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Research Paper

Reassessment of historical sections from the Paleogene marine margin of the Congo Basin reveals an almost complete absence of Danian deposits

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ABSTRACT

The early Paleogene is critical for understanding global biodiversity patterns in modern ecosystems. During this interval, Southern Hemisphere continents were largely characterized by isolation and faunal endemism following the breakup of Gondwana. Africa has been proposed as an important source area for the origin of several marine vertebrate groups but its Paleogene record is poorly sampled, especially from sub-Saharan Africa. To document the early Paleogene marine ecosystems of Central Africa, we revised the stratigraphic context of sedimentary deposits from three fossil-rich vertebrate localities: the Landana section in the Cabinda exclave (Angola), and the Manzadi and Bololo localities in western Democratic Republic of Congo. We provide more refined age constraints for these three localities based on invertebrate and vertebrate faunas, foraminiferal and dinoflagellate cyst assemblages, and carbon isotope records. We find an almost complete absence of Danian-aged rocks in the Landana section, contrary to prevailing interpretations over the last half a century (only the layer 1, at the base of the section, seems to be Danian). Refining the age of these Paleocene layers is crucial for analyzing fish evolution in a global framework, with implications for the early appearance of Scombridae (tunas and mackerels) and Tetraodontiformes (puffer fishes). The combination of vertebrate fossil records from Manzadi and Landana sections suggests important environmental changes around the K/Pg transition characterized by an important modification of the ichthyofauna. A small faunal shift may have occurred during the Selandian. More dramatic is the distinct decrease in overall richness that lasts from the Selandian to the Ypresian. The Lutetian of West Central Africa is characterized by the first appearance of numerous cartilaginous and bony fishes. Our analysis of the ichthyofauna moreover indicates two periods of faunal exchanges: one during the Paleocene, where Central Africa appears to have been a source for the European marine fauna, and another during the Eocene when Europe was the source of the Central Africa fauna. These data indicate that Central Africa has had connections with the Tethyian realm.

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1. Introduction

The Paleocene (66–56 Ma) is a key time period that follows the Cretaceous–Paleogene (K–Pg) mass extinction. During this period, major biotic turnovers occurred and many groups of modern vertebrates appeared and/or began to diversify. Such crucial episodes have been observed in terrestrial vertebrates including lizards and snakes (Longrich et al., 2012), birds (Ericson et al., 2006), and mammals (O'Leary et al., 2013), and marine vertebrates including ray-finned fishes (Friedman, 2009; Friedman and Sallan, 2012; Sibert and Norris, 2015; Guinot and Cavin, 2016), elasmobranchs (Kriwet and Benton, 2004; Noubhani, 2010; Guinot et al., 2012; Guinot and Cavin, 2016; Belben et al., 2017), and crocodylomorphs (Puértolas-Pascual et al., 2016). Among invertebrates, cephalopods reflect this extinction in the disappearance of ammonites (Landmann et al., 2015); bilvaves have also been affected by this mass extinction (Raup and Jablonski, 1993; Jablonski and Raup, 1995). However, such dramatic patterns are not observed in all animal groups: in contrast to most other Mesozoic vertebrates, testudines were apparently little affected by the K/Pg extinction event (Lyson et al., 2011; Holroyd et al., 2014).

Besides the radiation of modern groups of vertebrates and invertebrates, the Paleogene period (66–45 Ma) exhibits climatic fluctuations, although potential links between climate and vertebrate evolution are a matter of some debate (Zachos et al., 2001). Several terrestrial taxa (e.g., mammals, reptiles) disappeared before or during the Paleocene Eocene Thermal Maximum (PETM, 56 Ma; Wing et al., 2005; Gingerich, 2006; Smith et al., 2006), the warmest period of the last 65 million years. Although the PETM brought dramatic changes in terrestrial ecosystems, the signal observed in marine ecosystems is different. Concerning crocodylians, Mannion et al. (2015) found no evidence for transient biodiversity increases driven by the short-term PETM interval, although in Africa, Europe and North America, a small decrease of crocodyliform dyrosaurid diversity is apparent; notably tomistomines appear in the record, to the apparent detriment of the gavialoid crocodylians (Bardet et al., 2017). Tomczik (2014) further noted that fish morphotypes change little through the PETM, with no evidence for an excursion biota during the warmest interval, suggesting that fish experienced fewer geographic range shifts than might be expected. Noubhani (2010) noted only few major elasmobranch disappearances during the early Ypresian in Morocco.

Although the early Paleogene holds an important key to understanding global vertebrate (and invertebrate) biodiversity patterns, the record is incomplete as most terrestrial vertebrate research has focused primarily in North America, Europe, and Asia. In the Southern Hemisphere, continents and their terrestrial faunas experienced isolation and endemism following the breakup of Gondwana, and the fossil record is relatively sparse. Therefore, Africa might represent a key piece of the Gondwanan puzzle for understanding past migrations and patterns of modern biodiversity. Indeed, African marine habitats have been proposed as a center of origin for several groups of aquatic vertebrates, including whale sharks (Rhincodontidae), devil rays (Mobulidae) and palaeophiid snakes (Rage and Wouters, 1979; Noubhani and Cappetta, 1997; Adnet et al., 2012).

Fossil fishes from the African Paleogene have been described since the early 20th century (reviewed in Murray, 2000), primarily from northern and western sites, including Morocco (Arambourg, 1952; Cappetta, 1981, 1983; Noubhani and Cappetta, 1997), Algeria and Tunisia (Priem, 1903; De Stefano, 1915; Mahboudi et al., 1984), Egypt (Case and Cappetta, 1990; Underwood et al., 2011), Mali (Longbottom, 1984), Niger (White, 1934; Cappetta, 1972; Dikouma et al., 1994), Nigeria (White, 1926, 1955; Stevens et al., 2011), Togo (Stromer, 1910), Cameroon (Jaekel, 1895, 1904). In addition, Jubb and Gardiner (1975) reported teeth of several shark species from Paleogene deposits in South Africa, and Böhm (1926) described several elasmobranchs and actinopterygians from marine deposits in the diamond fields of Namibia. Yet the majority of fossiliferous localities document faunas that are stratigraphically limited, and therefore do not elucidate long-term faunal trends, nor the impact of climate change on faunal patterns. A phosphate series in Morocco represents the only exception: sections there record the first half of the Paleogene (Arambourg, 1952; Yans et al., 2014; Bardet et al., 2017), documenting strong affinities with the South-Tethyian region.

In this context, the Paleogene fossiliferous localities of western central Africa (Angola and Congo) are critical for understanding Cenozoic African faunal dynamics. Numerous fossil localities were documented in this area during Belgian expeditions of the early 20th century. At least 47 fossil localities were excavated or analyzed in the framework of Edmond Dartevelle's paleontological expeditions in 1933 and 1937–1938, gathering a large and unique collection of Mesozoic–Cenozoic vertebrates from the western margin of the Congo Basin, along the coastal area of Angola to Gabon (Dartevelle and Casier, 1943). Most of these sections yielded shells and echinoids, and many preserved fish remains. Among them, the early Paleogene localities of Landana in the Cabinda exclave, and the Manzadi and Bololo sections in DR Congo (Fig. 1) were particularly rich in vertebrate fossils with associated rock samples, providing sufficient stratigraphic context for age refinements using contemporary methodologies (e.g., Carbon isotopic research).

Because Landana appears to have recorded the first half of the Paleogene (Dartevelle and Casier, 1959), it may represent a southern equivalent of the phosphate series of Morocco. Such context is critical for exploring the evolution and affinities of marine faunas (e.g., origination, migration) in different regions of Africa.

Here we present refined age constraint for the Landana, Manzadi and Bololo sections based on invertebrate and vertebrate fossils, foraminiferal assemblages, palynomorphs, and carbon

Figure 1. Map of the margin of the Congo Basin showing the Landana, Manzadi, and Bololo fossil sections in western central Africa.

isotope records (i.e., carbon isotope ratios of bulk organic matter). Taken together, these lines of evidence help to characterize the evolution of early Paleogene faunas of West Central Africa, and to explore their paleobiogeographic implications.

2. Geographical, geological, and paleontological context

The Landana section (Cabinda exclave, Angola) is located along the west coast of Africa within the marine Congo Basin, 2–3 km south of the Shiloango river mouth (Fig. 1). The Congo Basin is one of several N–S oriented basins of the West–Central Coastal Province, whose development is related to Atlantic post-rift dynamics (Late Cretaceous–Holocene) (Brownfield and Charpentier, 2006; Brownfield, 2016).

The Landana section was reported for the first time by Pechuel-Loesche (1876), and the fossil content of the material that he collected was briefly described by Lenz (1877, 1878). Around the same time, a general lithological description was made by Freire d'Andrade in 1877 (Choffat, 1905), followed by a much more detailed log by Diderrich, containing lithological and paleontological information (Cornet, 1906). In 1913, Bequaert conducted a short expedition to Landana to collect fish, crocodilian, and turtle fossils (Bequaert, 1923). He provided an updated description of the Landana section, differentiating between ancient and recent sediments, measuring strike-dip and lateral lithological modifications, and describing recent erosional patterns. In the earliest detailed paleontological studies of the Landana section, the main part of the sequence was assigned to the Paleocene (layers 1–29; Dollo, 1912; Leriche, 1913; Dollo, 1914; Bequaert, 1923), with only the upper part of the section (layers 30–31) attributed to the middle-late Eocene (Dartevelle, 1952). Overlying sediments (not studied here) were interpreted as Miocene (or younger) sediments composed of reworked Eocene material. The sedimentology is here updated based on Dartevelle's; this will be described in detail in a forthcoming article.

The Manzadi and Bololo localities and sections, described and sampled by Dartevelle in 1933 (Dartevelle and Casier, 1943, p. 26–32), are located ~80 km southeast of the Landana section, in the Kongo Central Province of the DR Congo (Fig. 1). Based on fossils, lower layers of Manzadi have been interpreted as Maastrichtian in age, and upper layers have been interpreted as Danian (Dartevelle and Casier, 1959, p. 386–389, p. 412; see also Piérard, 1956), whereas the Bololo localities have been interpreted as Miocene sediments composed of reworked Eocene material (Dartevelle and Casier, 1959, p. 401–402).

3. Material and methods

3.1. Stratigraphic sections and rock samples

The lithological sequence of the Landana section has been subdivided into 32 sedimentary layers ("*couches*" in Dartevelle and Casier, 1943) (Fig. 2). Sedimentological material used for chemostratigraphy and biostratigraphy in this study represents part of the original sample set collected during Dartevelle's 1933 and 1937–1938 expeditions (see Dartevelle, 1935). The 32 successive lithostratigraphical units that are considered here are those defined by Dartevelle for the Landada section (Dartevelle and Casier, 1943, p. 54–62), corresponding to intervals recognized by Bequaert (1923) (layers 1–24) but extended by Dartevelle to cover upper parts of the sequence (layers 25–32).

Rock samples and fossils were cataloged and stored as part of the geological and paleontological collections of the Royal Museum for Central Africa (RMCA) at Tervuren, Belgium. For some layers, several specimens are available, but no information about sampling levels within the layers is contained in the notebooks and other documents by Dartevelle that belong to the RMCA archives. The samples were therefore considered to represent the middle of each layer. This implies that isotopic trend interpretations must be made with caution, especially for thick layers (e.g., layer 26; ~4 m thick) and for layers represented by several samples (e.g., layer 26; 3 samples).

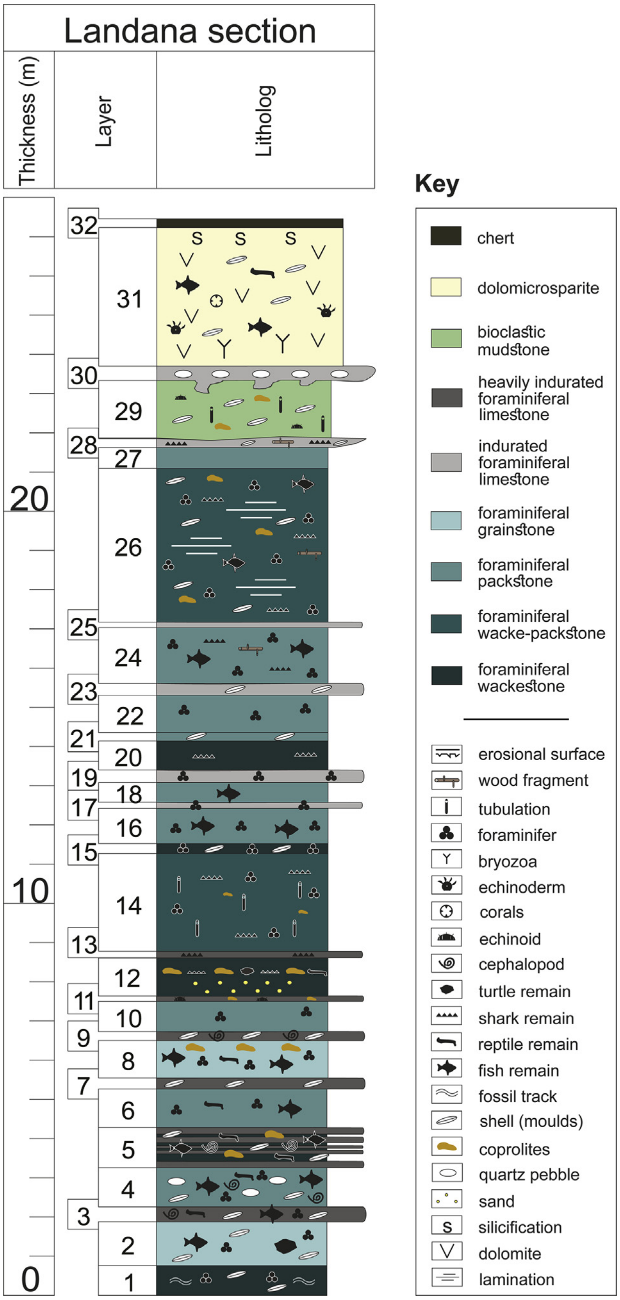


Figure 2. Lithology of the Landana section. Layer thickness is based directly on data provided in Dartevelle and Casier (1943), although sedimentology is updated in the present study.

The lithological sequences of the Manzadi and Bololo localities are composed of different smaller sections ("*Point*" in Dartevelle and Casier, 1943): *Points* IV and VI for Manzadi; *Points* I, II, III and IV for Bololo (only *Points* I and IV are discussed in the present paper). Further field exploration was conducted in September 2014, allowing additional sampling at Manzadi and Bololo.

3.2. Bulk organic carbon isotopes

Carbon isotope ratios of bulk organic matter (Dispersed Organic Carbon [DOC] or Particulate Organic Carbon [POC]) were measured for 53 samples (including replicas) spanning ~27 m of the succession in the Landana section according to the procedure used by Yans et al. (2010), Storme et al. (2012) and Noiret et al. (2016). Samples were prepared at the University of Namur (Belgium) and isotope measurements were performed at the Friedrich-Alexander University at Erlangen (Germany). Bulk sediment samples of about 40 g each were first dried and then cleaned, removing surface oxidation to exclude potential sources of degraded organic matter. Samples were powdered and treated with HCl 25% for 2 h to remove all carbonates. Soluble salts were removed by repetitive centrifuging (4000 rpm) until the neutral solution was obtained. Finally, the residue was dried at ~35 °C and powdered again in an agate mortar. Aliquot of decarbonated powder was measured with a standard LECO carbon analyzer (CS-200) to determine total organic carbon (TOC). Each sample was weighed into tin capsules and rolled into balls for continuous flow combustion and isotopic analysis using a Carlo Erba EA1110 elemental analyzer coupled to a mass spectrometer (Thermo Finnigan Delta Plus XP). Analyses were performed combusting the samples at 1025 °C. Measured isotopic compositions were calibrated with the inter-laboratory international standards USGS40. Organic δ^{13}C values are normalized to the international PDB standard (VPDB, Vienna Peedee Belemnite). Precision of analyses is within 0.07‰ (1σ).

3.3. Planktonic foraminifera

The planktonic foraminifera biozonation from the Landana section published by Lys et al. (1979) followed Berggren (1969)'s zonal definition. Enhanced with new observations and data collection, the stratigraphic scheme of Landana (Lys et al., 1979) is updated here according to Berggren et al. (1995), Berggren and Pearson (2005) tropical to subtropical paleogene zonations and bioevents (compiled in Wade et al., 2011; Anthonissen and Ogg, 2012).

In the Royal Museum of Central Africa (Tervuren, Belgium), two series of collection slides are dedicated to Landana: one main collection with calcareous microfossils from almost all layers (Dartevelle collection numbers: 5317, 5319, 5321 to 5324, 5326 to 5327, 5329, 5331 to 5335, 5340, 5343, 5345 to 5350, 5353 to 5355, 5357 to 5360, 5370, 5373, 5379 and RG collections numbers: 16,301 to 16,314, 16,316 to 16,320, 16,322 to 16,325, 16,327 to 16,340, 16,391, 16,393, 16,394) and a collection of Max Meijer with slides containing identified species (Dartevelle collection numbers: 5323, 5332, 5359, 5366, 5369).

All the figured specimens of Lys et al. (1979) have been stored in the Muséum National d'Histoire Naturelle (MNHN, Paris, France) since they have been photographed (Lys collection numbers: ML105 to ML116). The MNHN collections also house pieces of sediments and washed sediment residues.

The 38 slides of the main collection have been reinvestigated. They contain diverse calcareous microfossils (ostracods, benthic and planktonic foraminifera). Almost all layers are represented in this historical material except layers 20, 28, 29, 30 and 31. From one to three collection slides exist per layer; different collection slides from the same layer are assumed to represent different levels within a layer without certainty about their relative stratigraphic positions within that layer. Lys et al. (1979) did not specify collection methodology hence it is not possible to ascertain whether collection slides correspond to all calcareous microfossils in each washed sediment sample or simply random picking of the microfossil content. Moreover, as Maurice Lys, Max Meijer and Georgette Glaçon who co-authored the paper of Lys et al. (1979), worked on these samples over more than two decades, it is unclear whether collection slides have been updated or changed over time.

Due to some discrepancies between slide content and the distribution table (Table 1; p. 40) of Lys et al. (1979), new preparations were made for those samples from the Dartevelle expedition that remained available. Using standard methods, sediments were soaked in a peroxide solution and subsequently washed over 63 μm and 1 mm sieves. The planktonic foraminifera have been extracted and identified from this fraction (63 μm–1 mm).

3.4. Palynological methodology

Twenty-three samples from the Manzadi and Bololo sections (11 samples collected during Dartevelle's expedition in 1933 and 12 samples collected during the expedition in 2014) were analyzed and processed at the palynology lab of the department of Geology, Ghent University (Belgium). The samples were prepared using standard maceration techniques as described by Wood et al. (1996). After cleaning and oven-drying about 50 g of sediment was processed. Carbonates and silicates were removed by the addition of hydrochloric acid (2N) and warm hydrofluoric acid (40%), respectively. The remaining organic residues were subsequently placed in an ultrasonic bath for about 30 s and sieved on a nylon screen with a 10 μm mesh size. The organic fraction >10 μm was then mounted on microscope slides using liquid glycerol gelatin and later covered with a coverslip and sealed with transparent nail polish. The microscope slides were systematically scanned in non-overlapping traverses using a Zeiss Axioskop A2 transmitted light microscope with a magnification of up to 1000× and equipped with a Zeiss Axiocam MRc5 camera.

It is worth noting that the samples from the Landana section were palynologically analyzed as well. The results of this extensive study, notably the dinoflagellates, will be formally described and presented in a subsequent paper.

3.5. Sources used for the analysis of the evolution of the invertebrates and vertebrates

Biostratigraphic distributions used for the present research represent a compilation of data from the existing literature available for the Landana, Manzadi and Bololo sections. These data concern both vertebrates and invertebrates. We updated the systematics of the fossils found in these sections, especially that of the elasmobranchs.

We assembled this compilation to expand upon work by previous authors that focused only on specific groups. Until now, a global analysis of the invertebrate and vertebrate faunas of these sections was lacking.

Invertebrate data were examined for patterns in bivalves (Vincent et al., 1913; Freneix, 1979), echinoids (Dartevelle, 1952, 1953), and cephalopods (Vincent et al., 1913; Miller, 1951). Gastropods,

Table 1
Number of bilvave, echinoid, cephalopod, elasmobranch, actinopterygian, crocodyliform, squamate, and testudine species recorded in Landana, Manzadi, and Bololo sections.

Group	Landana	Manzadi	Bololo
Bivalvia	17	24	2
Echinoidea	7	0	1
Cephalopoda	4	0	0
Elasmobranchii	45	17	26
Actinopterygii	21	10	4
Crocodyliformes	1	0	0
Squamata	1	0	0
Testudines	3	0	0

including those studied by Vincent et al. (1913), are not considered in the present paper due to uncertain stratigraphic distribution.

Vertebrate data were examined for elasmobranchs and actinopterygians (Leriche, 1913; Dartevelle and Casier, 1943, 1949, 1959; Casier, 1960; Taverne, 2009, 2017), for crocodyliforms (Dollo, 1914; Swinton, 1950; Jouve and Schwarz, 2004), for squamates (Antunes, 1964), and for testudines (Dollo, 1912, 1914, 1924; Wood, 1973; Myers et al., 2017).

The number of taxa considered for each group is presented in Table 1. Faunal lists are available in Supplementary materials 1–3.

4. Results

4.1. Carbon isotopes on organics

Sample fraction of each layer of the Landana section (layers 1–31) was measured for bulk organic carbon isotopes ($\delta^{13}C_{org}$).

Organic carbon isotope records of the Landana section appear to be more fragmented than predicted. Contrary to other published isotopic Paleogene records that base their interpretations on hundreds of isotopic values, the Landana section provides 53 isotopic values from 31 layers in the ~27 m section.

Isotopic values ($\delta^{13}C_{org}$) for the Landana section range from −25.9‰ (layer 3) to −29.4‰ (layers 15 and 26) (Table 2). The major $\delta^{13}C_{org}$ trends observed from base to top throughout the Landana section are as follow (Table 2):

(1) Highly-fluctuating $\delta^{13}C_{org}$ values between layers 2 and 9 (average $\delta^{13}C_{org} = -27.2‰$) that shift towards lighter values in layers 10–12c (average $\delta^{13}C_{org} = -28.6‰$).
(2) Relatively light values for layers 14 and 15 (−29.3‰ and −29.4‰) that shifts to heavier values in the layer 16 (−28.0‰).
(3) Gradual $\delta^{13}C_{org}$ negative shift between layers 19 and 24 (from −27.0‰ to −28.9‰).
(4) High-amplitude variability (~2.5‰) within layer 26: sample LAND28287 (−29.1‰); sample LAND28288 (−27.4‰) and sample LAND28290 (−26.6‰).
(5) Three layers at the top of the section (layers 29–31) show no reliable isotopic trend (from −28.2‰ to −26.8‰).

Table 2
$\delta^{13}C_{org}$ (‰) and TOC (%) data for Landana section. TOC (%) analyses were performed on decarbonated material.

Landana section			
Label	Layer	$\delta^{13}C_{org}$ (‰)	TOC (%)
LAND28306	31	−26.8	0.18
LAND28304	30	−27.3	0.51
LAND28296	29	−28.2	0.17
LAND28293	28	−26.2 ($n = 4$)	0.67 ($n = 4$)
LAND28291	27	−27.8	2.45
LAND28287	26	−29.1 ($n = 5$)	2.81 ($n = 5$)
LAND28290	26	−26.6 ($n = 4$)	8.33 ($n = 4$)
LAND28288	26	−27.4 ($n = 4$)	9.72 ($n = 4$)
LAND28284	25	−28.1	6.04
LAND28283	24	−28.9	8.65
LAND118827	23	−28.1	6.46
LAND28281	22	−28.4	10.40
LAND28280	21	−27.5	6.82
LAND57029	20	−28.7	5.42
LAND118826	19	−27.0	6.70
LAND28278	18	−29.0	7.76
LAND 28277	17	−28.8 ($n = 2$)	4.02 ($n = 2$)
LAND28276	16	−28.0	5.19
LAND28275	15	−29.4 ($n = 3$)	5.78 ($n = 3$)
LAND28274	14	−29.3 ($n = 4$)	7.65 ($n = 4$)
LAND28273	13	−28.7	7.72
LAND28269	12c	−28.3	4.77
LAND28272	12	−28.5	1.80
LAND118818	11	−28.5	3.13
LAND28267	10	−29.1	4.14
LAND118817	9	−28.0	5.11
LAND28258	8	−26.6	0.17
LAND28264	7	−27.6	6.71
LAND118816	6	−27.9	6.11
LAND28323	5	−26.4	2.49
LAND28253	4	−28.1	2.98
LAND28250	3	−25.9	0.54
LAND28248	2	−26.9	0.41
LAND28247	1	−28.2	2.04

4.2. Planktonic foraminifera assemblage of the Landana section

Planktonic foraminifera are scarce or absent in the lower part of the section. They become common from the layer 7 (Fig. 3). Within layers 1–11, foraminiferal assemblages remain species-poor and mainly composed of the small globular species *Parasubbotina pseudobulloides* (Plummer, 1927), *Subbotina triloculinoides* (refer to Figs. 4–16 in Plummer, 1927) and broken specimens of *Praemurica inconstans* (Subbotina, 1953).

According to the stratigraphic distribution table (Table 1; p. 40) of Lys et al. (1979), morozovellids first appear in layer 12c (Fig. 3). However, we observed two small specimens of *Morozovella angulata* (White, 1928) in layer 2 in a slide from the main collection. Surprisingly, the slides from the same level in the Max Meijer's collection also present several specimens and different species of morozovellids. New residue analyses confirm the abundant presence of *M. angulata* and *Morozovella aequa* (Cushman and Renz, 1942) in layer 2 (Fig. 3). The index species *Igorina albeari* (refer to Figs. 4–11 in Cushman and Bermudez, 1949) was discovered indicating that layer 2 belongs to the *I. albeari* lowest-occurrence Subzone P3b, contrary to the biostratigraphic scheme of Lys et al. (1979). First occurence of *M. aequa* is frequently included in *Acarinina subsphaerica* partial range Subzone P4b (Berggren et al., 1995; Wade et al., 2011; Anthonissen and Ogg, 2012). But, *M. aequa* has low latitudinal preferences (Arenillas, 2012): for instance, in Spanish sections of Caravaca and Zumaia, Arenillas (2012) indicates scarce occurrences of *M. aequa* in *M. angulata* Lowest-occurrence Zone P3. It makes sense that this species has appeared earlier in Landana. An ambiguity is that one slide from the main collection contains a single specimen of *Globoconusa daubjergensis* (refer to Figs. 4–19 in Bronnimann, 1953), not reported in the distribution table of Lys et al. (1979), a taxon that is not expected to occur beyond the *Globanomalina compressa* (Plummer, 1927)/*P. inconstans* Lowest-occurrence Subzone P1c. This species was not identified in the newly washed sediments from layer 2. Thus, the specimen from the slide might correspond to contamination or to a rare reworked specimen. In subsequent layers (layers 5 and 7), Lys et al. (1979) have recovered *G. daubjergensis*. But in Meijer's slide from layer 7, the specimens identified as *G. daubjergensis* are unambiguously *Parvularugoglobigerina alabamensis* (refer to Figs. 4–18 in Liu and Olsson, 1992), a taxon that occurred up to the *I. albeari* lowest-occurrence biozone Subzone P3b. The wall structure is a distinctive character distinguishing the two species; *G. daubjergensis* presents a microperforate wall structure with an outer surface covered by abundant small pustules whereas *P. alabamensis* exhibits some pore-mounds. In addition, Lys et al. (1979) recognized *G. compressa* in layer 5 (Fig. 3); this specimen is not figured in Lys et al. (1979) and was not found in the material collection. In layer 7, *G. compressa* specimens were isolated in Meijer's slide but not reported in the distribution table of Lys et al. (1979). Nonetheless, the occurrences indicate that layer 7 is still included in the zone P3. *Morozovella* was absent between layers 2 and 12 in both Lys et al. (1979) and the present reinvestigation, perhaps indicating

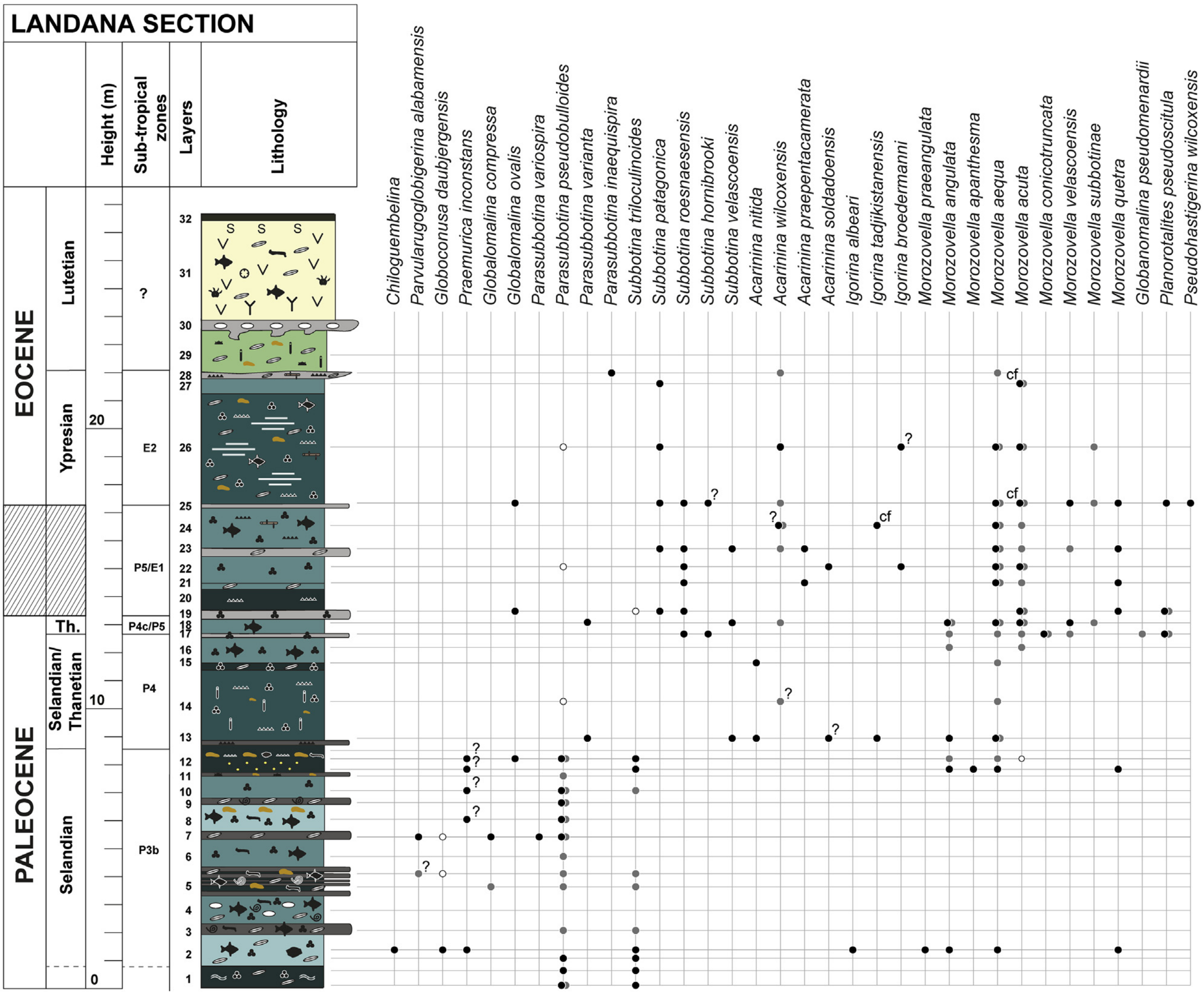


Figure 3. Planktonic foraminifera assemblages of the Landana section. Grey and black dots respectively indicate identifications from Lys et al. (1979) and from this study (new washed sediments and Lys and Meijer collection slide). White dots correspond to misidentified forms.

unfavorable conditions for the genus during that interval. Precise stratigraphic constraint for layer 1 remains elusive, but it likely falls between the *G. compressa*/*P. inconstans* Lowest-occurrence Subzone P1c and the Subzone P3b.

Layers 12 and 13 show a major change with a strong increase in planktonic foraminiferal abundance and richness. Morozovellids prevail in layer 12. Lys et al. (1979) recorded *Morozovella acuta* (Toulmin, 1941) and *M. angulata* (Fig. 3) in layer 12c, but curiously the collection slides do not contain any of these keeled species. The figured specimen of *M. acuta* (Lys et al., 1979: plate III; Fig. 5) is poorly preserved and captured only in lateral view, hence, the identification remains difficult to validate. Although absent in their distribution table, Lys et al. (1979) figured a spiral side of *M. aequa* in layer 12c (Lys et al., 1979; plate III, Fig. 8). Presence of morozovellids in layer 12 was confirmed through analysis of additional sample preparations. Three levels of layer 12 were washed (lower part = C12i-28272; middle part = C12c-28184 and C12m-28271; upper part = C12s-28269) from which only the lower part of the layer preserved planktic foraminifera including *M. aequa*, *M. angulata*, *Morozovella apanthesma* (refer to Figs. 4–12 in Loeblich and Tappan, 1957) and *Morozovella quetra* (Bolli, 1957). The presence of *M. acuta* – recorded by Lys et al. (1979) – suggests that layer 12 might already belong to the *Globanomalina pseudomenardii* (Bolli, 1957) Taxon-range zone P4 but *M. acuta* was not identified in new residues. One of us (DD) found the figured specimen described as *M. acuta* by Lys et al. (1979: plate III) in the MNHN collection; it has been reexamined (Figs. 4–7). New observations suggest that this specimen, not bounded by a thick flange (Figs. 4–9) and having strongly recurved sutures on the spiral side likely belongs to *M. angulata*; layer 12 can still be assigned to the *I. albeari* lowest-occurrence biozone Subzone P3b. In the next layer (layer 13), *M. angulata* and *M. aequa* are common in both the historical slides and in newly washed sediments and are associated with *Acarinina nitida* (Martin, 1943) indicating that layer 13 should already belong to the Zone P4.

In younger layers, index forms remain scarce. Lys et al. (1979) have indicated occurrences of *G. pseudomenardii* in layer 17 (Fig. 3). Hence, this layer is interpreted as no younger than the P4c/P5 (*Acarinina soldadoensis* (Brönnimann, 1952)/*G. pseudomenardii* Concurrent-range Subzone P4c/*Morozovella velascoensis* (Cushman, 1925) Partial-range Zone P5) transition (Berggren et al., 1995; Wade et al., 2011). The interval bracketed by layers 13 and 17 would be included in Zone P4. With the presence of *Morozovella subbotinae* (Morozova, 1939) (Lys et al., 1979), layer 18 should be no older than the P4c (Berggren et al., 1995; Wade et al., 2011; Anthonissen and Ogg, 2012). Layer 19 preserves first occurrences of *Planorotalites pseudoscitula* (Glaessner, 1937) (Figs. 3 and 4), having earliest occurrences in the *M. velascoensis* Partial-range Zone P5 (Pearson et al., 2006). The occurrence of *Pseudohastingerina wilcoxensis* (Cushman and Ponton, 1932) (Figs. 4-2) in layer 25 indicates the base of the *P. wilcoxensis*/*M. velascoensis* Concurrent-range Zone E2 (Berggren and Pearson, 2005). Therefore, layers 19–24 (Fig. 3) belong to the P5/E1 interval (Zone P5/*Acarinina sibaiyaensis* El Naggar, 1966 Lowest-occurrence Zone E1).

Layer 27 is the last reinvestigated layer. It contains rare planktonic foraminifera. Among them, *M. acuta* has been identified, suggesting that the layer belongs to the Zone E2 (Fig. 3). Lys et al. (1979) recorded *Acarinina wilcoxensis* (Cushman and Ponton, 1932) and *M. aequa* in layer 28. Lys et al. (1979) suggested that the layer has been reworked. Pending further evidence, we interpret layer 28 as still Ypresian in age (Fig. 3).

Finally, comparing the distribution table of Lys et al. (1979) and the present revision, it appears that the planktonic richness of the Landana section has been largely underestimated (Fig. 3). Since most of the previous work was performed between the 50s and the 80s, such a discrepancy may relate to methodological differences as the use of scanning electron microscopy become more common beginning in the 80s.

4.3. Palynomorphs of the Bololo and Manzadi sections

An overview of the organic-walled palynomorphs recovered from the Bololo and Manzadi samples is depicted in Table 3.

Recovery was generally poor with low overall abundances and very low diversity among dinoflagellate cysts, acritarchs, pollen and spores. Fungal spores make up an important part of the assemblages, but these most likely represent modern contaminations. The Bololo samples contained three identifiable dinoflagellate cyst specimens: 1 specimen of *Glaphyrocycsta* sp. A and 2 specimens of *Muratodinium*? sp. A (Fig. 5). All three specimens are relatively fragmentary. In-situ specimens of *Glaphyrocysta* sp. A and *Muratodinium*? sp. A were also recorded from layer 28 in the Landana section (unpublished data). Some fragmentary, potentially reworked, specimens were recorded in layer 29.

No dinoflagellate cyst specimens were recovered from samples collected at Manzadi in 2014.

4.4. Invertebrates

4.4.1. Echinoidea

Layer 11 preserves one *Spatangoïdes* (heart urchin) (Fig. 6) (Dartevelle, 1952). The assemblage preserved in layers 30 and 31 of the section is more diverse: indeed, six taxa are recognized (Fig. 6) – none of them is similar to the *Spatangoïdes* known from layer 11.

No echinoids were recovered in Manzadi area, and only *Schizaster douvillei* is recorded from Bololo but without precise locality information (Dartevelle, 1952, 1953).

4.4.2. Bivalvia

Following Freneix (1979), three distinct faunas can be established for Landana section. The first fauna (eight taxa; Fig. 6) – *Ostrea* (*Cymbulostrea*) *dartevellei* – was itself separated by Freneix (1979) into two slightly different assemblages, ranging respectively from layers 2 to 5, and from layers 6 to 11. The second fauna (three taxa; Fig. 6) *Pycnodonte* (*Eupycnodonte*) *eovicenti* assemblage – ranges from layers 14–28. The third fauna – *Pycnodonte* (*Eupycnodonte*) *eovicenti* – is typical of layers 29, 30 and 31 (six taxa; Fig. 6).

Two species at Bololo – *Pycnodonte* (*Epycnodonte*) cf. *vincenti* (*Point* IV) and *Cubitostrea plicata congica* (*Points* I and IV) – are present in layers 29–31 of the Landana section.

Bivalves from Manzadi (*Point* IV) have been well described and discussed in Dartevelle and Brebion (1956), Dartevelle and Freneix (1957), and Freneix (1959) and are not extensively discussed here as they derive from Maastrichtian sediments.

4.4.3. Cephalopoda

In Landana, four cephalopods have been identified (Vincent et al., 1913; Miller, 1951). Two distinct assemblages can be recognized: the first one, which includes the cephalopods *Hercoglossa didderichi* and *Cimomia landanensis*, ranges of layers 3–6 (Fig. 6); the second one, which includes *Deltoidonautilus caheni* and *Eutrephoceras dartevellei*, ranges from layer 26 to layer 31 (Fig. 6). *E. dartevellei* is a nautilid, whereas the other three species belong to the hercoglossid subfamily.

Cephalopods are unknown from Manzadi and Bololo sections.

4.5. Vertebrates

4.5.1. Elasmobranchii

Elasmobranchs are the most diverse vertebrates in the Landana, Manzadi, and Bololo sections. Several species have a short stratigraphic distribution. Therefore, this appears to be among the best vertebrate groups for examining biostratigraphy and correlation across Paleogene localities in western Central Africa.

The oldest assemblage recognized in the Landana section ranges from layer 1 to layer 18 (Fig. 7). This assemblage is characterized by typical Paleocene species, and by the presence of the torpediniform *Eotorpedo*. This assemblage can be divided in two groups: (1) a fauna that shows a high richness (layers 1–12); (2) a less diverse fauna (layers 13–18). Maximum richness is reached in layer 12c: 17 species are known for this particular layer ["*couche à coprolithes*" *sensu* Bequaert, 1920 (Dartevelle and Casier, 1943)]. Interestingly, five of the 17 elasmobranch species have been only discovered in layer 12c.

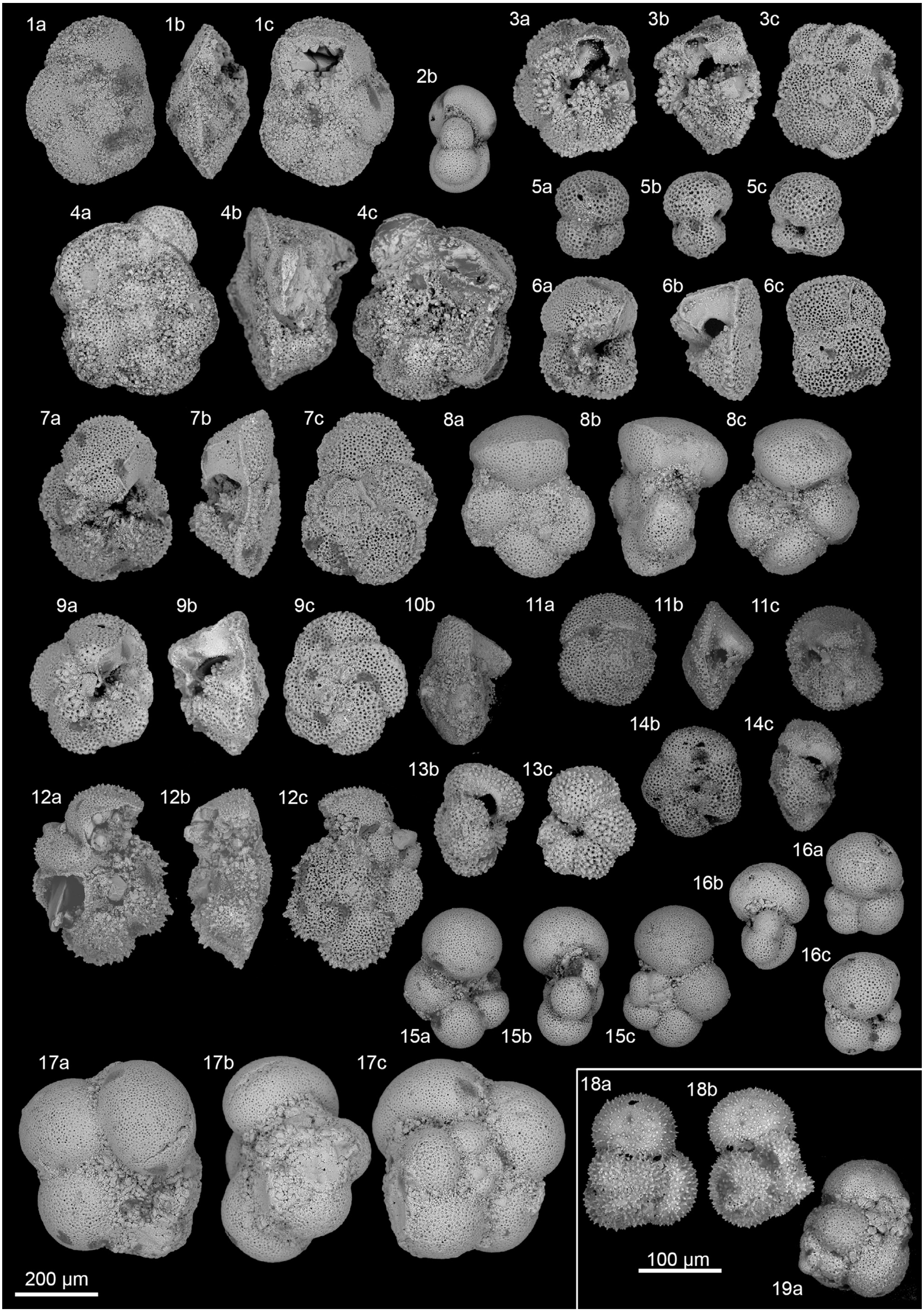
Layers 19–24 also preserve very few taxa: only four (Fig. 7). Among them, three species are recorded in the previous layers – however, the validity of the long-living taxon ?*Carcharias substriatus* remains questionable (Cappetta et al., 2006). The only new occurence is mitsukurinid *Striatolamia striata*; it first occurs in layer 24.

Layers 25–28 preserve nine taxa, but only five are recorded in overlying layers. Two species are first recorded in the layer 28 (Fig. 7).

The latest assemblage recognized herin begins in layer 29 (Fig. 7). It is characterized by the first occurrence of 22 new species, along with the disappearance of taxa known since the base of the section (*Myliobatis sulcidens*, ?*C. substriatus*, *Odontaspis speyeri*) and also since layer 24 (*S. striata*).

Notably, the identification of several specimens may need to be revised (e.g., ?*C. substriatus*), as their stratigraphic distribution is unusual (e.g., *Myliobatis dixoni*, *Eotorpedo hilgendorfi*, and *Ginglymostoma subafricanum* in Selandian layers; *Myliobatis* cf. *toliapicus* in Paleocene layers; *Otodus obliquus*, *Abdounia beaugei*, and *Myliobatis* cf. *toliapicus* in Lutetian layers), but this is beyond the scope of the present paper. If these determinations are correct, they will extend the stratigraphic record of numerous elasmobranchs.

The elasmobranch fauna of the upper layers of Manzadi shares only few species with that of Landana such as *Cretolamna appendiculata*, *O. speyeri*, and *Myliobatis n'zadinensis*. Moreover, the Carcharhiniformes (very abundant in Landana) and Torpediniformes (present but only represented by one species in Landana) are missing in Manzadi.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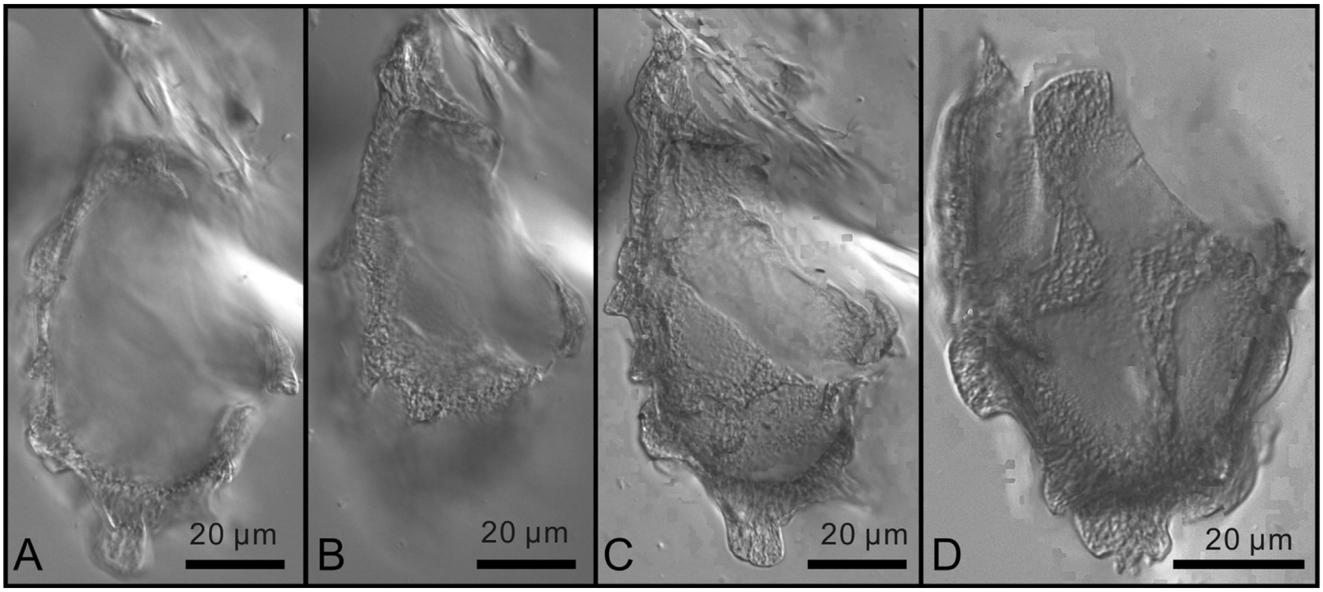

Figure 5. Dinoflagellate cysts of *Muratodinium*? sp. A are from the Bololo section clearly showing the spongy nature of the periphragm. (C and D) Z-stack images.

The elasmobranch fauna of Bololo is more similar to that of the Landana section, with 10 species shared. Except *M. dixoni* and *Otodus obliquus*, all the shared species are known only from layers 30 and 31 (Lutetian layers). Notably, Orectolobiformes and Torpediniformes are absent in Bololo; however, these two orders are poorly represented in Landana. Bololo also differs in preserving two elasmobranch families unknown in Landana: Alopiidae (thresher sharks) and Hemigaleidae (weasel sharks) – but this is not a reflection of differences in facies.

4.5.2. *Actinopterygii*

The actinopterygians are also good biostratigraphic markers because of their short temporal ranges and high species richness (Fig. 7).

Layers 1–6 in the Landana section display the highest richness (7 taxa) recorded in the Paleocene part of the section (Fig. 7). Two taxa of this fauna are recorded in layers 7–11 (Fig. 7); one taxon, *Sphyraenodus multidentatus*, occurs only in layer 8. Only one taxon (*Pycnodus praecursor*) known from layer 1 to layer 6 is represented in layer 12c, while four new taxa are known in layer 12c; these data could suggest either a faunal shift or a shift in environment at this time (i.e., between layers 5 and 6, and between layer 12 and layer 12c) (Fig. 7). Among the new taxa recorded in layer 12c, only *Eotrigonodon jonesi* and *Cybium angustidens* are known in younger layers, respectively in layers 18 and 26. The upper part of the section (layers 29–31) illustrates the maximum richness of actinopterygians with 10 new species recognized (Fig. 7).

The fauna of Manzadi *Point* IV can be distinguished from that of Landana in preserving Alepisauriformes and Elopiformes, and by the absence of Perciformes, Osteoglossiformes and Siluriformes – well-known groups in Landana. The two faunas share the presence of Anguilliformes and Tetraodontiformes. The fauna of Bololo resembles that of Landana: except for the trichiurid *Lepidopus castellobrancoi*, all other Bololo actinopterygians are recorded in the Landana section.

4.5.3. *Squamates*

Snake vertebrae from layers 31 and 32 (Lutetian) of Landana section have been identified as *Palaeophis* aff. *typhaeus* (Antunes, 1964) (Fig. 7). Interestingly, the species *Palaeophis typhaeus* is a typical component of the European Lutetian costal marine fauna that has been included by Rage et al. (2003) in the 'advanced' *Palaeophis* group based on the lateral compression of the vertebrae indicating a strong adaptation for an aquatic life. The massively built square shaped vertebrae from Landana more closely resemble those of *Palaeophis maghrebianus* from the Ypresian of Morocco (Arambourg, 1952; Houssaye et al., 2013) and *P. vastaniensis* from the Ypresian of India (Rage et al., 2008; Smith et al., 2016). These are both characterized by less compressed vertebrae than the condition observed in *P. typhaeus*. This morphological difference alters interpretations of the Landana species. A thorough description of the latter has recently been presented in comparison to the numerous other *Palaeophis* species (Folie et al., 2016). Snake remains are unknown in Manzadi and Bololo sections.

4.5.4. *Testudines*

The bothremydid (side-necked) turtle *Taphrosphys congolensis* – originally referred to *Bantuchelys* and *Podocnemis* by Dollo (1912, 1914, 1924) exhibits a broad stratigraphic distribution: it ranges from layer 2 to layer 16 according to Dollo (1924) (Fig. 7). Wood

Figure 4. Scanning electron micrographs of planktonic foraminifera (a: spiral side, b: lateral view; c: ombilical side) from the Landana section. Collections housed in the RMAC under the numbers DV xxxx, RG xxxxx and RGP xxxxx; Specimen house in the MNHN under the numbers MNHN.F.ML105.1. 1. *Planorotalites pseudoscitula* (Glaessner, 1937) (layer 25, Lys's collection, RGP 16337); 2. *Pseudohastigerina wilcoxensis* (Cushman and Ponton, 1932) (layer 25, Lys's collection, RGP 16337); 3. *Morozovella velascoensis* (Cushman, 1925) (layer 18, Lys's collection, RGP 16331); 4. *Morozovella conicotruncata* (Subbotina, 1947) (layer 17, Lys's collection, RGP 16329); 5. *Subbotina patagonica* (Todd and Kniker, 1952) (layer 23, Lys's collection, RGP 16335); 6. *Morozovella aequa* (Cushman and Renz, 1942) (layer 22, Lys's collection, RGP 16334); 7. *Morozovella acuta* (Toulmin, 1941) (layer 26, Lys's collection, RGP 16340); 8. *Morozovella quetra* (Bolli, 1957) (layer 19, Lys's collection, RGP 16332); 9. *Morozovella angulata* (White, 1928) (layer 13, extracted from RG 28273); 10. *Morozovella angulata* (layer 12c, MNHN.F.ML105.1, figured by Lys et al., 1979: Planche III; Fig. 5); 11. *Igorina albeari* (Cushman and Bermudez, 1949) (layer 2, extracted from RG 28249); 12. *Morozovella apanthesma* (Loeblich and Tappan, 1957) (layer 12i, extracted from RG 28272); 13. *Acarinina wilcoxensis* (Cushman and Ponton, 1932) (layer 18, Lys's collection, RGP 16331); 14. *Acarinina nitida* (Martin, 1943) (layer 15, extracted from RG 28272); 15. *Parasubbotina pseudobulloides* (Plummer, 1927) (layer 2, Lys's collection, RGP 16302); 16. *Subbotina triloculinoides* (Plummer, 1927) (layer 1, Lys's collection, RGP 16301); 17. *Parasubbotina variospira* (Belford, 1984) (layer 7, Lys's collection, RGP 16312); 18. *Parvularugoglobigerina alabamensis* (Liu and Olsson, 1992) (layer 7, Meijer's collection, DV 5332); 19. *Globoconusa daubjergensis* (Bronnimann, 1953) (layer 2, Lys's collection, RGP 16305).

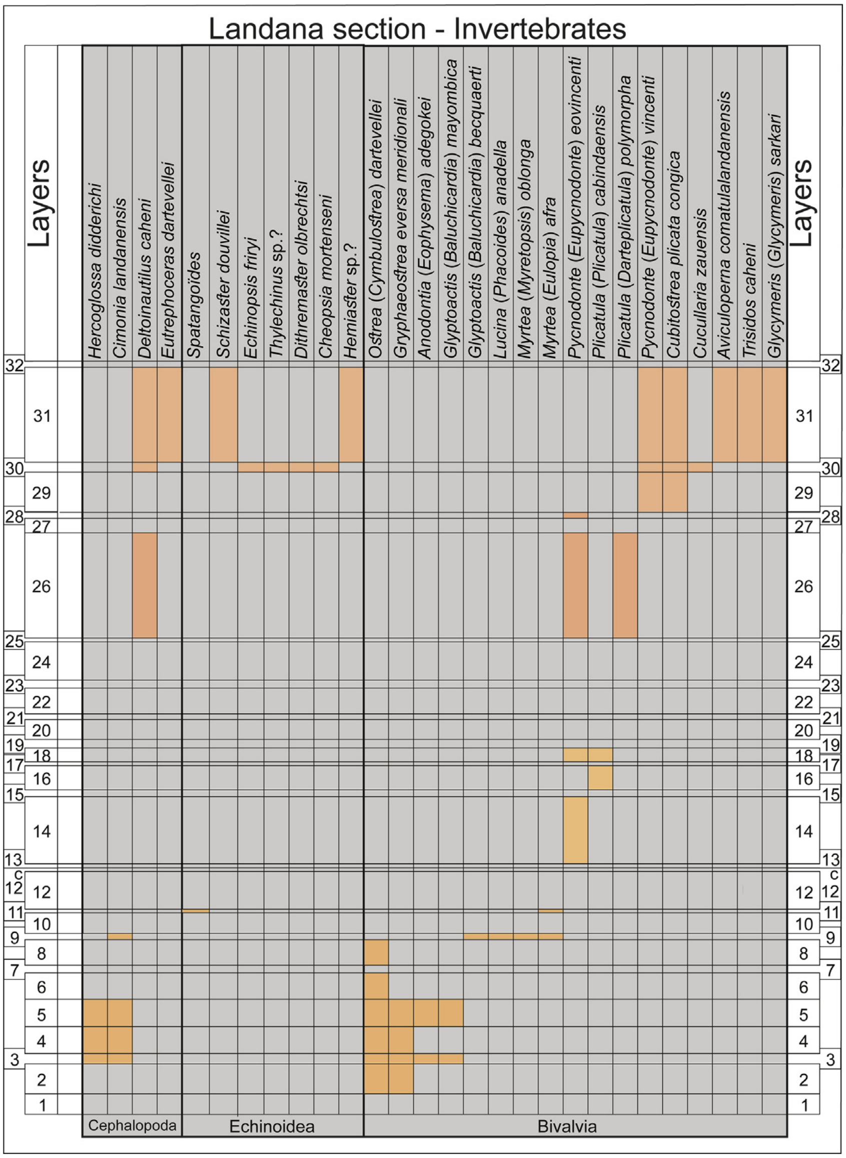

Figure 6. Stratigraphic distribution of the invertebrates recorded in the section of Landana. Orange shades indicate the presence of the taxon. Remark: Dartevelle (1952, 1953) did not provide precise information concerning the stratigraphic distribution of the echinoids he found, hence data presented here are based on the RMCA catalog.

(1973) indicated that this turtle ranges up to layer 18, nevertheless this information is not supported by the catalog of the RMCA.

Wood (1973) hypothesized the presence of a possible toxochelyid based on a partial carapace and a mandible found in layers 4 and 12, respectively. Gaffney et al. (2006) suggested that the lower jaw (layer 12) actually belongs to *T. congolensis*. Recently, Myers et al. (2017) described a cheloniid skull discovered in Landana in 2012. They erected a new durophagous pan-cheloniid species *Cabindachelys landanensis*, to which they refer the partial carapace described by Wood (1973). This allows to consider that this species is at least present in layer 4.

Myers et al. (2017) also described a turtle humerus collected differing from humeri of chelonioids and *Taphrosphys*, thus indicating the presence of a third turtle taxon at Landana. Its stratigraphic position is uncertain regarding the layer designation defined by Dartevelle and Casier (1943), but it probably came from the base of the section (≈layers 4–8; Selandian).

Turtle remains are as yet unknown or undescribed in Manzadi and Bololo sections.

4.5.5. *Crocodyliformes*

The only crocodyliform ever described from the Paleogene of western central Africa is the dyrosaurid *Congosaurus bequaerti* from the Landana section (Fig. 7). It is represented by numerous specimens including an almost complete skeleton (Dollo, 1912; Swinton, 1950; Jouve and Schwarz, 2004). Several unidentified isolated remains of crocodyliforms are present along the Landana section but the occurrence of *C. bequaerti* is confirmed only in layer 8 (Selandian). Crocodyliform remains are unknown in Manzadi and Bololo sections.

5. Discussion

5.1. *Integrated bio-chemostratigraphy of the Landana section: new age calibration of the Landana section*

Interpretations of the isotopic record magnitude and long-term profile can be biased by major modifications in sedimentation rates. Therefore, the consistent updated planktonic biostratigraphy of the

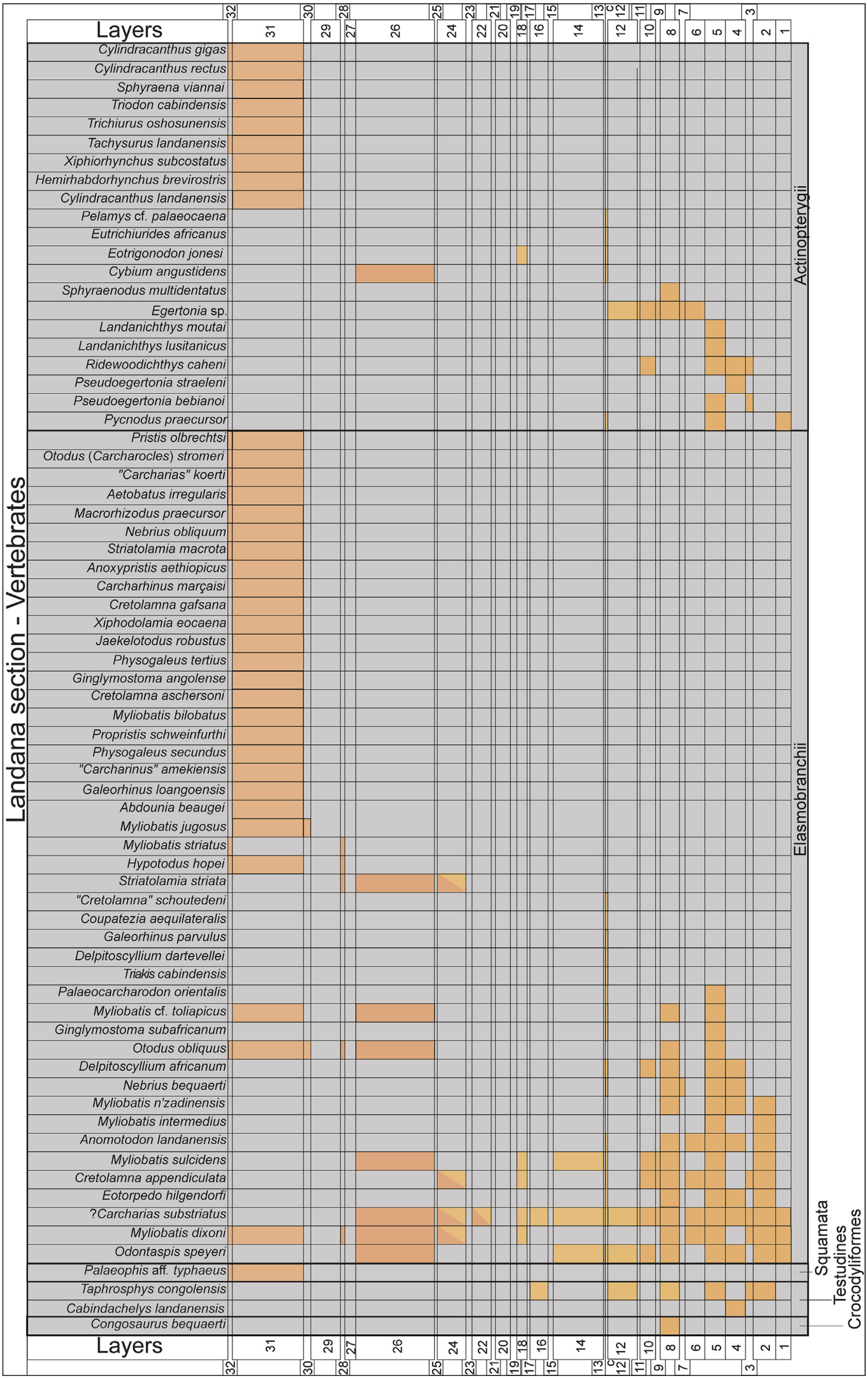

Figure 7. Stratigraphic distribution of vertebrates recorded in the Landana section. Orange shades indicate presence of a taxon.

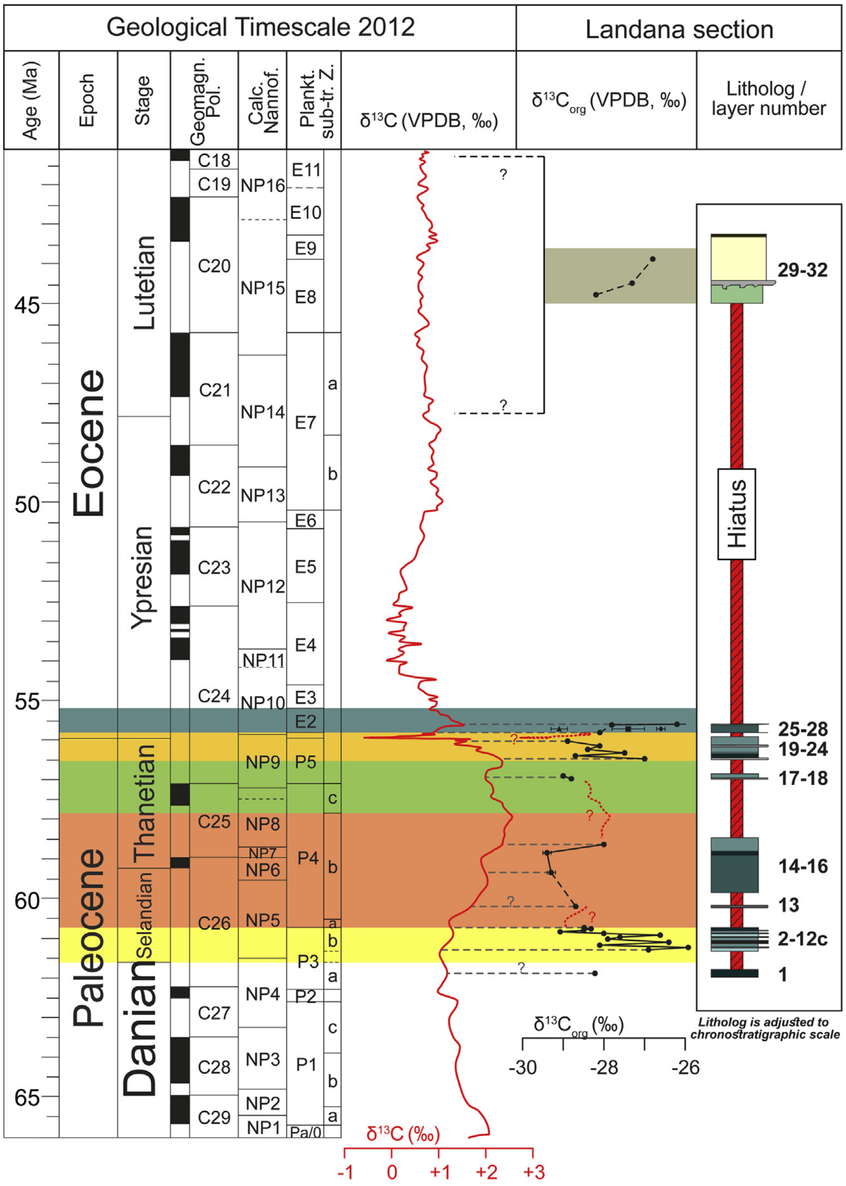

Figure 8. Correlation of the organic carbon ($\delta^{13}C_{org}$) isotope curve of the Landana section (this study) with the standard marine composite bulk carbonate ($\delta^{13}C_{carb}$) isotope curve of the Ypresian (Vandenberghe et al., 2012) and with the calcareous nannofossil and planktonic sub-tropical zones (this study).

Landana section, as well as the invertebrate and vertebrate faunas, provided strong reference tie-points for $\delta^{13}C_{org}$ calibrations to the standard $\delta^{13}C$ record.

The $\delta^{13}C_{org}$ record of the Landana section (Fig. 8) highlights some fractioned part of the well-known secular $\delta^{13}C$ patterns during the Paleocene and early Eocene interval, as previously reported for many years in "high-resolution" records (e.g., Stott et al., 1996; Zachos et al., 2001; Giusberti et al., 2007; Galeotti et al., 2010; Zachos et al., 2010; Westerhold et al., 2011; Coccioni et al., 2012; Vandenberghe et al., 2012; Galeotti et al., 2017).

Our succession starts in the Danian, characterized by a long-term $\delta^{13}C$ negative trend up to isotopic minima values around the Danian–Selandian transition. Layer 1 cannot be attributed to a specific planktonic foraminiferal zone. The four vertebrate taxa recorded in layer 1 are found in other layers (for instance, *M. dixoni* is known until layer 32); they thus do not differentiate the fauna of layer 1 from faunas recorded in the other parts of the section. We make the assumption that layer 1 is probably connected to the upper Danian (P3a?). Evidence in favor of this interpretation includes: (1) dinoflagellate cyst observations suggesting a Danian age (unpublished data) and (2) punctual isotopic value (−28.2‰, Table 2) of this layer 1 is somewhat lighter than overlying isotopic values (average $\delta^{13}C_{org}$ for layers 2–9 = −27.3‰). Heavier isotopic values would be subjected to a lower position in the isotopic record as highlighted in the standard isotopic curve (Fig. 8).

The bottom part of the Landana section (layers 2–12c) reveals a foraminiferal assemblage of the P3b Zone, that corresponds to the early Selandian (Schmitz et al., 2011). Although isotopic value fluctuations of ~2‰ between layers 2 and 9, the $\delta^{13}C_{org}$ record of the Landana section in this interval is relatively constant with an average $\delta^{13}C_{org}$ of −27.3‰. Layers 10–12c tend to indicate a ~1‰ shift towards lighter values (−28.7‰).

Collectively, layers 2–12c record several endemic elasmobranchs (e.g., *Myliobatis intermedius*, *Anomotodon landanensis*), limiting their use for lateral correlations. These layers include several elasmobranchs usually recorded in Danian African faunas:

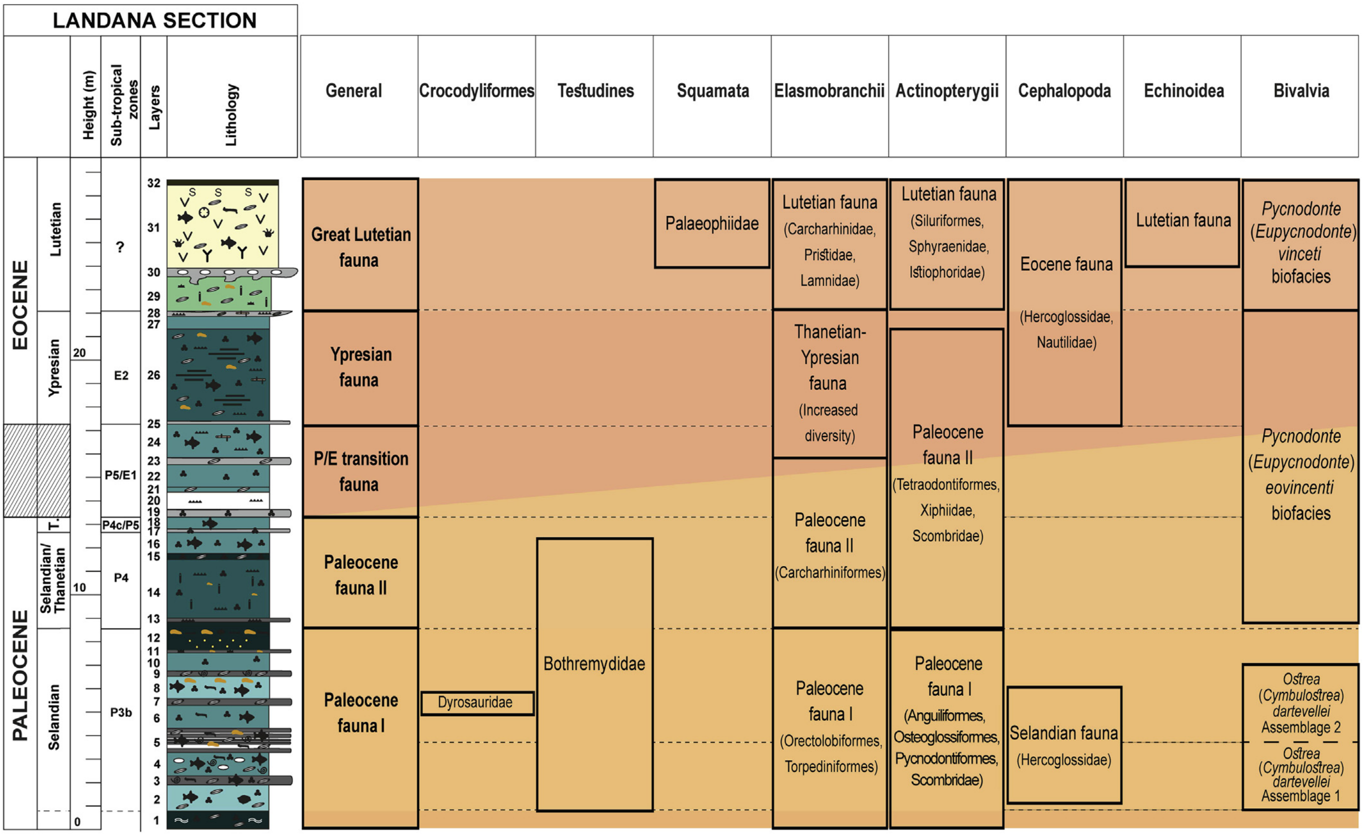

Figure 9. Faunal successions established for invertebrates and vertebrates recorded in the Landana section. Abbreviation: T. = Thanetian.

the ginglymostomatid *G. subafricanum*, triakid *Galeorhinus parvulus*, and the myliobatid *Myliobatis n'zadinensis*; *G. subafricanum* is notably recorded only in the Danian of the phosphates of Morocco (Arambourg, 1952; Noubhani and Cappetta, 1997). Other species in layers 2–12c are generally recorded throughout the Paleocene in Africa (e.g., *Delpitoscyllium africanum*, *Palaeocharcharodon orientalis*). Few taxa are even recorded in Ypresian (e.g., *C. appendiculata*, *Otodus obliquus*, *M. sulcidens*). More generally, most vertebrates recorded in layers 2–12c are generally characteristic of Paleocene faunas and do not specify a precise age for these layers, with the exception of the three elasmobranchs more typical of Danian faunas (see above). It is thus difficult to infer a Selandian age based only on the vertebrate fauna.

Layers 13–16 show a different planktonic assemblage than the interval between layers 2 and 12c and can be referred to the P4 Zone spanning ~2.5 Ma from the middle Selandian to the middle Thanetian. The standard isotopic record for this interval is characterized by a gradual long-term shift toward lighter δ^{13}C values. Isotopic data for this interval struggle to highlight a strong correlation with standard isotopic records. Nevertheless, the light $\delta^{13}C_{org}$ values of the layers 14 and 15 (−29.3‰ and −29.4‰) are followed up by heavier value (layer 16, −28.0‰) and are thus probably linked to the very late Selandian–early Thanetian. As a consequence, despite the long duration of the P4 Zone and the lack of samples for this time interval, we tentatively correlate these layers to the middle P4b (=late Selandian–early Thanetian) (Fig. 8). The vertebrate and invertebrate faunas fossilized in layers 13–16 do not provide conclusive evidence to support or refute either a Selandian or a Thanetian age inferred based on the foraminiferal assemblages.

Based on the foraminiferal assemblages, layers 17–18 are enclosed within the P4c/P5 Zone (middle-latest Thanetian). The long-term negative δ^{13}C trend (Fig. 8; Vandenberghe et al., 2012) beginning in the middle Thanetian (~chron C25n; P4b/P4c zones) up to the isotopic minimum values of the early-middle Ypresian (~C24n; E4 biozone; Fig. 8) directly follows the isotopic positive trend of the Selandian/early Thanetian (layers 14–16 in the Landana section) (Fig. 8).

Between layers 19 and 24, the $\delta^{13}C_{org}$ record shifts towards lighter values (−27.0‰ to −28.9‰) (Fig. 8). The foraminiferal assemblages indicate P5 or E1 Zone (Paleocene/Eocene transition). The Paleocene–Eocene isotopic event (PETM-CIE) characterizing the stage boundary is not observed in the succession of Landana. Two hypotheses can be proposed to explain this: (1) the PETM-CIE could be recorded in the sediments between layers 19 and 24 or above, but sampling resolution is inadequate to observe it; (2) the PETM-CIE is not recorded in the section and occurs within multiple hiatuses between layers 19 and 24 or above. The second hypothesis is more likely because (1) the Landana section exhibits multiple extended hiatuses and (2) the probability of recording such a brief event (~200 ka; e.g., McInerney and Wing, 2011) in an extended section is very small. Consequently, the rapid isotopic shift between layers 19 and 24 corresponds to the negative long-term isotopic trend initiated in the middle Thanetian close to the C25r/C25n chron reversal (e.g., Schmitz et al., 2011) and not to the PETM-CIE.

Ichthyofauna does not constrain definitive dating for the layers 19–24, hence this fauna offers no greater refinement from ages inferred using foraminiferal assemblages (P5 to E1 Zone; ≈Paleocene/Eocene transition; Fig. 3).

Foraminiferal assemblages between layers 25 and 28 indicate the E2 Zone, attributed to the post-CIE recovery and just at the initiation of the standard long-term δ^{13}C negative trend that peaks to minimum values in the early–middle Ypresian (Fig. 8).

Table 3
Qualitative assessment of the palynomorphs recovered from the Bololo and Manzadi sections. Dino = Dinoflagellate cyst; Acrit. = Acritarchs; Frag. = Fragments; Rem. = Remains; AOM = Amorphous Organic Matter; Conta. = Contamination; Com. = Comments.

	Sample#	Section	Dino. & Acrit.	Pollen & Spores	Fungal Spores	Plant Frag.	Animal Rem.	AOM	Conta.	Com.
2014 Expedition	B-M-1	Bololo		x	x	x	x	x	x	
	B-M-2	Bololo		x	x	x	x	x	x	
	B-M-3	Bololo		x	x	x	x	x	x	
	B-M-3 (1)	Bololo		x	x	x	x	x	x	
	B-M-4	Bololo	x	x	x	x	x	x	x	1 specimen of *Glaphyrocysta* sp. A; 1 dinoflagellate spp.
	B-M-5	Bololo	x	x	x	x	x	x	x	2 specimens of *Muratodinium*? sp. A
	M-K-1	Manzadi		x	x	x	x	x	x	
	M-K-2	Manzadi		x	x	x	x	x	x	
	M-K-3	Manzadi		x	x	x	x	x	x	
	M-K-4 (1)	Manzadi		x	x	x	x	x	x	
	M-K-4(s)	Manzadi								not fertile
1933 Dartevelle Expedition	P4C1/27,498	Bololo		x	x	x	x	x	x	
	P4C4/27,506	Bololo				x		x	?	barely fertile
	P4C2/27,447	Manzadi		x	x	x	x	x	x	
	P4C4/27,448	Manzadi		x	x	x	x	x	x	
	P4C6/27,450	Manzadi		x	x	x	x	x	x	
	P4C11/27,455	Manzadi		x	x	x	x	x	x	
	P4C13/27,457	Manzadi		x	x	x	x	x	x	
	P4C17/27,461	Manzadi								not fertile
	P4C22/27,464	Manzadi		x	x	x	x	x	x	
	P6C1/27,429	Manzadi		x	x	x	x	x	x	
	P6C2/27,432	Manzadi			x	x		x	?	barely fertile
	P6C6/27,439	Manzadi				x		x	?	barely fertile

Layer 26 has three distinct samples (LAND28287, LAND28288 and LAND28290) with three $\delta^{13}C_{org}$ respective average values of −29.1‰, −27.4‰ and −26.6‰ (Fig. 8; Table 2). No indication of the respective stratigraphic position of the samples within layer 26 were recorded by Dartevelle during his sampling. Freneix (1979), in her study on bivalves from the Landana section, described the anomalous presence of a unique valve of *Plicatula* (*Darteplicatula*) *polymorpha* Bellardi in layer 26. She formulated the hypothesis that this specimen was secondarily deposited in layer 26; it could have come, due to erosion, from deposits higher in the geological section. As previously suggested by Dartevelle and Casier (1943, p.59): « *La couche 26 […] profondément ravinée par des dépôts plus récents.* » (« *The layer 26 […] deeply incised by recent deposits* »). Gully erosion and reworking of fossils from the top of the section may explain the high variability of isotopic values of the 3 samples in layer 26.

The elasmobranch fauna of layers 25–28 corresponds to a mix between taxa recorded from the Paleocene and Ypresian (e.g., *S. striata*, *Otodus obliquus*, *M. sulcidens*) and taxa generally first recorded in the Ypresian (e.g., *Striatolamia macrota*, *Myliobatis striatus*) (Fig. 8). Therefore, the elasmobranch fauna agrees well with the updated planktonic biostratigraphy (i.e., biozone E2; Fig. 3).

Dartevelle and Casier (1959) hypothesized that the fauna in layer 29 was most congruent with layers 27 and 28, not with layers 30 and 31. We interpret the bivalve fauna first recorded in layer 29 (Freneix, 1979) to reflect a profound modification in the aquatic fauna, suggesting that layers 29, 30 and 31 represent a common temporal block. The three uppermost layers of the Landana section studied here (layers 29–31) are clearly distinctive from a sedimentological perspective, relative to the rest of the section (Fig. 8). No foraminifers were found in layer 29 (bioclastic mudstone) nor in layers 30 and 31 (indurated dolomicrosparite) (Fig. 3). Isotopic data (three samples) are insufficient to yield a consistent isotopic trend. The record of the odontaspidid “*Carcharias*” *koerti* (layer 31; Fig. 7), known only from Lutetian, including in phosphates of Morocco, supports a Lutetian age for this part of the section. Moreover, the presence of endemic carcharhinids *Carcharhinus amekiensis* and Moroccan *Carcharhinus marçaisi* also agrees with this hypothesis, considering that first representatives of *Carcharhinus* are currently dated to Lutetian (e.g. Kriwet, 2005; Cappetta, 2012). Consequently, a Lutetian age for these peculiar layers is supported by the ichthyofauna. Moreover, the bivalve assemblage recorded in these layers suggests a Lutetian age (Freneix, 1979). Therefore, we hypothesize an important hiatus (∼7–14 Ma?) in the section between layers 28 and 29. If true, almost the entire Ypresian stage is likely missing from the Landana section.

As a consequence of the new analyses, the fossil record of the Landana section appears to be more fragmented than predicted and spans a very long time interval, estimated at ∼14–20 Ma (Selandian–Lutetian), including six hiatuses (Fig. 8). The possible depositional hiatuses occurred between layers 1 and 2, layers 12c and 13, layers 16 and 17, layers 18 and 19, layers 24 and 25, and layers 28 and 29 (Fig. 8). It is worth keeping in mind that we interpreted only several spot samples. Moreover, we have no idea precisely where in the layer the analyzed samples come from. Therefore, we have no clue if the analyzed samples are representative for the entirety of the layer. As a consequence, there is a chance that the missing time periods are simply contained in the un-sampled portions.

The new results presented here, as with those provided by Lys et al. (1979), significantly differ from the preliminary ages proposed by Dartevelle and Casier (1959) in that the importance of the early Paleocene in the section (hypothesized as extending from layer 1 to layer 26) appears to have been overestimated in those earlier interpretations (Fig. 3; Table 4).

Moreover, as previously mentioned, the foraminiferal assemblages suggest that layers 2–12c correspond to the Selandian rather than exclusively to the Danian (Figs. 3 and 6) – this result partially agrees with that of Lys et al. (1979) (layers 6–12). Consequently, the record of the Danian is very short or absent in the Landana section; perhaps corresponding only to layer 1.

Table 4
Comparison of the age of the layers of the Landana section proposed by Dartevelle and Casier (1959), Lys et al. (1979), and this study.

Layers	Dartevelle and Casier (1959)	Lys et al. (1979)	This study
31	Lutetian	Not studied	Lutetian
30			
29	Landenian (late Paleocene)		
28		early Eocene	Ypresian
27			
26	Montian (early Paleocene)		
25			
24			Thanetian/Ypresian transition
23			
22			
21			
20			
19			
18			Thanetian
17		late Paleocene	
16			
15			
14			
13			
12c		middle Paleocene	Selandian
12			
11			
10			
9			
8			
7			
6			
5		early Paleocene	
4			
3			
2			
1			Danian?

This very weak record of Danian deposition at Landana is one of the primary results of the present study and it refines the age of numerous macrofossil records discovered throughout the locality.

A late Paleocene age (=Thanetian) as proposed by Lys et al. (1979) for layers 13–17 is potentially supported for the layers 14–16 by our new data. However, it is worth keeping in mind that the foraminiferal assemblages recorded from layer 13 to layer 16 correspond to P4 Zone, a zone that spans ~2.5 Ma from the middle Selandian to the middle Thanetian (Fig. 3).

Our results suggest that layers 19–24 were deposited around the Paleocene/Eocene boundary. However, Lys et al. (1979) interpreted layers 18–24 as reflecting Ypresian deposition. Our data suggest that these layers were instead deposited around the Paleocene/Eocene boundary and thus are not considered to be Ypresian here (Figs. 3 and 6). We do, however, interpret layers 25–28 as Ypresian in age (Figs. 3 and 6).

Dartevelle and Casier (1959) considered layers 31 and 32 as Lutetian, whereas Freneix (1979) considered layers 29, 30, and 31 as Lutetian (Table 4). A Lutetian age for layers 29–32 is based on vertebrate and invertebrate records (see above) as these layers contain no foraminifers and $\delta^{13}C$ record is not sufficient. Layer 32 is a chert bed which probably records a regional discontinuity and might correspond to a major Lutetian denudation event in the Congo Basin (De Putter et al., 2016). Hence, the age determination for any Lutetian intervals recorded in Landana remains unresolved (Fig. 8).

5.2. Characterization of the Landana faunas

The Landana deposits record a rich invertebrate and vertebrate fauna, and this richness (Tables 1 and 5), combined with the long fossil record (Selandian to Lutetian), establishes several faunal successions (Fig. 9).

Fauna in layers 1–5 (Paleocene fauna I on Fig. 9) exhibit broad species richness: 2 turtles, 15 elasmobranchs, 7 actinopterygians, 2 cephalopods and 4 bivalves are recorded in these levels. This level of taxonomic richness is only found in the peculiar layer 12c and in the Lutetian (Fig. 10).

The case of *G. subafricanum*, *G. parvulus*, and *Myliobatis n'zadinensis* is interesting because these taxa are present in Selandian sediments at Landana, while they are considered to be restricted to Danian in the other fossiliferous localities. Perhaps these elasmobranch fossils were reworked in the Selandian deposits. Alternatively, these species may have survived until the Selandian in western central Africa. In any case, this discrepancy highlights the need for a closer examination of elasmobranchs from the Landana section.

A small decrease in faunal richness occurs between layers 5 and 6 (i.e., during the Selandian) (Figs. 7 and 8; Table 5). This is characterized by numerous disappearances (especially among actinopterygians), and just one appearance (*Egertonia* in layer 6). Despite several new appearances (Table 5), the fauna that ranges from layer 6 to layer 12 is generally less speciose than the first five layers (Fig. 10). However, it is worth noting that taxa recorded from layer 6 to layer 12 are globally similar to those in lower layers of the section (i.e., layers 1–5).

Layer 12c is unusual, as noted by previous authors (Bequaert, 1920; Dartevelle and Casier, 1943) due to (1) the facies structure (i.e., abundance of coprolites): and (2) the abundance of vertebrates it contains. For instance, five elasmobranchs are known only from this layer (Table 5), notably including the sole occurrence of the superfamily Dasyatoidea at Landana. Also recorded are the first occurrences of the Carcharhiniformes (ground sharks), Tetraodontiformes (puffer fishes), Xiphiidae, and Trichiuridae. The vertebrate record thus suggests an increase in faunal richness at Landana during deposition of layer 12c. Further understanding of this faunal transition requires deeper sedimentologic and paleoenvironmental analyses.

The disappearance of several elasmobranchs, and more generally of the Torpediniformes (sawfishes), Pycnodontiformes, and Scombridae occurs between layer 12c and layer 13 (Table 5). Moreover, a new bivalve assemblage – *Pycnodonte* (*Eupycnodonte*) *eovicenti* assemblage – is recorded in layers 14 (late Selandian–early Thanetian) to 28 (Ypresian) (Fig. 7; Table 5).

A decrease in faunal richness is reflected in layers 13–18 (Paleocene fauna II on Fig. 9; Fig. 10). Only the turtle *Taphrosphys* (unknown after layer 17), five elasmobranchs, and one actinopterygian are recorded in layers 13–18. Surprisingly, only one of the new actinopterygians that are first observed in layer 12c – *E. jonesi* (Tetraodontiformes) – is recorded in these layers.

The numerous disappearances, together with a new bivalve fauna, reinforce the impression of a faunal shift at Landana between layer 12c and layer 13 (i.e., during the Selandian). This could represent bias due to the large depositional hiatus present between these two layers (Fig. 8). Future analyses of this turnover should take into account faunal modification together with environmental information recorded in layer 12c.

Fauna recorded in layers 19–24 (P/E transition fauna on Fig. 9) are even less rich than in layers 13–18 (Fig. 10), with only four elasmobranchs recorded. Invertebrate and vertebrate faunal composition is largely similar to that of underlying layers. Only layer 24 differs in recording (1) the last occurrence of *C. appendiculata*, a cretoxyrhinid (mackerel sharks) recorded since layer 2 in Landana, and (2) the appearance of *S. striata* – marking the beginning of an increase in faunal richness that culminates in the Lutetian (Fig. 10).

Table 5
Pertinent data used for reconstructing the faunal successions in Landana section.

Layers	-	Cephalopods	Elasmobranchs	Actinopterygians	Squamates	Events
Between layers 5 and 6	Decrease in diversity	Disappearance of several cephalopods	Disappearance of *Myliobatis intermedius*	Disappearance of two scombrid (*Landanichtys moutai* and *L. lusitanicus*) and two anguilliform (*Pseudoegertonia straeleni* and *P. bebianoi*) species Appearance of *Egertonia*	-	Decrease of the faunal diversity
Layer 8	-	-	-	Appearance of *Sphyraenodus*	Occurrence of *Congosaurus*	-
Layer 9	Diversification of the bivalve fauna	Brief reappearance of *Cimomia landanensis*	-	-	-	-
Layer 12c	-	-	Five elasmobranchs are known only from this layer: *Coupatezia aequilateralis*, "*Cretolamna*"*schoutedeni*, *Triakis cabindensis Galeorhinus parvulus*, and *Delpitoscyllium dartevellei* Unique occurrence of Dasyatoidea Appearance of Carcharhiniformes (ground sharks)	Appearance of four species Appearance of Tetraodontiformes (puffer fishes), Xiphiidae, and Trichiuridae	-	Increase of the faunal diversity
Between layers 12c and 13	-	-	Disappearance of *Palaeocarcharodon orientalis*, *Anomotodon landenensis*, *Ginglymostoma subafricanum*, and *Nebrius bequaerti* Disappearance of Torpediniformes	Disappearance of Pycnodontiformes and Scombridae	-	Faunal shift? Decrease of the faunal diversity
Layer 14	Occurrence of two new bivalves: *Pycnodonte* (*Eupycnodonte*) *eovicenti* and *Plicatula* (*Plicatula*) *cabindaensis*.	-	-	-	-	
Layer 17	-	-	-	-	Disappearance of *Taphrosphys*	Decrease in diversity
Layer 19	-	-	-	Disappearance of *Eotrigonodon jonesi*	-	Decrease in diversity
Layer 24	-	-	Appearance of the *Striatolamia striata*	-	-	Beginning of the increase of the faunal diversity
Between layers 24 and 25	-	-	Disappearance of *Cretolamna appendiculata*	-	-	-
Layers 25 to 28	Appearance of *Plicatula* (*Darteplicatula*) *polymorpha*	Appearance of cephalopod *Deltoidonautilus*	Appearance of *Striatolamia macrota* and *Myliobatis striatus*	-	-	Increase of the faunal diversity
Between layers 26/28 and 29/31	New bivalve fauna	Appearance of the nautilid *Eutrephoceras*	Disappearance of *Striatolamia striata*, *Myliobatis sulcidens*, ?*Carcharias substriatus* and *Odontaspis speyeri* Appearances of 24 species Appearance of the Carcharhinidae (requiem sharks) Lamnidae (*Macrorhizodus*), and Pristidae (sawfishes)	Disappearance of *Cymbium angustidens* Appearances of nine species Appearance of the Siluriformes, Istiophoridae, and Sphyraenidae	First appearance of *Palaeophis*	Faunal shift

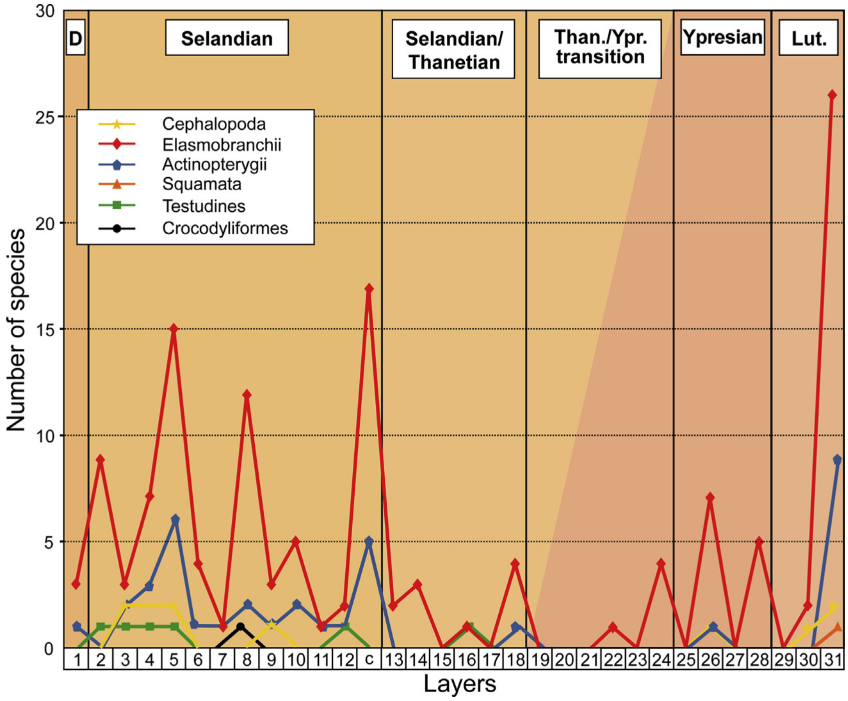

Figure 10. Richness of the Cephalopoda, Elasmobranchii, Actininopterygii, Squamata, Testudines, and Crocodyliformes throughout the Landana section. Abbreviation: D. = Danian.

Faunal richness in layers 25–28 (Ypresian fauna on Fig. 9) is distinctly higher than in the underlying layers 13–24 (Fig. 10). This is notably characterized by the reappearance of cephalopods (in layer 26) (Fig. 6; Table 5). As the majority of taxa recorded in these layers appear to continue in distribution from underlying layers, the icthyofauna seems not to have been profoundly affected by the PETM event. This agrees with the previous study of Noubhani (2010) and Tomczik (2014) who noted little change through the PETM in ichthyofauna of the Pacific, tropical Atlantic, and phosphates of Morocco.

Several disappearances occurred between the Ypresian and Lutetian periods: four elasmobranchs and one actinopterygian known in Ypresian sediments are absent from the Lutetian sediments (Fig. 7; Table 5). In contrast, numerous taxa are first recorded in layer 31 (Lamnidae, Carcharhinidae, Pristidae, Istiophoridae, Siluriformes, Sphyraenidae, new bivalve assemblage). As a result, fauna in layers 29–32 (Great Lutetian fauna on Fig. 9) are almost entirely different from those in underlying layers (Figs. 5 and 7). Indeed, among the 27 elasmobranchs described from layers 29–32, only four are known from lower layers. A relatively high richness of the echinoids (six taxa) is also notable (Fig. 6). Significant differences observed between the Ypresian and Lutetian faunas may reflect an important faunal turnover.

To summarize, the layers 2–12c (Selandian) represent the richest Paleocene section at Landana, illustrated by the presence of elasmobranchs, actinopterygians, cephalopods, bivalves, the crocodyliform *Congosaurus*, and testudines *Taphrosphys* and *Cabindachelys* (Fig. 10). An important decrease in overall richness begins in layers 13 (Selandian). As a consequence, a small faunal shift is suggested, but this requires further documentation. Moreover, if the layers 13–18 appear to be Selandian in age, it would imply that this faunal shift occurred during the Selandian. This decrease is accentuated during the Thanetian-Ypresian transition (layers 19–24) (Fig. 10). Richness increases during the latter portion of the Ypresian recorded in Landana (layers 25–28) (Fig. 10). Finally, the Lutetian records a complete renewal of the fauna with a number of species equal to that recorded in the Selandian layers (Fig. 10).

5.3. Landana as a reference section for Central Africa: comparison with the fauna from Bololo and Manzadi sections

Refining the age and faunal characterization of the Landana section is useful in interpreting the age of other fossiliferous sections in Central Africa. Here we compare the fauna of Landana with those of Bololo and Manzadi. Manzadi and Bololo localities are composed of different smaller sections (=*Point*).

Concerning Manzadi, we here discuss only *Points* IV and VI of those explored in this area (Dartevelle and Casier, 1943) as they provide the richests faunas.

The vertebrate fauna is similar in the four layers recognized at *Point* IV; only the occurrence of *Serratolamna serrata* at the top of the section suggests faunal distinctiveness from deposits at the base. The elasmobranch (presence of three families unknown in the Landana section) and actionopterygian (presence of Aulopiformes, Elopiformes, and *Congorhynchus*) faunas from this *Point* are clearly distinctive from those recorded anywhere in the Landana section (Table 6). The same argument can be made for the molluscs (Dartevelle and Freneix, 1957) (Table 6).

As numerous taxa are restricted and/or abundant in the Maastrichtian (Table 6), we interpret *Point* IV as Mesozoic in age; a Maastrichtian age for this *Point* is further supported by the presence of mosasaurs (Lingham-Soliar, 1994). However, four taxa that are generally found in Cenozoic sections of Landana are also present in *Point* IV: the myliobatid *Myliobatis n'zadinensis*, the odontaspidid *O. speyeri*, the anguilliforms *Pseudogertonia*, and the pycnodontiform *P. praecursor*. These taxa were perhaps present in the Maastrichtian of Central Africa, although a definitive conclusion requires a systematic revision of these taxa.

The *Point* VI locality at Manzadi lacks the Maastrichtian elasmobranch and actinopterygian taxa that support a Maastrichtian age for *Point* IV (e.g., Anacoracidae, Sclerorhynchidae, Alepisauriformes). The majority of elasmobranchs from *Point* VI, as well as the sole actinopterygian found at this *Point*, *Pseudogertonia bebianoi*, are generally found in Landana sections (Table 7).

Table 6
Information concerning the fauna from Manzadi *Point* IV and inferred age for this locality. Invertebrate and vertebrate taxa are listed in Supplementary material 2.

Taxa		Landana	Remarks	Inferred age
Elasmobranchs	Anacoracidae (*Squalicorax*)	unknown in Landana	Species known from Santonian to Maastrichtian	Santonian-Maastrichtian
	Serratolamnidae (*Serratolamna*)	unknown in Landana	Species only known in Maastrichtian	Maastrichtian
	Sclerorhynchidae (*Schizorhiza, Ctenopristis*)	unknown in Landana	Species only known in Maastrichtian	Maastrichtian
	Myliobatis n'zadinensis	Layers 2–8	-	Already present in Maastrichtian? or misidentification?
	Odontaspis speyeri	Layers 1–26	-	Already present in Maastrichtian? or misidentification?
Actinopterygians	Alepisauriformes	unknown in Landana	Abundant in Maastrichtian	Maastrichtian?
	Elopiformes	unknown in Landana	Abundant in Maastrichtian	Maastrichtian?
	Congorhynchus	unknown in Landana	Maastrichtian-Paleogene	Maastrichtian?
	Pseudogertonia bebianoi	Layers 3–5	-	Already present in Maastrichtian? or misidentification?
	Pycnodus praecursor	Layers 1–12c	-	Already present in Maastrichtian? or misidentification?
	Cimolichthys manzadiensis	unknown in Landana	Restricted to the Mesozoic	Mesozoic
	Stratodus apicalis	unknown in Landana	Restricted to the Mesozoic	Mesozoic
Molluscs	Entire fauna	unknown in Landana	Maastrichtian in age (Dartevelle and Freneix, 1957)	Maastrichtian

Point VI is hence interpreted as Cenozoic in age. Dartevelle and Casier (1959) proposed a Paleocene age for this locality. A Selandian age is, in our point of view the most plausible hypothesis based on the combination of elasmobranch taxa recovered. However, we refrain from placing a precise age on this locality as the fauna includes some taxa known elsewhere from the Selandian (e.g., *Myliobatis n'zadinensis*) through the Lutetian (e.g., *Rhinoptera raeburni*) (Table 7). A reworking of Paleocene fossils is possible, but it cannot be tested with available evidence. To conclude, the differences observed between *Points* IV and VI at Manzadi implies that Manzadi localities preserves fossils found elsewhere from least two distinct time periods.

The Bololo area also includes different localities with *Point* I revealing the most vertebrate taxa (Dartevelle and Casier, 1943, 1959). Among the 26 elasmobranchs recovered in Bololo, only 10 are known from the Landana section. Most of the 10 taxa – except *Otodus obliquus* and *M. dixoni* that have a wide stratigraphic distribution – are known only in the Lutetian segment of the Landana section (layers 29–31) (Table 8). Interestingly, elasmobranchs from Bololo include the first appearance of the Alopiidae and Hemigaleidae, and a broad sample of the Carcharhinidae These taxa are not recorded from Landana and are typically characteristic of Miocene faunas. Most of the actinopterygians from Bololo are found in the Lutetian part of the Landana section (e.g., Xiphiidae); only the trichiurid *L. castellobrancoi* is unknown from the Landana section. The bivalves known from Bololo are found in deposits interpreted as Lutetian at Landana (Table 8).

In their study of the fossil fishes from Congo and Angola, Dartevelle and Casier (1959) noted that Bololo fauna correspond to a mix of Eocene and Miocene fossils known from elsewhere, suggesting that the Eocene taxa had been reworked into later deposits. Our analyses of the Landana section support that notion, and we agree that 10 of the taxa could be interpreted to reflect a Lutetian age fauna that has been reworked. Alternatively, Bololo might represent transitional fauna capturing the latest occurrences of Paleogene taxa and the earliest occurrences of fauna more common in the early Neogene.

Point II and *Point* III also suggest a mix of elasmobranchs typically seen in the Lutetian and Miocene (based on the presence of the Miocene species *Galeocerdo aduncus* and *Hemipristis serra*).

Point IV from Bololo, however, is unique in that it preserves elasmobranchs known only from Paleogene deposits in Landana (Table 9). Consequently, our observation agrees with that of Dartevelle and Casier (1959) that *Point* IV is clearly not Miocene. Among the six taxa that have been specifically determined, four are recorded only in the Lutetian part of the Landana section (Table 9), while the two other species are known from the Selandian to the Lutetian in Landana. These data indicate a possible Lutetian age, at least, for layers 3 and 4 of *Point* IV. The age of layer 2 is less certain as it only includes the long-living taxon *Otodus obliquus*.

Table 7
Information concerning the fauna from Manzadi *Point* VI and inferred age for this locality. Invertebrate and vertebrate taxa are listed in Supplementary material 2.

Taxa		Landana	Remarks	Inferred age
Elasmobranchs	*Delpitoscyllium africanum*	Layers 4–13	-	Paleocene
	Otodus obliquus	Layers 5–32	Long-living taxon in Landana	-
	Myliobatis dixoni	Layers 1–32	Long-living taxon in Landana	-
	Myliobatis n'zadinensi	Layers 2–8	-	Paleocene (Selandian)
	Odontaspis speyeri	Layers 1–26	Long-living taxon in Landana	-
	Rhinoptera raeburni	unknown in Landana	Lutetian	Lutetian
Actinopterygian	*Pseudogertonia bebianoi*	Layers 3–5	-	Paleocene (Selandian)

Table 8
Information concerning the fauna from Bololo *Point* I and inferred age for this locality. Invertebrate and vertebrate taxa are listed in Supplementary material 3.

Taxa		Landana	Remarks	Inferred age
Elasmobranchs	*Otodus obliquus*	Layers 5–32	Long-living taxon in Landana	(reworked?)
	Myliobatis dixoni	Layers 1–32	Long-living taxon in Landana	(reworked?)
	Carcharhinid *C. egertoni*, *G. aduncus*, and *G. mayumbensis*	unknown in Landana	Miocene taxa Broad diversification of the Carcharhinidae	Miocene
	Alopiidae (*Alopias latidens*, *A. subexigua*)	unknown in Landana	Species known in Oligocene and Miocene	Oligocene-Miocene
	Hemigaleidae (*Hemipristis serra*)	unknown in Landana	Species known in Oligocene and Miocene	Oligocene-Miocene
	Other elasmobranchs	Known in the Lutetian part of Landana section (layers 29–31)	-	Lutetian (reworked?)
Actinopterygians	Xiphiidae (*Cylindracanthus*)	Layers 31–32	Xiphiidae are abundant in the Lutetian of Landana	Lutetian (reworked?)
	Trichiurus oshosunensis (Trichiuridae)	Layer 31	-	Lutetian (reworked?)
	Lepidopus castellobrancoi (Trichiuridae)	Unknown in Landana	-	-
Bivalves	*Pycnodonte* (*Eupycnodonte*) cf. *vincenti*	*Pycnodonte* (*Eupycnodonte*). *vincenti*: Layers 29–31	-	Lutetian (reworked?)
	Cubitostrea plicata congica	Layers 29–31	-	Lutetian (reworked?)

Table 9
Information concerning the fauna from Bololo *Point* IV and inferred age for this locality. Invertebrate and vertebrate taxa are listed in Supplementary material 3.

Taxa		Landana	Remarks	Inferred age
Elasmobranchs	*Pristis olbrechti*	Layers 31–32	Lutetian	Lutetian
	Aetobatus irregularis	Layers 31–32	Lutetian	Lutetian
	Physogaleus tertius	Layer 31	Lutetian	Lutetian
	"*Carcharias koerti*"	Layers 31–32	Lutetian	Lutetian
	Myliobatis dixoni	Layers 1–32	Long-living taxon in Landana	-
	Otodus obliquus	Layers 5–32	Long-living taxon in Landana	-

As mentioned earlier, only three identifiable dinoflagellate cyst specimens (*Glaphyrocysta* sp. A and *Muratodinium*? sp. A) were recovered from all samples collected at Bololo. In-situ specimens of these particular taxa were recorded from layer 28 at Landana (Ypresian; unpublished data). Some fragmentary, potentially reworked, specimens were also recorded in layer 29 (Lutetian). The Point IV Bololo dinoflagellate cyst specimens, which are also relatively fragmentary, are therefore likely either in-situ Ypresian specimens, or similarly to as at Landana, reworked specimens in younger, likely Lutetian as suggested by the elasmobranch fossils, deposits.

To summarize, Bololo provides fossiliferous localities that contain taxa consistent with both Lutetian and Miocene age faunas. This may reflect a similar situation as that at Manzadi where two different periods (Maastrichtian and Selandian) have been recorded in closely situated sections. Alternatively, the pattern could reflect a transitional fauna deposited sometime between the Lutetian and Miocene.

5.4. *Comparison with the phosphate basins of Morocco*

The phosphates of Morocco range from the end of the Cretaceous (Maastrichtian) to the base of the middle Eocene (Lutetian); this is the longest interval of all phosphate deposits from the Mediterranean and Atlantic "Phosphogenic Provinces". These marine sediments record the evolution of northwestern African faunas and are characterized by their remarkable richness in fossil vertebrate remains, documenting a palaeobiodiversity "hot-spot" at the Cretaceous–Paleogene turnover (Bardet et al., 2017).

These phosphates are also interesting in light of intensive revisions to the vertebrate record (notably from the Oulad Abdoun, Ganntour, Meskala and Souss basins) over the last 20 years, making the area a reference for the evolution of the marine and terrestrial (notably mammals) vertebrates in North Africa. A recent comprehensive review of Moroccan phosphates by Bardet et al. (2017) permits comparisons with the deposits of Landana described herein.

The elasmobranch assemblages recovered from the phosphates of Morocco do not permit recognition of the Selandian. As a consequence, the elasmobranch fauna from the Selandian portion of the Landana section has no equivalent in Morocco. However, the Danian and Thanetian phosphorite levels in Morocco may include a portion of the Selandian, as carbon isotope chemostratigraphic analyses recently performed in the Ouled Abdoun phosphate Basin demonstrate that Bed IIa, including several mammalian fossils, could be Selandian–early Thanetian in age (Yans et al., 2014). Therefore, future biostratigraphic characterization of the Selandian based on selachian assemblages in the phosphate series could provide fruitful comparisons with the Landana section.

The elasmobranch faunas of Landana are clearly less rich than those of the Moroccan region; for instance, almost 250 elasmobranch species are described from the Moroccan hot-spot (Bardet et al., 2017), *versus* 45 species from the Landana section (Table 10). It is worth mentioning that the elasmobranch fauna recorded from the phosphates of Morocco has been revised since the initial works of Arambourg (1935, 1952) (e.g., Cappetta, 1981, 1984, 1985, 1988, 1989, 1992; Noubhani, 1993; Noubhani and Cappetta, 1994, 1995, 1997), and that a more thorough revision of Landanan elasmobranchs remains to be conducted.

The elasmobranch faunas from the Paleogene of Morocco are characterized by a constant increase in richness (Bardet et al., 2017; Fig. 10). Faunas at Landana do not reflect this trend (Fig. 10), although some similarities between the faunas are recognizable. Notably, the Lamniformes and Myliobatiformes are clearly the most abundant groups in both Morocco (Bardet et al., 2017) and Landana (Table 11), whereas the Torpediniformes are poorly represented in both locales.

Table 10
Number of vertebrate families, genera and species in the Landana section by major taxonomic ranks.

Groups	Families	Genera	Species
Elasmobranchii	13	27	45
Actinopterygii	11	16	21
Squamata	1	1	1
Testudines	2	2	3
Crocodyliformes	1	1	1
Total	**28**	**47**	**71**

Moroccan and Landana faunas share 22 elasmobranch taxa (based on Noubhani and Cappetta, 1997, Table 4). Paleocene and Eocene broad comparisons (favored over more fine-scale comparisons due to a paucity of Selandian in Morocco and a lack of Danian at Landana), reveal that the stratigraphic distribution of elasmobranchs is fairly congruent between the two locales, with a few notable exceptions (Tables 12 and 13; see section 5.5. Paleobiogeographic implications).

Contrary to the pattern observed for elasmobranchs, actinopterygian faunas from Landana are equivalent in richness to those from Morocco, although the Moroccan fossils published by Arambourg (1952) require closer examination (Bardet et al., 2017). The two areas share the presence of Osteoglossidae and, above all, show similar richness in Perciformes (particularly in the presence of Scombridae, Sphyraenidae, Xiphiidae, and Trichiuridae).

Moreover, one can note that some elasmobranch and actinopterygian groups recorded in Morocco are unknown from Landana (e.g., Albuliformes). In contrast, one can note the absence of Anguilliformes in Morocco (Table 12).

The dyrosaurids from Morocco are the most abundant crocodyliforms through the Paleocene (Arambourg, 1952; Buffetaut, 1979; Jouve, 2004; Jouve et al., 2005a, b). They reached peak in richness in the Thanetian, during which time five species are currently recognized (Bardet et al., 2017). This clearly contrasts with the poor stratigraphic extension of *Congosaurus* at Landana, which is restricted to the Selandian (layer 8).

Table 11
Number of families, genera and species for the different orders of Elasmobranchii in the Landana section.

Orders	Families	Genera	Species	Age
Orectolobiformes	1	3	6	Selandian–Lutetian
Lamniformes	5	11	17	Selandian–Lutetian
Carcharhiniformes	2	5	8	Thanetian–Lutetian
Torpediniformes	1	1	1	Selandian
Myliobatiformes	2	3	10	Selandian–Lutetian
Rajiformes	1	3	3	Lutetian

In general, testudines from Landana do not display a richness equivalent to that observed in the phosphates of Morocco where three families are recorded during the Cenozoic: Bothremydidae, Cheloniidae, and Sandownidae (Tong and Hirayama, 2002; Gaffney et al., 2006; Tong and Hirayama, 2008; Tong and Meylan, 2013; Bardet et al., 2017). The Bothremydidae are the most abundant turtles in the Paleogene of the phosphates of Morocco (nine taxa ranged from the Danian to Ypresian: Gaffney et al., 2006; Bardet et al., 2017). Only one bothremydid is known in the Landana section (*Taphrosphys*) – and only during the Paleocene. Myers et al. (2017) described a cheloniid skull from Landana. Cheloniids are represented by four species in the Paleogene phosphates of Morocco (Hay, 1908; Tong and Hirayama, 2002, 2008; Jalil et al., 2009). The presence of a cheloniid in Landana is thus not surprising, and phylogenetic analyses performed by Myers et al. (2017) suggest that the Angolan taxon is related to *Euclastes acutirostris* from the Danian-Thanetian phosphate strata in Morocco (Jalil et al., 2009).

Palaeophiidae is one of the ophidian families that adapted to various freshwater and marine environments (Rage et al., 2008). *Palaeophis* was a near-shore and estuarine dweller that lived in shallow marine, brackish, and likely freshwater environments. The genus is represented perhaps as early as the Maastrichtian in the phosphates of Morocco (Rage and Wouters, 1979), or even the Campanian in Mali (Rage and Werner, 1999). *Palaeophis* became more abundant and broadly distributed during the Eocene, as exemplified in the fossil record of the phosphates of Morocco (Bardet et al., 2017). As a result, the appearance of this genus in Landana fits with the faunal turnover that characterizes the Lutetian part of the section, congruent with general trends observed for this peculiar snake genus.

In summary, the vertebrate fauna from Morocco and Central Africa share similar compositions (e.g., presence of the same reptile groups) and trends through time, with very few differences in faunal composition and stratigraphic distribution. The Landana fauna appears less diverse than the Moroccan fauna, particularly during the Thanetian and Ypresian. These differences may reflect local environmental conditions (e.g., persistence of Pycnodontiformes and Tetraodontiformes). Alternatively, taphonomic/

Table 12
List and information concerning the elasmobranchs and actinopterygians taxa that distinguish Landana from the phosphates of Morocco.

	Taxa	Landana	Phosphates of Morocco	Remarks
Elasmobranchs	Carcharhinidae (beginning of the diversification)	Lutetian	Ypresian	-
	Pristidae	Lutetian	Ypresian	Taphonomic and/or collecting bias?
	Rajiformes	Only in the Lutetian	From the Maastrichtian to the Ypresian	Southward dispersal during the Eocene?
	Hexanchiformes	Absent	Present	Taphonomic and/or collecting bias?
	Squaliformes	Absent	Present	Taphonomic and/or collecting bias?
	Pristiophoriformes (sawsharks)	Absent	Present	Taphonomic and/or collecting bias?
	Squatiniformes (angel shark)	Absent	Present	Taphonomic and/or collecting bias?
	Heterodontiformes (bullhead sharks)	Absent	Present	Taphonomic and/or collecting bias?
Actinopterygians	Sphyraenidae	Lutetian	Ypresian	Southward dispersal during the Eocene?
	Pycnodontiformes	Known in the Paleocene	Only in Maastrichtian	Persistence of Cretaceous faunal elements in western Central Africa
	Tetraodontiformes	Known in the Paleocene and Eocene	Only in Maastrichtian	Persistence of Cretaceous faunal elements in western Central Africa
	Anguilliformes	Present	Absent	Difference in local environmental conditions?

Table 13
List and information concerning the elasmobranch taxa that support dispersal events.

Taxa	Landana	Phosphates of Morocco	North America and Europe	Dispersal direction
Myliobatis dixoni	Since Selandian	Since Thanetian	Since Thanetian in Europe	Northward dispersal during the Paleocene
Myliobatis sulcidens	Since Selandian	Since Thanetian	-	
Eotorpedo hilgendorfi	Since Selandian	Since Thanetian	-	
Cretolamna schoutedeni	Since Selandian	Since Thanetian	-	
Otodus obliquus	Since Selandian	Since Thanetian	Since Thanetian in Europe	
Carcharias substriatus	Since Selandian	Since Thanetian	-	
Carcharhinidae	Lutetian (first appearance)	Known in Thanetian and Ypresian	-	Southward dispersal during the Eocene
Pristidae	Lutetian (first appearance)	Known in Thanetian and Ypresian	-	
Aetobatus irregularis	Lutetian (first appearance)	Known in Thanetian and Ypresian	-	
Cretolamna ascheroni	Lutetian (first appearance)	Known in Thanetian and Ypresian	-	
Ginglystoma angolense	Lutetian (first appearance)	Known in Thanetian and Ypresian	-	
Hypotodus hopei	Lutetian (first appearance)	Known in Thanetian and Ypresian	Known in Selandian in Europe	
Striatolamia striata	Paleocene/Eocene transition (layers 24–28)	Thanetian	Known in Selandian in Europe	
Xiphodolamia eocaena	Lutetian (first appearance)	Unknown in Morocco	Known since the Ypresian in North America and Europe	
Jaekelotodus robustus	Lutetian (first appearance)	-	Since Thanetian in Europe	
Physogaleus secundus	Lutetian (first appearance)	Thanetian in Europe	-	

collecting bias in recording small pristid and batoid specimens may also explain differences among these collections.

5.5. *Paleobiogeographic implications*

Paleobiogeographic affinities of vertebrates and invertebrates from Landana have been discussed by previous authors (Dartevelle and Casier, 1959; Freneix, 1979). Primary results indicate that elasmobranchs and actinopterygians from the Paleogene marine margin of the Congo Basin show clear affinities with the Paleogene faunas of Morocco (Dartevelle and Casier, 1959; see above). New data from Landana permit a closer comparison with contemporaneous records from Morocco, North America, and Europe (Table 13). Based on these data, we hypothesize two dispersal events.

Dartevelle and Casier (1959) noted that the affinities between the Central African and European sections become more pronounced during the Eocene (layers 27–32 in their article) than observed in the Paleocene (layers 0–26 in their article). They attribute this pattern to an expansion of tropical ecosystems northward following the Thanetian. Our analysis based on elasmobranchs suggest two possible faunal exchanges between the two African basins: during the Paleocene, Central Africa appears to have been a source for the Moroccan elasmobranch fauna (i.e., northward dispersal), whereas the opposite is suggested during the Eocene (i.e., southward dispersal) (Table 13). Our conclusions suggest a more complex history than initially recognized by Dartevelle and Casier (1959), logically based on a more complete fossil record.

Systematics of the elasmobranchs recorded from Morocco have received relatively more attention than have elasmobranch fauna from Central Africa, which has not been substantially revised since the work of Dartevelle and Casier in the 1950’s. As a systematic revision is beyond the scope of this paper, our paleobiogeographic hypotheses should be refined through careful reexamination of elasmobranch collections housed at the RMCA, particularly in light of recent reexamination of Antarctic Eocene records (Kriwet, 2005; Engelbrecht et al., 2016).

It is also worth mentioning that an integrated review of marine and freshwater fossil actinopterygians of the African continent is also warranted (Murray, 2000). Current data suggest that the actinopterygian fauna from Central Africa is congruent with that recorded in the Phosphates of Morocco, with differences at the specific level. More specifically, fishes from the Maastrichtian of Manzadi (Table 14) support exchange between Central Africa and North Africa during Mesozoic. Other actinopterygians support the existence of exchange between Central Africa and the Tethys region (Table 14). Yet the absence of Anguilliformes in Morocco is intriguing and implies that these actinopterygians did not disperse along the North African coast, but perhaps rather via an epicontinental sea.

The Bothremydidae likely originated and radiated in Gondwana. The Taphrosphyini (tribe that includes *Taphrosphys*) are present in North America, and abundant in the Paleogene of Morocco, and are also found in the Maastrichtian of Mali, Niger, Egypt, and America (Gaffney et al., 2006; Pérez-García, 2016), as well as in the Cenozoic of Europe (Pérez-García, 2016). The species found in Landana supports connection with the Tethys region and northern Africa.

Table 14
List and information concerning the actinopterygian taxa that support geographic contacts.

Taxa	Manzadi *Point* IV (Maastrichtian)	Landana	Phosphates of Morocco (Maastrichtian)	Remarks
Enchodus bursauxi	Present	Absent	Present	Contact between western Central Africa and North Africa during Mesozoic
Enchodus elegans	Present	Absent	Present	Contact between western Central Africa and North Africa during Mesozoic
Stephanodus libycus	Present	Absent	Present	Contact between western Central Africa and North Africa during Mesozoic
Stratodus apicalis	Present	Absent	Present	Contact between western Central Africa and North Africa during Mesozoic
Anguilliformes	Present	Present	Absent	Contact between western Central Africa and the Tethys region
Perciformes	Absent	Present	Present	Contact between western Central Africa and North Africa during Cenozoic

The cheloniid seem to exhibit Laurasian affinities based on abundance in Europe and North America (Hirayama, 1997). The testudines fauna from the Selandian of Landana is congruent with those recorded in the Tethyian area at that time.

Interestingly, Dyrosauridae and Palaeophiidae have recently been described from the Ypresian of India (Smith et al., 2016). Palaeophiidae are broadly distributed in the Tethyian region: as mentioned earlier, they are documented since the Maastrichtian in Morocco (Rage and Wouters, 1979). Moreover, they are recorded in Europe since the P/E boundary (Kristensen et al., 2012). Contrary to palaeophiids, dyrosaurids have not been reported from Europe with the possible exception of one record from the Cenomanian of Portugal (Buffetaut and Lauverjat, 1978). Concerning the Indian dyrosaurid, notably represented by a coracoid, Smith et al. (2016) note that this bone resembles *C. bequaerti* from the Paleocene of Landana, Angola, more than that of *Dyrosaurus maghribensis* from the phosphates of Morocco. As envisaged by Smith et al. (2016), the Indian Dyrosauridae might correspond to remnants of ghost lineages that reached the Indian subcontinent during the late Cretaceous. Alternatively they might have dispersed from North Africa and passed along the southern margin of the Tethys to reach the Indian subcontinent.

Echinoids from Landana, as noted by Dartevelle (1952, 1953), are similar to those in what are now Senegal (*Echynopsis friryi*, *S. douvillei*), Egypt (*Cheopsia mortensini*) and Algeria (*S. douvillei*). Bivalves from layers 2 to 12 (Selandian) have affinities with South American and African taxa (Freneix, 1979). Layers 13/14 to 28 exhibit taxonomic similarity to faunas derived from the Indo-Mediterranean region (Freneix, 1979). Lutetian taxa are actually closer to those from Egypt, than from northwestern Africa.

To summarize, the Landana fauna displays African and Tethysian affinities. The shallow-marine fauna at the mouth of the Congo River was clearly connected to the Tethyan Sea via northwestern Africa. This conclusion is reinforced by the present study, incorporating recent work on vertebrates from the phosphates of Morocco (Bardet et al., 2017). The fauna is largely congruent with that of northern Africa, suggesting periodic faunal exchange. However, dispersals along the Tethyan Sea – at least its southern margin (e.g., Egypt, India) – via an epicontinental waterway cannot be ruled out and can be investigated in the future. This might help explain any differences seen with northern Africa.

5.6. Additional remarks on the potential connections between Central Africa and Tethyan area

Mesozoic break-up of Gondwana between western Africa and eastern South America affected the tectonic differentiation of the African craton (Brownfield, 2016). Subsidence of the Chad and Iullemmeden basins during the late Mesozoic and early Cenozoic favored a marine transgression, covering northern Africa by a shallow sea: most of Morocco, Tunisia, Algeria, Libya and Egypt were underwater, and the Tethys Sea reached into Mali and Niger through central-northern Africa, and reached the Atlantic through the Gulf of Guinea (Reyment, 1980; Petters, 1981; Mateer et al., 1992; Smith et al., 1994; Guiraud et al., 2005; Kelechi, 2017). This marine connection, present in the Late Cretaceous between the Tethys and the Atlantic, was still in evidence through the Paleocene; palaeoreconstructions show the connection between the Tethys and the Atlantic Ocean to have closed by the middle Eocene (Reyment, 1980; Guiraud et al., 2005). This connection allowed trans-Saharan dispersals, and marine fishes were widespread in deposits across the region (Murray, 2000). An epicontinental connection is supported by the bivalves, anguilliformes, and possibly the dyrosaurids recorded in Landana. In contrast, elasmobranch faunal patterns appear to instead be rooted in dispersals from Morocco.

Additional work is needed to elucidate: (1) potential connections between the coastal areas and the Congo Basin; (2) the presence of synchronous Paleogene deposition within this basin and (3) a potential connection between the Paleogene Congo Basin and a northern outlet, towards the present-day Central African Republic. Current research suggests that the Congo River basin underwent a starvation period with condensed sedimentation in the Late Cretaceous and Paleogene (Anka et al., 2010), a view based on offshore geophysics in the Congo fan that needs further documentation both in onshore basinal and basin margin areas (Linol et al., 2015; De Putter et al., 2015, 2016). Our present state of knowledge does not document a direct connection between Landana and the Tethyan area via the onshore Congo Basin and a Paleogene Trans-Saharan Corridor. The hypothesis of a peri-continental connection, possibly via the Gulf of Guinea, is perhaps more likely.

6. Conclusions

Here we provide refined age constraint for the Landana (Angola) fossil-bearing deposits, using new data (carbon isotopes, foraminiferal assemblages, and palynomorphs) together with interpretations of previously collected fossils. We suggest that this section recorded only a very short part of the (upper?) Danian, parts of the Selandian and Thanetian, the very beginning of the Ypresian, and a portion of the Lutetian. Invertebrate and vertebrate faunas recorded in Landana exhibit African and Tethysian affinities. Therefore, Central Africa likely retained at least periodic connections with the Tethys region, representing part of a gigantic marine realm.

Our study of the Landana section also demonstrates that invertebrate and vertebrate faunas exhibit faunal shifts congruent with global perturbations thought to have affected the entire Atlantic coast, and Landana is hence part of a general African pattern. For instance, we found the profound modification in elasmobranch and actinopterygian faunas observed globally and locally during the Maastrichtian/Danian transition (i.e., K-Pg mass extinction). Yet differences noted between Landana and other African sites suggest that Landana represents a slightly different ecosystem, perhaps not surprising due to latitudinal differences. For instance, it is possible that Landana provided a longer refuge for several typically-Cretaceous faunal elements.

Integrating datasets and refining age estimates for the Landana section is pivotal for exploring faunal evolution in a global framework, especially for rich Gondwanan ichthyofaunas including the Scombridae (tunas and mackerels) and Tetraodontiformes (puffer fishes). The bony fish *Landanichtys* is a prime illustration: this Landanan genus is indeed considered the oldest fossil scombrid ever discovered (Dartevelle and Casier, 1959; Bannikov, 1981; Beckett and Friedman, 2016). Hence further age constraint could have profound impact on our understanding of the evolution of the mackerels.

Refined ages will allow better understanding of the evolution of fossil faunas throughout Western Central Africa, making Landana a critical reference section for the region. Moreover, the integration of Landana, Manzadi, and Bololo provides critical information concerning the evolution of the Central African marine fauna (e.g., during the K-Pg mass extinction). Finally, the Landana section records a dramatic decline in species richness during the Selandian (layers 13–18), Thanetian and Ypresian, emphasizing the importance of expanding collection efforts across numerous latitudes with well-documented reference sections. Future work exploring global patterns in species distributions will benefit from renewed interest in the age and depositional setting at Landana.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.gsf.2018.06.002.

References

Adnet, S., Cappetta, H., Guinot, G., Notarbartolo di Sciara, G., 2012. Evolutionary history of the devilrays (Chondrichtyes: Myliobatiformes) from fossil and morphological inference. Zoological Journal of the Linnean Society 166, 132–159.

Anka, Z., Séranne, M., di Primio, R., 2010. Evidence of a large upper-Cretaceous depocentre across the continent-ocean boundary of the Congo-Angola Basin. Implications for paleo-drainage and potential ultra-deep source rocks. Marine and Petroleum Geology 27, 601–611.

Anthonissen, D.E., Ogg, J.G., 2012. Appendix 3: cenozoic and Cretaceous biochronology of planktonic foraminifera and calcareous nannofossils. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), The Geological Time Scale 2012. Elsevier Science, Oxford, pp. 1083–1127.

Antunes, M.T., 1964. O neocretacico e o cenozoico do litoral de Angola. Junta de Investigaçoes do Ultramar, Lisboa, pp. 1–255.

Arambourg, C., 1935. Note préliminaire sur les vertébrés fossiles des phosphates du Maroc. Bulletin de la Société géologique de France 5, 413–439 (in French).

Arambourg, C., 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes et Mémoires du Protectorat de la République française au Maroc, Direction de la Production industrielle et des Mines, Division des Mines et de la Géologie. Service géologique du Maroc 92, 1–372 (in French).

Arenillas, I., 2012. Patterns of spatio-temporal distribution as criteria for the separation of planktic foraminiferal species across the Danian-Selandian transition in Spain. Acta Palaeontologica Polonica 57, 401–422.

Bannikov, A.F., 1981. Sistematicheskoye polozheniya sostav i proiskhozhdenikye semeystva Scombridae. Voprosy Ikhtiologii 21, 200–208. Unknown translator. Transferred to electronic copy and edited by Mark Uhen and Michell Kwon, Smithsonian Institution, 2007.

Bardet, N., Gheerbrant, E., Noubhani, A., Cappetta, H., Jouve, S., Bourdon, E., Pereda Suberbiola, X., Jalil, N.-E., Vincent, P., Houssaye, A., Sole, F., Elhoussaini Darif, K., Adnet, S., Rage, J.-C., de Lapparent de Broin, F., Sudre, J., Bouya, B., Amaghzaz, M., Meslouh, S., 2017. Les Vertébrés des phosphates crétacé-paléogènes (72.1-47.8 Ma) du Maroc. Mémoires de la Société Géologique de France 180, 351–452 (in French).

Beckett, H.T., Friedman, M., 2016. The one that got away from Smith Woodward: cranial anatomy of *Micrornatus* (Acanthomorpha: Scombridae) revealed using computed microtomography. In: Johanson, Z., Barrett, P.M., Richter, M., Smith, M. (Eds.), Arthur Smith Woodward: His Life and Influence on Modern Vertebrate Palaeontology. Geological Society, London, Special Publications, vol. 430, pp. 337–353.

Belben, R.A., Underwood, C.J., Johanson, Z., Twitchett, R.J., 2017. Ecological impact of the end-Cretaceous extinction on lamniform sharks. PLoS One 12 (6), e0178294. https://doi.org/10.1371/journal.pone.0178294.

Bequaert, J., 1920. Végétation du Bas-Chiloango et limite occidentale de la forêt du Mayumbe. Revue Zoologique Africaine, Supplément Botanique, p. 21 (in French).

Bequaert, J., 1923. Observations géologiques faites au cours d'un voyage dans l'Enclave de Cabinda et la Bas-Congo. Bulletin de la Société belge de Géologie de Paléontologie et d'Hydrogéologie 33, 18–28 (in French).

Berggren, W.A., 1969. Paleogene biostratigraphy and planktonic foraminifera of Northern Europe. In: Proc. 1st Intern. Conf. Plankt. Microfossils, Geneva (Brill, Leiden), vol. 1, pp. 121–160.

Berggren, W.A., Kent, D.V., Swisher III, C.C., Aubry, M.-P., 1995. A revised cenozoic gochronology and chronostratigraphy. In: Berggren, W.A., Kent, D.V., Aubry, M.-P., Hardenbol, J. (Eds.), Geochronology Time Scales and Global Stratigraphic Correlation. B, SEPM, Tulsa, Oklahoma, pp. 129–212.

Berggren, W.A., Pearson, P.N., 2005. A revised tropical to subtropical Paleogene planktonic foraminiferal zonation. Journal of Foraminiferal Research 35, 279–298.

Böhm, J., 1926. Über tertiäre Versteinerungen von den Bogenfelsen diamantfeldern. In: Kaiser, E. (Ed.), Die Diamantwuste Sud-westafrikas. Dietrich Reimer, Berlin, pp. 55–87.

Brownfield, M.E., 2016. Assessment of undiscovered oil and gas resources of the West-Central Coastal Province, west Africa. In: Brownfield, M.E. (Ed.), Geologic Assessment of Undiscovered Hydrocarbon Resources of Sub-saharan Africa. U.S. Geological Survey Digital Data Series 69-GG, p. 41.

Brownfield, M.E., Charpentier, R.R., 2006. Geology and total petroleum systems of the west-Central coastal Province (7203), west Africa. U.S. Geological Survey Bulletin 2207-B, 1–52.

Buffetaut, E., 1979. *Atlantosuchus coupatezi*, n. g., n. sp., un nouveau Dyrosauride (Crocodylia, Mesosuchia) des phosphates montiens du Maroc. Bulletin trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre 66, 85–90 (in French).

Buffetaut, E., Lauverjat, J., 1978. Un crocodilien d'un type particulier dans le Cénomanien de Nazaré. Comptes Rendus Sommaire des Seances de la Société Géologique de France 2, 79–82 (in French).

Cappetta, H., 1972. Les Poissons crétacés et tertiaires du Bassin des Iullemmeden (République du Niger). Palaeovertebrata 5, 179–251 (in French).

Cappetta, H., 1981. Additions à la faune de sélaciens fossiles du Maroc. 1 : sur la présence des genres Heptranchias. Alopias et Odontorhytis dans l'Yprésien des Ouled Abdoun Geobios 14, 563–575 (in French).

Cappetta, H., 1983. Additions à la faune de sélaciens fossiles du Maroc. 2: Révision de Raja praealba Arambourg, 1952, espèce de l'Yprésien des Ouled Abdoun. Tertiary Research 5, 1–8 (in French).

Cappetta, H., 1984. Découverte du genre Gymnura (Batomorphii, Myliobatiformes) dans le Thanétien des Ouled Abdoun, Maroc. Observations sur la denture de quelques espèces actuelles. Geobios 17, 631–635 (in French).

Cappetta, H., 1985. Sur une nouvelle espèce de Burnhamia (Batomorphii, Mobulidae) dans l'Yprésien des Ouled Abdoun, Maroc. Tertiary Research 7, 27–33 (in French).

Cappetta, H., 1988. Les Torpédiniformes (Neoselachii, Batomorphii) des phosphates du Maroc. Observations sur la denture des genres actuels. Tertiary Research 10, 21–52 (in French).

Cappetta, H., 1989. Sélaciens nouveaux ou peu connus du Crétacé supérieur du Maroc. Mesozoic Research 2, 11–23 (in French).

Cappetta, H., 1992. Nouveaux Rhinobatoidei (Neoselachii, Rajiformes) à denture spécialisée du Maastrichtien du Maroc. Remarques sur l'évolution dentaire des Rajiformes et des Myliobatiformes. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 187, 31–52 (in French).

Cappetta, H., 2012. Chondrichthyes II Mesozoic and Cenozoic Elasmobranchii: Teeth, Handbook of Paleoichthyology. verlag Dr. Friedrich Pfeil, Stuttgart-New York.

Cappetta, H., Buffetaut, E., Cuny, G., Suteethorn, V., 2006. A new elasmobranch assemblage from the lower Cretaceous of Thailand. Palaeontology 49, 547–555.

Case, G.R., Cappetta, H., 1990. The eocene selachian fauna from the rayum depression in Egypt. Palaeontographica Abt A 212, 1–30.

Casier, E., 1960. Notes sur la Collection des Poissons Paléocènes et Eocènes de l'Enclave de Cabinda (Congo). Annales du Musée Royal du Congo Belge Tervuren Belgique A Minéralogie Géologie Paléontologie 1, 1–48 (in French).

Choffat, P., 1905. Contribution à la connaissance géologique des Colonies portugaises d'Afrique. Nouvelles données sur la zone littorale d'Angola. Communicaçôes dos Serviços Geologicos de Portugal 1, 1–48 (in French).

Coccioni, R., Bancalà, G., Catanzarit, R., Fornaciari, E., Frontalini, F., Giusberti, L., Jovane, L., Luciani, V., Savian, J., Sprovieri, M., 2012. An integrated stratigraphic record of the Paleocene-lower Eocene at Gubbio (Italy): new insights into the early Paleogene hyperthermals and carbon isotopes excursions. Terra Nova 24, 380–386.

Cornet, J., 1906. Notes sur la Géologie du Mayombe Occidental. Mémoires et Publications de la Société des Sciences des Arts et des Lettres du Hainaut 9, 36–38 (in French).

Dartevelle, E., 1935. Note préliminaire sur l'Eocène de la zone littorale du Congo. Bulletin de la Société Belge de géologie de paléontologie et d'hydrogéologie 44, 25–27 (in French).

Dartevelle, E., 1952. Echinidés fossiles du Congo et de l'Angola, introduction historique et stratigraphique. Annales du Musée du Congo Belge Sciences Géolgiques 8, 1–70 (in French).

Dartevelle, E., 1953. Les Echinides fossiles du Congo et de l'Angola. 2^e partie : description systématique des Echinides fossiles du Congo et de l'Angola. Annales du Musée Royal du Congo Belge 13, 1–240 (in French).

Dartevelle, E., Casier, E., 1943. Les Poissons fossiles du Bas-Congo et des régions voisines. Annales du Musée du Congo Belge Sciences Géolgiques Série 3 (II), 1–200 (in French).

Dartevelle, E., Casier, E., 1949. Les Poissons fossiles du Bas-Congo et des régions voisines. Annales du Musée du Congo Belge Sciences Géolgiques Série 3 (II), 201–256 (in French).

Dartevelle, E., Brebion, P., 1956. Mollusques du Crétacé de la Côte occidentale d'Afrique du Cameroun à l'Angola. I- Gastéropodes. Annales du Musée Royal de l'Afrique Centrale Tervuren Belgique 15, 1–128 (in French).

Dartevelle, E., Freneix, S., 1957. Mollusques du Crétacé de la Côte occidentale d'Afrique du Cameroun à l'Angola. II- Lamellibranches. Annales du Musée Royal de l'Afrique Centrale Tervuren Belgique 20, 1–271 (in French).

Dartevelle, E., Casier, E., 1959. Les Poissons fossiles du Bas-Congo et des régions voisines. Annales du Musée du Congo Belge Sciences Géolgiques Série 3 (II), 257–568 (in French).

De Putter, T., Ruffet, G., Yans, J., Mees, F., 2015. The age of supergene manganese deposits in Katanga and its implications for the Neogene evolution of the African Great Lakes region. Ore Geology Reviews 71, 350–362.

De Putter, T., Bayon, G., Mees, F., Ruffet, G., Smith, T., 2016. Cenozoic Sedimentation History of the Congo Basin Revisited. SGF-asf “Source to Sink” Conference, Rennes, France, 30 Nov - 2 Dec 2016. Accessible online at: http://www.geosoc.fr/reunion/2016/S2S/workshop-book-abstracts.pdf.

De Stefano, G., 1915. Sopra alcuni ittiodontoliti dei forfati di Kalaa-Derda in Tunisia. Bolletino Della Societa Geologica Italiana 34, 263–272 (in Italian).

Dikouma, M., Lang, J., Laurin, B., Pascal, A., Salard-Cheboldaeff, M., 1994. Biostratigraphyof some Maastrichtian and Paleocene formations in the Iullemmeden basin (southern Niger). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 193, 55–79.

Dollo, L., 1912. Sur les premiers restes de tortues fossiles recueillis au Congo. Bulletin de l’Académie royale de Belgique 2, 8–9 (in French).

Dollo, L., 1914. Sur la découverte de Téléosauriens tertiaires au Congo. Bulletin de l’Académie royale de Belgique 7, 288–298 (in French).

Dollo, L., 1924. *Bantuchelys*, genre nouveau de tortues, découvert dans le Paléocène du Congo. Bulletin de la Classe des Sciences de l’Académie de Belgique 5, 613–635 (in French).

Engelbrecht, A., Mörs, T., Reguero, M.A., Kriwet, J., 2016. Revision of eocene antarctic carpet sharks (Elasmobranchii, Orectolobiformes) from seymour Island, antarctic peninsula. Journal of Systematic Palaeontology 15, 969–990.

Ericson, P.G., Anderson, C.L., Britton, T., Elzanowski, A., Johansson, U.S., Källersjö, M., Ohlson, J.I., Parsons, T.J., Zuccon, D., Mayr, G., 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. Biology Letters 2, 543–547.

Folie, A., Mees, F., De Putter, T., Smith, T., 2016. A new large species of the snake *Palaeophis* from the Lutetian marine margin of the Congo Basin, Cabinda, Angola. Journal of Vertebrate Paleontology Program and Abstracts 2016, 137.

Freneix, S., 1959. Mollusques du Crétacé de la Côte occidentale d’Afrique du Cameroun à l’Angola III.- Conclusions stratigraphiques et paléontologiques. Annales du Musée Royal de l’Afrique Centrale Tervuren Belgique 24, 1–126 (in French).

Freneix, S., 1979. Bivalves du Paléocène et de l’Eocène de l’Angola et du Zaïre. Musée Royal de l’Afrique Centrale Tervuren Belgique Annales 8, 53–206 (in French).

Friedman, M., 2009. Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. Proceedings of the National Academy of Sciences 106, 5218–5223.

Friedman, M., Sallan, L.C., 2012. Five hundred million years of extinction and recovery: a Phanerozoic survey of large-scale diversity patterns in fishes. Palaeontology 55, 707–742.

Gaffney, E.S., Tong, H.Y., Meylan, P.A., 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. Bulletin of the American Museum of Natural History 300, 1–700.

Galeotti, S., Krishnan, S., Pagani, M., Lanci, L., Gaudio, A., Zachos, J.C., Monechi, S., Morelli, G., Lourens, L., 2010. Orbital chronology of early eocene hyperthermals from the Contessa road section, central Italy. Earth and Planetary Science Letters 290, 192–200.

Galeotti, S., Moretti, M., Sabatino, N., Sprovieri, M., Ceccatelli, M., Francescone, F., Lanci, L., Lauretano, V., Monechi, S., 2017. Cyclochronology of the early eocene carbon isotope record from a composite Contessa road-bottaccione section (gubbio, central Italy). Newsletters on Stratigraphy 50, 231–244.

Gingerich, P.D., 2006. Environment and evolution through the Paleocene-Eocene thermal maximum. Trends in Ecology and Evolution 21, 246–253.

Giusberti, L., Rio, D., Agnini, C., Backman, J., Fornaciari, E., Tateo, F., Oddone, M., 2007. Mode and tempo of the Paleocene-Eocene thermal maximum in an expanded section from the Venetian pre-Alps. GSA Bulletin 119, 391–412.

Guinot, G., Cavin, L., 2016. ‘Fish’ (Actinopterygii and Elasmobranchii) Diversification Patterns through Deep Time: Biological Reviews, vol. 91, pp. 950–981.

Guinot, G., Adnet, S., Cappetta, H., 2012. An Analytical Approach for estimating fossil record and diversification events in sharks, skates and rays. PLoS One 7, e44632. https://doi.org/10.1371/journal.pone.0044632.

Guiraud, R., Bosworth, W., Thierry, J., Delplanque, A., 2005. Phanerozoic geological evolution of northern and central Africa: an overview. Journal of African Earth Sciences 43, 83–143.

Hay, O.P., 1908. The Fossil Turtles of North America, vol. 75. Publications of the Carnegie Institute of Washington, pp. 1–568.

Hirayama, R., 1997. Distribution and diversity of Cretaceous chelonioids. 225–241. In: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient Marine Reptiles. Academic Press, San Diego, CA, pp. 1–501.

Holroyd, P.A., Wilson, G.P., Hutchinson, G.P., 2014. Temporal changes within the latest Cretaceous and early Paleogene turtle faunas. GSA Special Papers 503, 299–312.

Houssaye, A., Rage, J.-C., Bardet, N., Vincent, P., Amaghzaz, M., Meslouh, S., 2013. New highlights about the enigmatic marine snake *Palaeophis maghrebianus* (Palaeophiidae; palaeophiinae) from the Ypresian phosphates (middle eocene) of Morocco. Palaeontology 56, 647–661.

Jablonski, D., Raup, D.M., 1995. Selectivity of end-Cretaceous marine bivalve extinction. Science 268, 389–391.

Jaekel, O., 1895. Unter-Tertiäre Selachier aus Südrussland. Mémoire du Comité Géologique St-Pétersbourg 9, 19–35 (in German).

Jaekel, O., 1904. In: Esch, E., Solger, F., Oppenheim, P., Jaekel, O. (Eds.), Uber einen Torpediniden und andere Fischreste aus dem Tertiär von Kamerun. Beitrage zur Geologie von Kamerun, Stuttgart, pp. 289–291 (in German).

Jalil, N.-E., de Lapparent de Broin, F., de, Bardet, N., Vacant, R., Bouya, B., Amaghzaz, M., Meslouh, S., 2009. *Euclastes acutirostris*, a new species of marine turtle (Cryptodira, Cheloniidae) from the Palaeocene phosphates of Morocco (Oulad Abdoun basin, Danian-Thanetian). Comptes Rendus Palevol 8, 447–459.

Jouve, S., 2004. Etude des crocodyliformes fini Crétacé-Paléogène du bassin des Oulad Abdoun (Maroc) et comparaison avec les faunes africaines contemporaines: systématique, phylogénie et paléobiogéographie. Unpublish. Ph.D. Thesis. Muséum National d’Histoire Naturelle, Paris, pp. 1–232 (in French).

Jouve, S., Schwarz, D., 2004. *Congosaurus bequaerti*, a Paleocene dyrosaurid (Crocodyliformes; Mesoeucrocodyla) from Landana (Angola). Bulletin de l’Institut Royal des Sciences Naturelles de Belgique Sciences de la Terre 74, 129–146.

Jouve, S., Bouya, B., Amaghzaz, M., 2005a. A short-snouted dyrosaurid (Crocodyliformes, Mesoeucrocodylia), from the palaeocene of Morocco. Palaeontology 48, 359–369.

Jouve, S., Iarochene, M., Bouya, B., Amaghzaz, M., 2005b. A new crocodyliform dyrosaurid from the Palaeocene of Morocco and a phylogenetic analysis of Dyrosauridae. Acta Palaeontologica Polonica 50, 581–594.

Jubb, R.A., Gardiner, B.G., 1975. A preliminary catalogue of identifiable fossil fish material from Southern Africa. Annals of the South African Museum 67, 381–440.

Kelechi, O.F., 2017. The southern benue trough and Anambra basin, southeastern Nigeria: a stratigraphic review. Journal of Geography Environment and Earth Science International 12, 1–16.

Kriwet, J., 2005. Addition to the eocene selachian fauna of Antarctica with comment on antarctic selachian diversity. Journal of Vertebrate Paleontology 25, 1–7.

Kriwet, J., Benton, M.J., 2004. Neoselachian (Chondrichthyes, Elasmobranchii) diversity across K-Pg boundary. Palaeogeography Palaeoclimatology Palaeoecology 214, 181–194.

Kristensen, H.V., Cuny, G., Rasmussen, A.R., Madsen, H., 2012. Earliest record of the fossil snake *Palaeophis* from the Paleocene/Eocene boundary in Denmark. Bulletin de la Société Géologique de France 183, 621–625.

Landmann, N.H., Goolaerts, S., Jagt, J.W.M., Jagt-Yazykova, E.A., Machalski, M., 2015. Ammonites on the brink of extinction: diversity, abundance, and Ecology of the order Ammonoidea at the Cretaceous/paleogene (K/Pg) boundary. Topics in Geobiology 44, 497–553.

Lenz, O., 1877. Petrefakten von der Loango-Küste (West-Afrika). Verhandlungen der Kaiserlich Königlichen Geologischen Reichsanstalt 1877, 278–279 (in German).

Lenz, O., 1878. Geologische Mittheilungen aus West-Afrika. Verhandlungen der Kaiserlich Königlichen Geologischen Reichsanstalt 1878, 148–153 (in German).

Leriche, M., 1913. Les poisons paléocène de Landana (Congo). Les gisements de Poissons paléocènes et éocènes de la côte occidentale d’Afrique. Annales du Musée du Congo Belge Sciences Géologiques Série 3 (1), 67–92 (in French).

Lingham-Soliar, T., 1994. First record of mosasaurs from the Maastrichtian (upper Cretaceous) of Zaire. Paläontologische Zeitschrift 68, 259–265.

Linol, B., de Wit, M.J., Guillocheau, F., de Wit, M.C.J., Anka, Z., Colin, J.-P., 2015. Formation and collapse of the Kalahari duricrust [‘African Surface’] across the Congo Basin, with implications for changes in rates of Cenozoic off-shore sedimentation. In: de Wit, M.J., Guillocheau, F., de Wit, M.C.J. (Eds.), Geology and Resource Potential of the Congo Basin, Regional Geology Reviews, pp. 193–210.

Longbottom, A.E., 1984. New Tertiary pycnodonts from the Tilemsi valley, republic of Mali. Bulletin of the british Museum of natural history. Geological Series 38, 1–26.

Longrich, N.R., Bhullar, B.-A.S., Gauthier, J.A., 2012. Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. Proceedings of the National Academy of Sciences 109, 21396–21401.

Lys, M., Meijer, M., Glaçon, G., 1979. Etude micropaléontologique des échantillons du Paléocène de la coupe de Landana, enclave de Cabinda, Angola. Musée Royal de l’Afrique Centrale Tervuren Belgique Annales 8, 1–52 (in French).

Lyson, T.R., Joyce, W.G., Knauss, G.E., Pearson, D.A., 2011. *Boremys* (Testudines, Baenidae) from the latest Cretaceous and early Paleocene of North Dakota: an 11-million-year range extension and an additional K/T survivor. Journal of Vertebrate Paleontology 31, 729–737.

Mahboudi, M., Ameur, R., Crochet, J.-Y., Jaeger, J.-J., 1984. Implications paleébiogéographiques de la découverte d’une nouvelle localité Eocène à vertébreés continentaux en Afrique nord-occidentale: El Kohol (Sud-Oranais, Algeérie). Geobios 17, 625–629 (in French).

Mannion, P.D., Benson, R.B.J., Carrano, M.T., Tennant, J.P., Judd, J., Butler, R.J., 2015. Climate constrains the evolutionary history and biodiversity of crocodylians. Nature Communication 6, 8438. https://doi.org/10.1038/ncomms9438.

Mateer, N.J., Wycisk, P., Jacobs, L.L., Brunet, M., Luger, P., Arush, M.A., Hendriks, F., Weissbrod, T., Gvirtzman, G., Mbede, E., Dina, A., Moody, R.T.J., Weigelt, G., El-Nakhal, H.A., Hell, J., Stets, J., 1992. Correlation of nonmarine Cretaceous strata of Africa and the Middle East. Cretaceous Research 13, 273–318.

McInerney, F.A., Wing, S.L., 2011. The paleocene-eocene thermal maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. Annual Review of Earth and Planetary Sciences 39, 489–516.

Miller, A.K., 1951. Tertiary Nautiloids of west-Costal Africa. Annales du Musée du Congo Belge 8, 7–89.

Murray, A.M., 2000. The palaeozoic, mesozoic and early cenozoic fishes of Africa. Fish and Fisheries 1, 111–145.

Myers, T.S., Polcyn, M.J., Mateus, O., Vineyard, D.P., Olímpio Gonçalves, A., Jacobs, L.L., 2017. A new durophagous stem cheloniid turtle from the lower Paleocene of Cabinda, Angola. Papers in Palaeontology 1–16. https://doi.org/10.1002/spp2.110. Online version.

Noiret, C., Steurbaut, E., Tabuce, R., Marandat, B., Schnyder, J., Storme, J.-Y., Yans, J., 2016. New bio-chemostratigraphic dating of a unique early Eocene sequence from southern Europe results in precise mammalian biochronological tie-points. Newsletters on Stratigraphy 49, 469–480.

Noubhani, A., 1993. Les sélaciens des bassins à phosphate du Maroc (Maastrichtien-Lutétien). Systématique, biostratigraphie, évolution et dynamique des faunes. Ph.D. Université de Montpellier II, pp. 1–293 (in French).

Noubhani, A., 2010. The selachians faunas of the Moroccan phosphate deposits and the KT mass-extinctions. Historical Biology 22, 71–77.

Noubhani, A., Cappetta, H., 1994. Révision des Rhombodontidae (Neoselachii, Batomorphii) des bassins à phosphate du Maroc. Palaeovertebrata 23, 1–49 (in French).

Noubhani, A., Cappetta, H., 1995. Batoïdes nouveaux ou peu connus (Neoselachii: rajiformes, Myliobatiformes) des phosphates maastrichtiens et paléocènes du Maroc. In: Herman, J., Van Waes, H. (Eds.), Elasmobranches et Stratigraphie. Belgian Geological Survey, Professional Papers, vol. 278, pp. 157–183 (in French).

Noubhani, A., Cappetta, H., 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des bassins à phosphate du Maroc (Maastrichtien-Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. Palaeo Ichthyologica 8, 1–327 (in French).

O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Luo, Z.X., Meng, J., Novacek, M.J., Perini, F.A., Randall, Z.S., Rougier, G.W., Sargis, E.J., Silcox, M.T., Simmons, N.B., Spaulding, M., Velazco, P.M., Weksler, W., Wible, J.R., Cirranello, A.L., 2013. The placental mammal ancestor and the post–K-Pg radiation of placentals. Science 339, 662–667.

Pearson, P.N., Olsson, R.K., Huber, B.T., Hemleben, C., Berggren, W.A., 2006. Atlas of Eocene Planktonic Foraminifera, vol. 41. Cushman Foundation Special Publication, pp. 1–513.

Pechuel-Loesche, E., 1876. Loango und die Loangoküste. Mitteilungen des Vereins für Erdkunde zu Leipzig 1876, 37–67.

Pérez-García, A., 2016. A new turtle confirms the presence of Bothremydidae (Pleurodira) in the Cenozoic of Europe and expands the biostratigraphic range of Foxemydina. The Science of Nature 103, 1–14.

Petters, S., 1981. Stratigraphy of Chad and Iullemmeden basins west Africa. Eclogae Geologicae Helvetiae 74, 139–159.

Piérard, H., 1956. Observations sur le Crétacé supérieur de la région située entre Bulu-Zambi et Bololo sur la rive nord du fleuve Congo (territoire du Bas-Fleuve, Congo belge). Musée Royal du Congo Belge Sciences Géologiques 17, 1–80 (in French).

Priem, M.F., 1903. Sur les Poisson fossiles des phosphates d'Algérie et de Tunisie. Extrait du Bulletin de la société Géologique de France série 4 (3), 393–406 (in French).

Puértolas-Pascual, E., Blanco, A., Brochu, C.A., Canudo, J.I., 2016. Review of the late Cretaceous-early paleogene crocodylomorphs of Europe: extinction patterns across the K-PG boundary. Cretaceous Research 57, 565–590.

Rage, J.-C., Wouters, G., 1979. Découverte du plus ancien Palaeopheidé (Reptilia, Serpentes) dans le Maestrichtien du Maroc. Geobios 12, 293–296 (in French).

Rage, J.-C., Werner, C., 1999. Mid-cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan: the earliest snake assemblage. Palaeontologia Africana 35, 85–110.

Rage, J.-C., Bajpai, S., Thewissen, J.G.M., Tiwari, B.N., 2003. Early eocene snakes from Kutch, western India, with a review of the Palaeophiidae. Geodiversitas 25, 695–716.

Rage, J.C., Folie, A., Rana, R.S., Singh, H., Rose, K.D., Smith, T., 2008. A diverse snake fauna from the early Eocene of Vastan Lignite Mine, at Gujarat, India. Acta Palaeontologica Polonica 53, 391–403.

Raup, D.M., Jablonski, D., 1993. Geography of end-Cretaceous marine bivalve extinctions. Science 260, 971–973.

Reyment, R.A., 1980. Paleo-oceanography and paleobiogeography of the Cretaceous South-Atlantic Ocean. Oceanologica Acta 3, 127–133.

Schmitz, B., Pujalte, V., Molina, E., Monechi, S., Orue-Etxebarria, X., Speijer, R.P., Alegret, L., Apellaniz, E., Arenillas, I., Aubry, M.-P., Baceta, J.-I., Berggren, W.A., Bernaola, G., Caballero, F., Clemmensen, A., Dinarès-Turell, J., Dupuis, C., Heilmann-Clausen, C., Orús, A.H., Knox, R., Martín-Rubio, M., Ortiz, S., Payros, A., Petrizzo, M.R., von Salis, K., Sprong, J., Steurbaut, E., Thomsen, E., 2011. The global stratotype section and points for the bases of the selandian (middle Paleocene) and Thanetian (upper Paleocene) stages at Zumaia Spain. Episodes 34, 220–243.

Sibert, E.C., Norris, R.D., 2015. New age of fishes initiated by the Cretaceous-paleogene mass extinction. Proceedings of the National Academy of Sciences 112, 8537–8542.

Smith, A.G., Smith, D.G., Funnell, B.M., 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, Cambridge.

Smith, T., Kumar, K., Rana, R.S., Folie, A., Solé, F., Noiret, C., Steeman, T., Sahni, A., Rose, K.D., 2016. New early Eocene vertebrate assemblage from western India reveals a mixed fauna of European and Gondwana affinities. Geoscience Frontiers 7, 969–1001. https://doi.org/10.1016/j.gsf.2016.05.001.

Smith, T., Rose, K.D., Gingerich, P.D., 2006. Rapid Asia-Europe-north America geographic dispersal of earliest eocene primate Teilhardina during the paleocene-eocene thermal maximum. Proceedings of the National Academy of Sciences 103, 11223–11227.

Stevens, N.J., Eastman, J.T., Odunze, S.O., Cooper, L.N., Obi, G.C., 2011. Paleocene ichthyofaunal and paleoenvironmental setting, Imo Formation, southeastern Nigeria. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 260, 289–296.

Storme, J.-Y., Devleeschouwer, X., Schnyder, J., Cambier, G., Baceta, J.I., Pujalte, V., Iacumin, P., Yans, J., 2012. Paleocene/Eocene boundary section at Zumaia (Basque-Catabric Basin) revisited: new insights from high resolution magnetic susceptibility and carbon isotope chemostratigraphy on organic matter ($\delta^{13}C_{org}$). Terra Nova 24, 310–317.

Stott, L.D., Sinha, A., Thiry, M., Aubry, M.-P., Berggren, W.A., 1996. Global $\delta^{13}C$ changes across the Paleocene-Eocene boundary: criteria for terrestrial-marine correlations. In: Knox, R.W.O.B., Corfield, R.M., Dunay, R.E. (Eds.), Correlation of the Early Paleogene in Northwest Europe, Geological Society Special Publication, vol. 101, pp. 381–399.

Stromer, E., 1910. Reptilien-und Fischreste aus dem marinen Alttertiär von Süd-Togo (Westafrika). Monatseerschten für Deutschen Geologischen Gesellschaft 39, 478–507 (in German).

Swinton, W.E., 1950. On *Congosaurus bequaerti* Dollo. Annales du Musée du Congo Belge Sciences Géologiques 8, 1–35 (in French).

Taverne, L., 2009. *Ridewoodichthys*, a new genus for *Brychaetus caheni* from the marine Paleocene of Cabinda (Africa): re-description and comments on its relationships within the Osteoglossidae (Teleostei, Osteoglossomorpha). Bulletin de l'Institut royal des Sciences naturelles de Belgique Sciences de la Terre 79, 147–153.

Taverne, L., 2017. New data on the osteoglossid fishes (Teleostei, Osteoglossiformes) from the marine danian (Paleocene) of Landana (Cabinda enclave, Angola). Geo-Eco-Trop 40, 297–304.

Tomczik, D.W., 2014. Fish Production and Diversity across the Paleocene–eocene Thermal Maximum: Evidence for Enhanced Export Production and Community Resilience. PhD. Univeristy of California.

Tong, H., Hirayama, R., 2002. A new species of *Tasbacka* (Testudines: Cryptodira: Cheloniidae) from the Paleocene of the Oulad Abdoun phosphate Basin, Morocco. – Neues. Jahrbuch für Geologie und Paläontologie 5, 277–294.

Tong, H., Hirayama, R., 2008. A new species of *Argillochelys* (Testudines: Cryptodira: Cheloniidae) from the Ouled Abdoun phosphate Basin, Morocco. Bulletin de la Société géologique de France 179, 623–630.

Tong, H., Meylan, P., 2013. Morphology and relationships of *Brachyopsemys tingitana* gen. et sp. nov. from the Early Paleocene of Morocco and recognition of the New Eucryptodiran turtle family: Sandownidae. In: Brinkman, D.B., Holroyd, P.A., Gardner, J.D. (Eds.), Morphology and Evolution of Turtles, Vertebrate Paleobiology and Paleoanthropology 13, Springer ScienceDordrecht, pp. 187–201.

Underwood, C.J., Ward, D.J., King, C., Antar, S.M., Zalmout, I.S., Gingerich, P.D., 2011. Shark and ray faunas in the middle and late eocene of the Fayum area, Egypt. Proceedings of the Geologists Association 122, 47–66.

Vandenberghe, N., Speijer, R., Hilgen, F.J., 2012. The Paleogene period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M., Ogg, G. (Eds.), The Geological Time Scale 2012. Elsevier Science, Oxford, pp. 855–921.

Vincent, E., Dollo, L., Leriche, M., 1913. Matériaux pour la Paléontologie du Bas- et du Moyen-Congo. Annales du Musée du Congo Belge Géologie Paléontologie Minéralogie Série III 1, 1–92 (in French).

Wade, B.S., Pearson, P.N., Berggren, W.A., Pälike, H., 2011. Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. Earth Science Reviews 104, 111–142.

Westerhold, T., Röhl, U., Donner, B., McCarren, H.K., Zachos, J.C., 2011. A complete high-resolution Paleocene benthic stable isotope record for the central Pacific (ODP Site 1209). Paleoceanography 26, PA2216.

White, E.I., 1926. Eocene fishes from Nigeria. Bulletin of the Geological Survey of Nigeria 10, 1–82.

White, E.I., 1934. Fossil fishes of sokoto Province. Bulletin of the Geological Survey of Nigeria 14, 1–78.

White, E.I., 1955. Notes on african Tertiary sharks. Bulletin of the Geological Survey of Nigeria 5, 319–325.

Wing, S.L., Harrington, G.J., Smith, F.A., Bloch, J.I., Boyer, D.M., Freeman, K.H., 2005. Transient floral change and rapid global warming at the Paleocene–Eocene boundary. Science 310, 993–996.

Wood, G.D., Gabriel, A.M., Lawson, J.C., 1996. Palynological techniques-processing and microscopy. In: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Application, Volume 1 Principles. American Association of Stratigraphic Palynologists Foundation, Dallas, pp. 29–50.

Wood, R.C., 1973. Fossil marine turtle remains from the Paleocene of the Congo. Annales du Musée Royal de l'Afrique Centrale Tervuren Belgique Sciences Géologiques 75, 2–35.

Yans, J., Gerards, T., Gerrienne, P., Spagna, P., Dejax, J., Schnyder, J., Storme, J.-Y., Keppens, E., 2010. Carbon-isotope of fossil wood and dispersed organic matter from the terrestrial Wealden facies of Hautrage (Mons basin, Belgium). Palaeogeography Palaeoclimatology Palaeoecology 291, 85–105.

Yans, J., Amaghzaz, M., Bouya, B., Cappetta, H., Iacumin, P., Kocsis, L., Mouflih, M., Selloum, O., Sen, S., Storme, J.-Y., 2014. First carbon isotope chemostratigraphy of the Ouled Abdoun phosphate Basin, Morocco; implications for dating and evolution of earliest African placental mammals. Gondwana Research 25, 257–269.

Zachos, J.C., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.

Zachos, J.C., McCarren, H., Murphy, B., Röhl, U., Westerhold, T., 2010. Tempo and scale of late Paleocene and early Eocene carbon isotope cycles: implications for the origin of hyperthermals. Earth and Planetary Science Letters 299, 242–249.