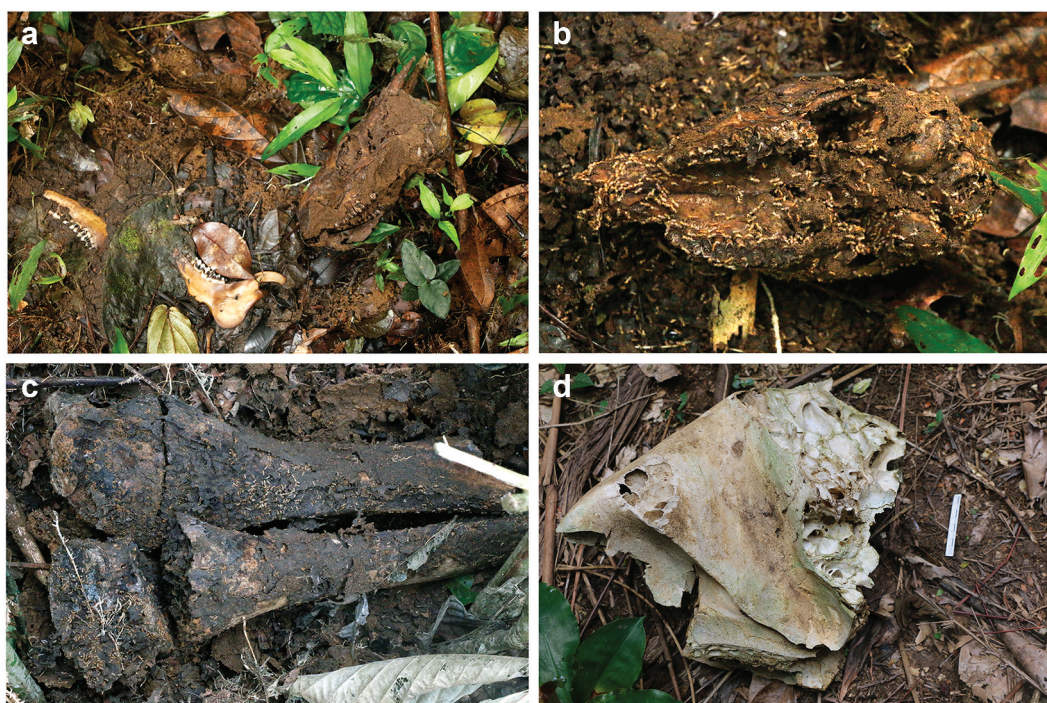
The faunal inventory reveals the absence of mammal species that accumulate vertebrate remains (hyenas, canids) (Rosas et al. 2021a). No abiotic accumulators were detected either. The main potential biotic accumulators (concentrators) are birds of prey: eagles and owls. In Kibale forest, Peterhans et al. (1993) note that the only multi-species bone concentrator is crowned hawk eagle (*S. coronatus*), similar to that reported by McGraw et al. (2006) in Ivory Coast's Tai Forest. However, some of these species tend to locate their feeders high in the canopy, so that in the fall of food scraps there is a wide dispersal of the remains. In any case, local guides and hunters report never having seen accumulations of mammal bones. Suids and small carnivores (e.g., civets) may be the scavengers. These ecological characteristics determine that the thanatocenosis is of a very low density, almost always scattered and

not aggregated. It was found, nevertheless, that in equatorial rain forest contexts humans are an accumulating agent of organic remains.

Some remains of animals hunted by humans have been found: elephants and duikers (Figure 4), but no remains from other non-anthropogenic causes of death. In the few remains found, two types of external surfaces can be detected. One is well preserved, with hardly any signs of weathering, cracking or desiccation. The few remains detected persist for years on the ground and in our observations we have not been able to appreciate the action of scavengers (suids, civets). Others are subject to the persistent action of termites, which very quickly cover the bones with mud aggregate formations (termite mounds) (Figure 4).

### Fossildiagenic processes

In relation to burial processes, there is a low rate of sedimentation/erosion in the jungle environment, with the superficial geological substratum being predominantly eluvial in character (Figure 2A-D). The low stratigraphic thickness is constant in all sections; with thicknesses ranging from 2 to 10 m. Figure 2E illustrates the characteristic stone line of ferrolitic nodules (Alen point 8) where the three horizons defined by Lecomte (1988) are clearly distinguished. The saprolite (H3), bedrock above which is a more or less thick horizon of disaggregated materials that still maintain, although partially altered, the original structure of the rock. Over this horizon, H1 is superimposed without interruption an accumulation horizon made of coarse fragments called 'stone line' (H2). The presence of prehistoric lithic materials accumulated in these structures is frequent. However, the name 'stone line' is currently very confusing, as both the materials that compose them and the details of their structure vary considerably. In any case, the existence of a clear stratigraphic unconformity defined by an accumulation of clasts (of different nature and composition) above which



**Figure 4.** Mammal bones found in the rainforest of Monte Alén National Park (Equatorial Guinea). A and B are duiker skull remains (*Philantomba monticola*); C and D are elephant bones (*Loxodonta cyclotis*). A, B and C shows the effects of termites on the bones. D shows the limited alteration of the bones, after years of being on the ground.

a homogeneous loose-clay horizon (H1) free of any coarse fragments is supported is a fact of observation in a multitude of stratigraphic profiles. As in the previous case, lithic materials have been documented in the H1 horizon.

Fluvial sediments occur close to the large estuaries of the Atlantic coast, especially those of Rio Campo and Rio Wele, being less abundant in Rio Muni, some of which are currently covered by mangroves. Figure 2F shows detrital sediments (gravels) from the channel bottom in the Rio Campo area. Some deposits corresponding to alluvial fans can also be distinguished. Recent taphocenosis has not been detected in any case, while the eluvial records and sedimentary deposits have not yielded any macroscopic palaeontological record. Charcoal remains, some of centimetre size, are occasionally preserved.

## Discussion and conclusions

The programme of archaeo-palaeontological surveys in the context of rainforest ratifies the secular absence of palaeontological record in these African ecological environments. However,

contrary to the most widespread opinion (Almécija et al. 2021), a first consideration that can be made is to rule out sampling factors, whether for historical, political or vegetation cover reasons, as a reason for the scarcity of palaeontological record. As a next step, and in order to understand the possible taphonomic factors that determine this lack, a programme of *in situ* observations has been designed, combining geological, ecological and biostratigraphic data from the present-day world, the results of which are summarised in Figure 5.

### Factors related to biogenic production

In the rainforest ecosystem there are a series of ecological factors that are not favourable for the formation of a palaeontological record. One of the most important of these is the spatial distribution of organisms. Compared to savannah or temperate environments, everything is more homogeneously distributed in the rainforest. The differentiation of biotopes is partially blurred by the extensive vegetation cover, which tends to homogenise the different elements of the landscape. We can say that the distribution

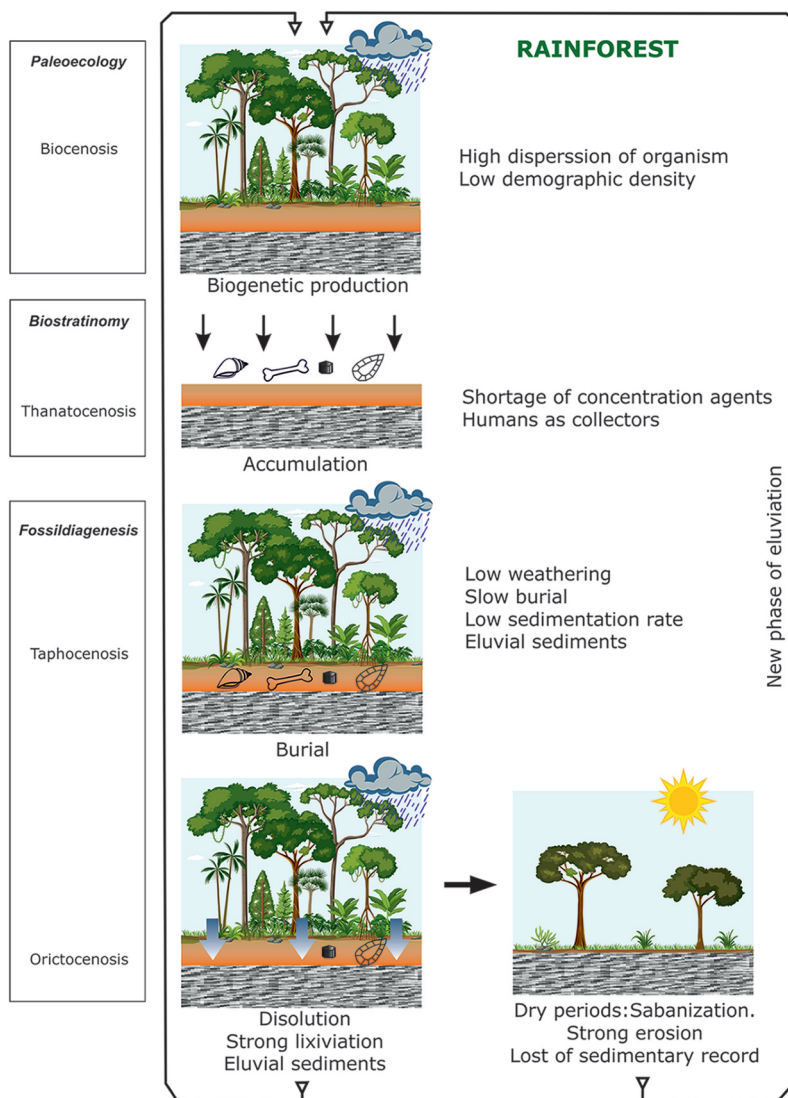


Figure 5. Diagram showing the main taphonomical processes affecting the present Atlantic African rainforests.

of animal biogenic production is homogeneously distributed in space. This phenomenon is clearly reflected in the different species of mammals, whose diversity is high but the number of individuals per species is relatively low. Another ecological factor somewhat related to the above is that in the African forest there are no large predators or scavengers that accumulate skeletal remains. A basic requirement for accumulating associations to occur is the presence of physical or biological factors that concentrate the elements produced. Without this factor, the remains are so dispersed as to make their detection very difficult, even if they are preserved. We have found that in the rainforest there are no accumulation agents. There is an exception to this. It was found that in equatorial rain forest contexts, humans are an accumulating agent of organic remains and a large number of skeletal remains from food residues are deposited near the houses (Rosas et al. 2021a). Human activity becomes, consequently, a potential generator of archaeo-palaeontological fossil record and it can infer it has been also during Pleistocene epochs. Consequently, the presence of prehistoric remains of lithic industry is a strong indicator that they could have been originally associated with skeletal remains, a common circumstance in the archaeo-palaeontological record since the origin of the genus *Homo*, or even earlier. Such skeletal remains have not been found in any of the sites detected in environments currently covered by rainforest.

### Biostratinomic factors

Some of the results of this work largely coincide with those reported by Tappen (1994) and Peterhans et al. (1993). For example, the scarcity of skeletal remains in the rainforest is remarkable, a fact also pointed out by Tappen (1994), despite intensive search effort. In contrast to other more open environments, or drier climatic conditions, very few bones are found on the surface in African rainforests. In fact, in the at least 20 transects carried out throughout the different campaigns, covering an average of 7 km/5.3 h, no bones have been found apart from remains clearly from human hunting (known from direct testimonies, or associated with traps, etc.) and these have also been scarce. Besides, local forest guides and hunters have been asked for bone remains and they declare the extreme scarcity of them. Very few cases of non-anthropogenic deaths have been detected. It has been proposed several times that in the rain forest soils are acidic and destroy skeletons quickly (Watson 1967; Gordon and Buikstra 1981; Retallack 1984; Peterhans et al. 1993). However, this is partly contradicted by the fact that the remains remain on the surface for long periods; a fact also observed by Tappen (1994). Furthermore, the surfaces of the bones are well preserved, with hardly any signs of weathering, similar to what has been found by other authors (Peterhans et al. 1993; Tappen 1994). Not being exposed to direct sunlight (ultra-violet light) and maintaining a constant humidity and temperature prevents cracking of the bones. Shipman (1981) points out that vegetation cover, as well as protection in the case of shelters and caves, delays the stages of weathering described by Berhrensmeier (1978), safeguarding the remains from rapid weathering more typical of savannah areas. This rules out that the rapid degradation of the remains is a limiting factor for their preservation, a widely held unjustified belief. Moreover, alteration soils and the formation of so-called 'stone lines' are widespread in Central African rainforests (Lecomte 1988). In these eluvial contexts, burial of the thanatocenoses is slow and skeletal remains (invertebrates, bones and teeth) can remain on the surface for a long time (Peterhans et al. 1993; Tappen 1994). This, however, raises a paradox: if bones remain at the surface for a long time, when large animals such as elephants or buffaloes are in the ecosystem, why are they not found?

Galdikas (1978) notes that the scavenging of wild pigs may play an important role in the destruction of pongid remains. At Gombe National Park, chimpanzee carcasses were rarely recovered, what was attributed to rapid destruction of the remains by scavengers, insects, and microorganisms (Goodall 1986). In our observations in the EG forests, the action of vertebrate scavengers could not be detected. However, a key element in scavenging functions in the rainforest ecosystem is played by ants (Fayle et al. 2011; Griffiths et al. 2018). Ferocity and abundance (up to 25% of animal biomass) can exert a very rapid action on the degradation of soft tissues of dead animals, although their effect on skeletal remains, possibly rapidly abandoned, is not well determined. The effect of termites on the preservation of skeletal remains is also unclear. Tappen (1994) reports a destructive biostratinomic action through the formation of small round pits on 59% of the remains studied in Ituri rain forest. More recently, Backwell et al., (2020) report on the effects of South African termites on present-day bones, resulting in individual striations, multiple fine parallel striations, pits, pitting and abrasion on bones. However, the formation of mud crusts around and inside the bones could also result in a protective effect favourable to the preservation of the bones, and perhaps their concealment. No doubt further in situ observations or experimental approaches could help to clarify these aspects.

### Fossildiagenetic factors

Other possible factors determining the formation of the palaeontological record are those related to post-burial chemical action and the erosion and disappearance of the geological record. From the comparative analysis of the different stratigraphic profiles, we can infer the action of at least two fossildiagenetic factors contrary to the formation of orictocenosis in rainforest environments. One of them would be the occasional presence of lithic industry and charcoal remains in situ can be interpreted as products of human activities (although it cannot be ruled out that some of the charcoal remains could come from natural fires) and their highly probable association with organic remains. The absence of palaeontological records in both eluvial and sedimentary environments in EG points to leaching as a destructive cause. An apparent exception, however, is the preservation of charcoal remains, also documented in other sites (Tovar et al. 2014). The high rainfall typical of the rainforest determines intense washing and leaching, which gives rise to ferrolitic soils, which are widespread in the study area. It is hypothesised that these vertical mobilisation processes are one of the main agents determining the dissolution of organic materials (Figure 5). In recent prehistoric archaeological contexts from rockshelters such as those from Ituri, Congo (Mercader et al. 2003) and Shum Laka, Cameroon (de Maret 2013), skeletal remains of both snails and mammals (bovids, primates, rodents, and carnivores) are preserved, although they are mainly teeth. Compared to open-air sites, the protective effect of a rocky cover, preventing the permanent washing away of sediments, emerges as a key factor for the preservation of skeletal remains. Outside East-Central Africa, an abundant osteological record from rainforest habitats is documented at the Fa-Hien Lena cave site, Sri Lanka (Wedage et al. 2019).

A second factor may be related to the almost constant presence of alteration soils of scarce stratigraphic thickness (somewhat thicker on Bioko Island) covering most of the surveyed territories seems to indicate the existence of widespread regional events of high erosion (Lerebours-Pigeonnière and Ovono 2001), something previously proposed in nearby areas of Gabon (Lecomte 1988), possibly associated with cold periods and sabanization (Maley

1996; Piñeiro et al. 2017). Such events would have dismantled previous stratigraphic records (Figure 5). The climatic transition periods, between the beginning of the loss of vegetation cover and the occasional persistence of heavy rainfall, draw strongly erosive phases.

Consequently, taking into account all the biogenic, biostratigraphic and fossil-diagenetic factors mentioned above, the discovery of palaeontological records of mammals should focus on more confined environments, among which rockshelters or other protected sites are of particular interest. The potential record contained in local accumulation sites such as tectonic pits (semigrabens), maars and small intramontane endorheic basins remains to be verified and will be the subject of future surveys. In any case, lack of sampling is ruled out as an explanation for the palaeontological desert from the African rainforest.

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