



## **Climate, flora and fauna changes in the Sahara over the past 500 million years**

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The present-day Sahara occupies an area of slightly over 8 million km<sup>2</sup> in Africa, between latitudes 16 and 32° N, circumscribed within the isohyet of 100 ± 50 mm mean annual rainfall. The hyperarid area alternately expanded and shrank on both sides of a seemingly narrow semi-permanent eremitic zone along the Tropic of Cancer during the course of the Quaternary epoch (1.7 Ma). The Cenozoic, Mesozoic and Paleozoic Sahara, in turn, has undergone drastic climatic changes as the African continent drifted northward from its Antarctic position to reach its present latitudinal situation. But, seemingly the Sahara was never the large desert it now is, with the exception perhaps of the Upper Triassic Lower Liassic epochs. The Pleistocene and Holocene contrasting climate changes induced large variations in flora and fauna distribution, as well as in geomorphic processes.

The flora shifted from that of typical desert to tropical savanna and Mediterranean forest or steppe, depending on period and location. Fauna, in turn, changed more in abundance than in nature, since the same groups have been in existence since the Upper Pliocene–Lower Pleistocene. Large mammals, for instance, were mainly of Afro-tropical kinship throughout the Pleistocene and Holocene, while small mammals, in contrast, were predominantly of Mediterranean origin over the same periods. And such is still the case. There were varying large degrees in density of occurrence, but relatively minor fluctuations in nature, in response to such environmental changes as lake and dune expansion and retreat, and even glacier expansion and melting at higher elevations. The present-day man-made expansion of desertic conditions to the north and south actually threaten both flora and fauna alike in the short- and medium-term. Most African large mammals, still present in the desert until the second half of the 19th century, have now become extinct, or are on the very verge of extinction in the Sahara (some may be surviving further south, and/or in the East Africa's parks network). The situation, however, is far less dramatic for the flora, which still includes almost 3000 species of vascular plants, although some species — of economic value or not — are in danger from the man-made destruction of their habitat.

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**Keywords:** Sahara; desert; climate change; biogeography; flora; fauna; natural resources; biodiversity; desertification

### **Outline of the present geographical situation and subdivisions of the Sahara**

Setting the present upper limit of the Sahara on the  $100 \pm 50$  mm isohyet of mean annual rainfall (MAR), proposed by the present author some 40 years ago, has now received a broad acceptance among climatologists, geographers and biologists (Le Houérou, 1959, 1995a).

Our interpretation of the 1:10 million scale colour map of the Ecologically Homogenous Territorial Units (EHTU) (Popov *et al.*, 1991) results in an area of 8.14 million km<sup>2</sup> for the 80 Saharan EHTU recognized in this map of acridian habitats within the 100 mm isohyet bond of MAR (Fig. 1).

Moreover, there are many possible subdivisions in our classifications of the Sahara available in terms of climate, environment, geomorphology, flora and fauna, not to mention crops, livestock and human populations (Monod, 1936, 1973; Capot-Rey, 1953; Cloudsley-Thompson, 1954, 1984a; Dubief, 1959, 1963; Le Houérou, 1959, 1986, 1990, 1992, 1995; Quézel, 1965, 1978; Schiffers, 1971).

The 80 EHTU mentioned above form six broad divisions.

- Northern Sahara lowlands: MAR > 25 mm, winter rains, elevation < 1000 m
- Southern Sahara lowlands: MAR > 25 mm, summer rains, elevation < 1000 m
- Sahara Highlands: MAR > 25 mm, winter and/or summer rains, elevation > 1000 m
- Oceanic Sahara lowlands: MAR > 25 mm, elevation < 1000 m, distance from the Atlantic < 50 km
- Central Sahara lowlands: MAR < 25 mm, no marked rain seasonality, elevation < 1000 m
- Red Sea lowland Sahara: MAR < 25 mm, winter rains, elevation < 1000 m

Each, in turn, can be subdivided into at least three to four sub-units, as shown in Figs 2 and 3 (Dubief, 1963; Quézel, 1978; Le Houérou, 1990).

These divisions and their characteristics should be kept in mind when assessing climatic, environmental and biological changes during the course of Pleistocene and Holocene epochs: different geographical areas of the Sahara may contemporaneously have harboured Mediterranean forest, Mediterranean steppe, tropical savanna and climatic desert. Conversely, a given geographical division may have alternately supported forest, steppe, savanna or desert in different times. Things are therefore globally much more complex than the semantic unit 'desert' might suggest; the natural temptation for oversimplification should, therefore, be strongly resisted if one is to avoid deeply erroneous conclusions.

The subject is made the more difficult as our present state of knowledge (and ignorance) varies from one period to the next. Generally speaking, the higher rainfall periods are better documented than hyperarid periods as the former permit conservation of much more datable elements of flora, fauna and sediments. There is, on the other hand, a decreasing gradient of the amount and accuracy of information on the changes from moist to dry environments, and from Holocene to Upper Pleistocene epochs.

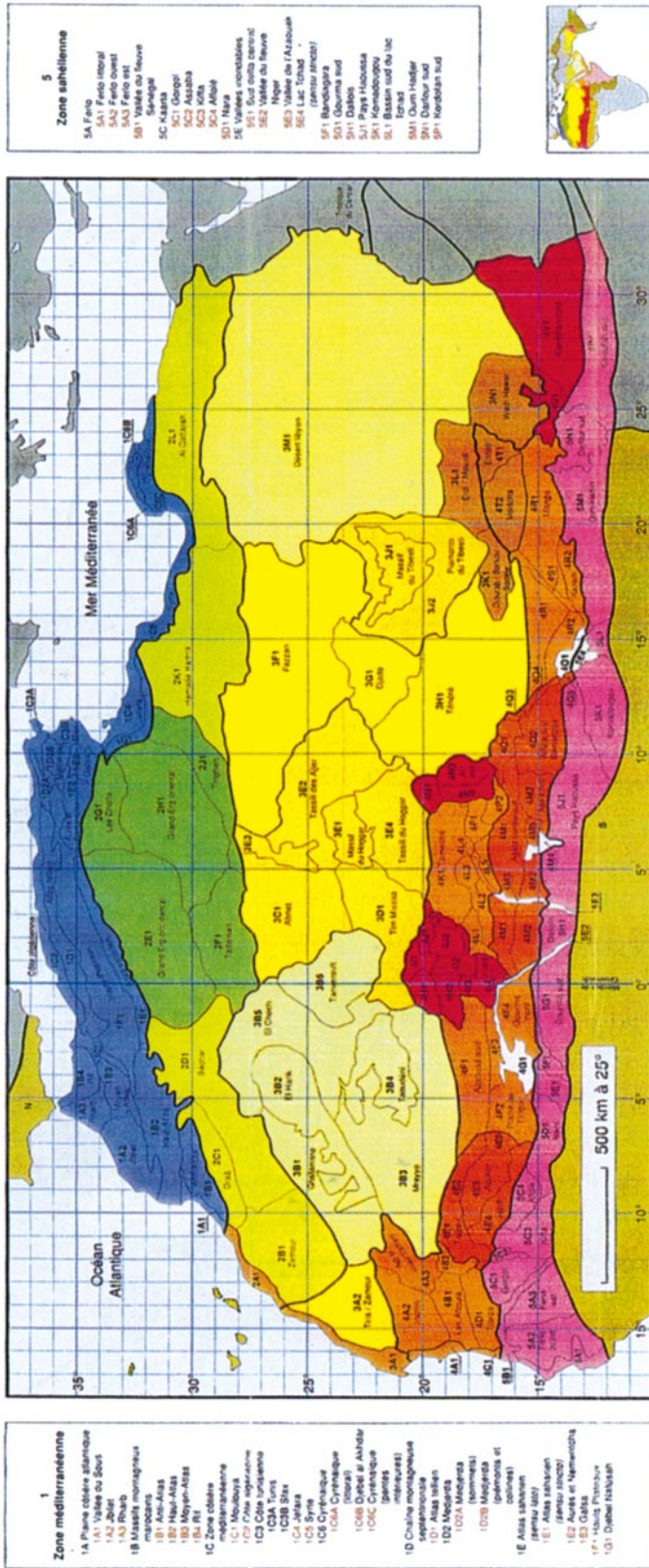
### **Climatic changes before the Quaternary period**

The African continent started its slow northward move from the Pangaeon South Pole continent in the Upper Silurian and Lower Devonian periods, some 400 million years ago (Ma).

**Figure 1.** (facing page). Ecologically Homogeneous Territorial Units (EHTU) (from Popov *et al.*, 1991).

G. B. POBOY, J.-F. BEAUKIN & J. GIGELT, 1991

Carte des unités territoriales écologiquement homogènes (UTEH)



- 1 Zone méditerranéenne**
- 1A Plaine côtière atlantique
  - 1A1 Vallée du Sous
  - 1A2 Zibit
  - 1A3 Zibit
  - 1B Massifs montagneux marocains
  - 1B1 Anti-Atlas
  - 1B2 Haut-Atlas
  - 1B3 Moyen-Atlas
  - 1B4 Rif
  - 1C Zone côtière méditerranéenne
  - 1C1 Moulouya
  - 1C2 Oued
  - 1C3 Côte saharienne
  - 1C4 Tiris
  - 1C5 Siba
  - 1C6 Jifara
  - 1C7 Bys
  - 1C8 Oued
  - 1C9 Oued
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  - 1C97 Oued
  - 1C98 Oued
  - 1C99 Oued
  - 1C100 Oued

- 5 Zone saharienne**
- 5A Fano
  - 5A1 Fano oriental
  - 5A2 Fano ouest
  - 5A3 Fano est
  - 5B Fano sud
  - 5B1 Fano sud-ouest
  - 5B2 Fano sud-est
  - 5C Kabara
  - 5C1 Gougl
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- 2 Zone méditerranéo-saharienne**
- 2A Agadir nord
  - 2B Zemmour
  - 2C Draa
  - 2D Grand Erg occidental
  - 2E Les Oueds
  - 2F Grand Erg oriental
  - 2G Hauts Plateaux
  - 2H Hauts Plateaux
  - 2I Hauts Plateaux
  - 2J Hauts Plateaux
  - 2K Hauts Plateaux
  - 2L Hauts Plateaux
  - 2M Hauts Plateaux
  - 2N Hauts Plateaux
  - 2O Hauts Plateaux
  - 2P Hauts Plateaux
  - 2Q Hauts Plateaux
  - 2R Hauts Plateaux
  - 2S Hauts Plateaux
  - 2T Hauts Plateaux
  - 2U Hauts Plateaux
  - 2V Hauts Plateaux
  - 2W Hauts Plateaux
  - 2X Hauts Plateaux
  - 2Y Hauts Plateaux
  - 2Z Hauts Plateaux

- 3 Zone saharienne**
- 3A Sahara occidental
  - 3A1 Agadir sud
  - 3A2 Tine / Zemmour
  - 3B Oued
  - 3B1 Oued
  - 3B2 Oued
  - 3B3 Oued
  - 3B4 Oued
  - 3B5 Oued
  - 3C Anad
  - 3C1 Anad
  - 3C2 Anad
  - 3C3 Anad
  - 3C4 Anad
  - 3C5 Anad
  - 3C6 Anad
  - 3C7 Anad
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  - 3C47 Anad
  - 3C48 Anad
  - 3C49 Anad
  - 3C50 Anad

- 4 Zone sahélo-saharienne**
- 4A Incha et Adjar mauritaines
  - 4A1 Incha (nord)
  - 4A2 Incha (sud)
  - 4A3 Incha (est)
  - 4A4 Incha (ouest)
  - 4A5 Incha (nord-est)
  - 4A6 Incha (nord-ouest)
  - 4A7 Incha (sud-est)
  - 4A8 Incha (sud-ouest)
  - 4A9 Incha (est-ouest)
  - 4A10 Incha (ouest-est)
  - 4A11 Incha (nord-sud)
  - 4A12 Incha (sud-nord)
  - 4A13 Incha (nord-est-sud)
  - 4A14 Incha (nord-ouest-sud)
  - 4A15 Incha (sud-est-nord)
  - 4A16 Incha (sud-ouest-nord)
  - 4A17 Incha (est-ouest-sud)
  - 4A18 Incha (ouest-est-nord)
  - 4A19 Incha (nord-sud-est)
  - 4A20 Incha (nord-sud-ouest)
  - 4A21 Incha (sud-nord-est)
  - 4A22 Incha (sud-nord-ouest)
  - 4A23 Incha (nord-est-sud-est)
  - 4A24 Incha (nord-est-sud-ouest)
  - 4A25 Incha (nord-ouest-sud-est)
  - 4A26 Incha (nord-ouest-sud-ouest)
  - 4A27 Incha (sud-est-nord-est)
  - 4A28 Incha (sud-est-nord-ouest)
  - 4A29 Incha (sud-ouest-nord-est)
  - 4A30 Incha (sud-ouest-nord-ouest)
  - 4A31 Incha (est-ouest-sud-est)
  - 4A32 Incha (est-ouest-sud-ouest)
  - 4A33 Incha (ouest-est-nord-est)
  - 4A34 Incha (ouest-est-nord-ouest)
  - 4A35 Incha (nord-sud-est-est)
  - 4A36 Incha (nord-sud-est-ouest)
  - 4A37 Incha (nord-sud-ouest-est)
  - 4A38 Incha (nord-sud-ouest-ouest)
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  - 4A40 Incha (sud-nord-est-ouest)
  - 4A41 Incha (sud-nord-ouest-est)
  - 4A42 Incha (sud-nord-ouest-ouest)
  - 4A43 Incha (nord-est-sud-est-est)
  - 4A44 Incha (nord-est-sud-est-ouest)
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  - 4A99 Incha (sud-est-nord-est-est-est)
  - 4A100 Incha (sud-est-nord-est-est-ouest)

- 5 Zone saharienne**
- 5A Fano
  - 5A1 Fano oriental
  - 5A2 Fano ouest
  - 5A3 Fano est
  - 5B Fano sud
  - 5B1 Fano sud-ouest
  - 5B2 Fano sud-est
  - 5C Kabara
  - 5C1 Gougl
  - 5C2 Assaba
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Ordovician (500–440 Ma) continental and shallow channel-sea sandstone deposits outcrop over large areas in the present Sahara (Furon, 1950, 1957; Fabre *et al.*, 1976), particularly in the Inner Tassili plateaux of the Ahaggar, around the Precambrian core (Suggarian, Pharuzian). These show evidence of erosion forms developed below and around a thick ice cap (Inlandsis) similar to those documented in Canada, Greenland and Scandinavia for the last Quaternary glaciation (*c.* 20,000 years ago). The Upper Ordovician glaciation (Caradoc and Ashgill) is actually one of the best documented worldwide, apart from the Pleistocene's, with striated bedrocks, U-shaped valleys, tillites, moraines, hydrolaccoliths and other ring-shaped structures ('kettles', 'pingos'), polygonal soils, etc., all typical of permafrost. All channel and glacial deposits show a slow northward sedimentation drift (Beuf *et al.*, 1971; Rognon *et al.*, 1972; Rognon, 1989*b*; Fabre *et al.*, 1976).

But the Ordovician glaciation occurred at a time when there was still no terrestrial vegetation on earth. The chief biological remains found were '*Bilobites*' and '*Tigillites*' imprints of mud-earth worms and arenicolous annelids (*Scolites*), sometimes very numerous (Rognon *et al.*, 1972). All this bears witness to the existence of the future Sahara in the Antarctic Pangaea up to *c.* 440 Ma.

When the Ordovician ice cap melted, huge amounts of water were released into a transgressing shallow, cold, hypo-saline Silurian (= Gothlandian) Sea characterized by graptolithic shale and clay deposits. These presently outcrop over large expansions across the Sahara from southern Morocco and Mauritania through Algeria and Libya (Fabre *et al.*, 1976). They, in particular, constitute the Intra-Tassilian trough of the Ahaggar.

The present-day Sahara was then exundated anew, with the deposition of thick lagoon and river sandy sediments of Devonian age (395–345 Ma) that constitute the Outer Tassili ring of plateaux around the nucleus of the Ahaggar massif. These

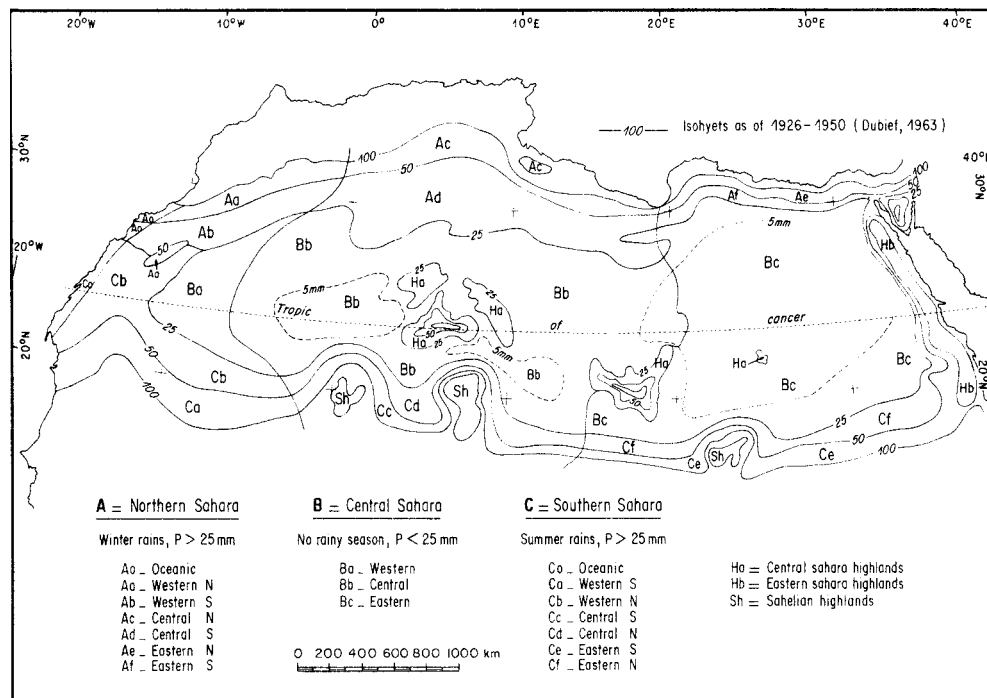
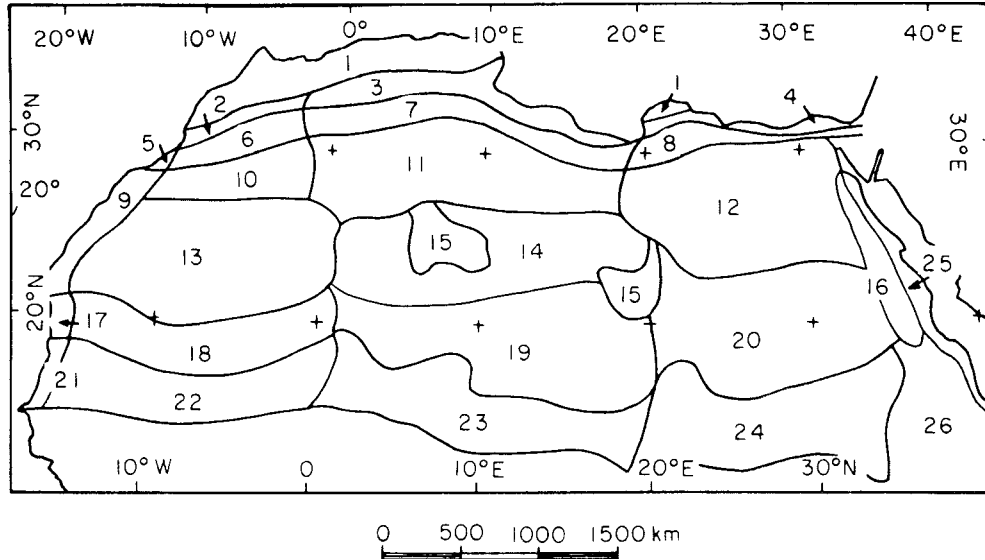


Figure 2. Biogeographic limits and subdivisions of the Sahara (Le Houérou, 1990, 1995).



**Figure 3.** Sketch of the phytogeographic subdivisions of the Sahara and neighbouring territories (from Quézel, 1978; Le Houérou, 1990, 1995).

- |  |  |
|--|--|
| 1 - Mediterranean region (semi-arid to hyper-humid zones)                            |  |
| 2 - Western arid steppic zone  | Mediterranean region<br>Ibero-Maghribian Domain                  |
| 3 - Central arid steppic zone  |  |
| 4 - Eastern arid steppic zone  |  |
| 5 - Oceanic Northern Sahara transition zone  |  |
| 6 - Western Northern Sahara transition zone  | Saharo-Arabian region<br>Northern Sahara                         |
| 7 - Central Northern Sahara transition zone  |  |
| 8 - Eastern Northern Sahara transition zone  |  |
| 9 - Oceanic Central Sahara   | Saharo-Arabian region  |
| 10 - NW Central Sahara   | Central Sahara Plains  |
| 11 - Northern Central Sahara   |  |
| 12 - NE Central Sahara   |  |
| 13 - Western Central Sahara  |  |
| 14 - Central Central Sahara  | Saharo-Arabian region & Mediterranean region<br>Sahara Highlands |
| 15 - Central Sahara Highlands  |  |
| 16 - Eastern Sahara Highlands  |  |
| 17 - Oceanic Southern Sahara   | Saharo-Arabian region<br>Southern Sahara                         |
| 18 - Western Southern Sahara   |  |
| 19 - Central Southern Sahara   |  |
| 20 - Eastern Southern Sahara   |  |
| 21 - Oceanic Sahel   | Sadano-Angolan region<br>Sahelian domain                         |
| 22 - Western Sahel   |  |
| 23 - Central Sahel   |  |
| 24 - Eastern Sahel   |  |
| 25 - Saharo-Arabian region, Eastern Sahara Zone, Red Sea shores                      |  |
| 26 - Sudano-Angolan region, East African & Erythreo-Sabeian domain, E-A Montane Zone |  |

Devonian sandstones are rich in iron oxides, red silts and clays as a result of chemical weathering on a continent that had become covered with terrestrial vegetation (Emberger, 1944).

Coral sea deposits as well as palæo landforms and rock weathering suggest a rainy climate with a mild to warm temperature. By the Upper Devonian and Lower Carboniferous periods (Fammenian, Tournaisian, Viséan, Namurian (350–320 Ma)) arboreal ferns, lycopods and horse-tails were already present in the continental deposits of the now Djado-Ennedi plateaux, suggesting a wet-tropical climate (Batton *et al.*, 1965; Busson, 1967, 1970, 1972).

Palæo-magnetic data suggest the Saharan area was already then in the vicinity of the Tropic of Capricorn, in a situation somewhat reminiscent of the present geographic setting of the Karroo or the Kalahari, but with a different climate (Rognon, 1989a).

Since the late Devonian period (345 Ma), throughout the Carboniferous epochs, most of the Sahara was, to a large extent, under a tropical sea until the Permian (280 Ma).

During the Permian and Lower Triassic periods (225 Ma), the sea slowly withdrew from the continent, from west to east, while Africa continued its northward drift. The terrestrial arboreal flora included ferns, lycopods, horsetails and primitive gymnosperms (Gingkoales, Cycadales, Bennettiales, Caytoniales, Araucariaceae). The fauna included dinosaurs (also present in the Karroo at the same time). Sediments included red clays and lacustrine limestone. All these characteristics suggest a sub-humid to hyper-humid tropical Saharan environment. In no way does this suggest a tropical desert, such as that present at the same time further north in Eurasia from Ireland to Poland, and particularly well documented by North Sea oil geologists (Rognon, 1989b).

The Permo-Carboniferous series constitutes the floor of the continental Intercalary (CI) and of its eastern Sahara counterpart the Nubian Sandstone (NS) formations. The CI and the NS are both most reminiscent of the Karroo formation of southern Africa, with close faunal kinships (Kilian 1930, 1937; Busson, 1970, 1972; Fabre *et al.*, 1976; Rognon, 1989b; Lefranc & Guiraud, 1990). Paleomagnetic data suggest the future Sahara was located between the Tropic of Capricorn and the Equator during the Permian period.

The first Triassic marine and continental sediments of Buntsandstein and Muschelkalk (225–210 Ma) were then topped with thick saline deposits of evaporites (gypsum, anhydrite, sodium chloride, dolomite) of the Keuper (Upper Trias, 210–190 Ma) and Lias (Lower Jurassic, 190–175 Ma).

All these suggest an arid climate, similar to large parts of the world during the same periods. Paleomagnetic information infer the future Sahara was between 5 and 10° S by the Lower Jurassic. Such latitudes correspond today with a tropical climate such as in the Sudano-Zambesian ecozone, while South America had not yet begun its westward drift off Africa. The CI and NS spread over time from the Permian to the Upper Cretaceous (Maestrichtian) periods. They outcrop over some 1.2 million km<sup>2</sup>; about two-thirds of which is located in the eastern Sahara (NS). NS also outcrops over 0.5 million km<sup>2</sup> in the eastern Sahel of the Sudan Republic. The CI contains one of the largest aquifer in the world (Guiraud, 1988). It is present over 0.8 million km<sup>2</sup> of the northern Sahara of Algeria, Tunisia and Libya, north of the Tropic of Cancer. The CI aquifer yields some 9.5 m<sup>3</sup> s<sup>-1</sup> of good to fair quality water from 110 boreholes and many foggaras (= qanats), with a total reserve estimated 6 × 10<sup>13</sup> m<sup>3</sup> (Gischler, 1979; Pallas, 1980; Lefranc & Guiraud, 1990; Margat, 1992; Guiraud & Bellion, 1995).

The NS aquifer of Kufra covers an area of 1.8 million km<sup>2</sup>, producing 4 m<sup>3</sup> s<sup>-1</sup> of excellent water (500 p.p.m. > total dissolved solids) seemingly dating back to a Palæo-Nile. The reserve is still unknown, but apparently huge. CI and NS waters seem much older than previously thought (UNESCO, 1972); according to recent isotopic <sup>36</sup>Cl datation they now appear to be aged over 30,000 years on the margins of the aquifer

and up to 100,000–500,000 in the central trough faults (Guiraud, 1993; Guiraud & Bellion, 1995).

The flora of the CI and NS was studied by Batton *et al.* (1965) and Busson (1967, 1970, 1972), and reviewed by Lefranc & Guiraud (1990). This review is summarized in Table 1.

The recorded fauna includes 12 species of bivalves, 20 species of dinosaurs, fishes, crocodiles etc. Lefranc & Guiraud (1990) conclude their review 'The Flora of the CI includes vegetal remains belonging to biotopes typical of high mountain forest, arid, semi-arid and mainly humid Mediterranean and tropical environments. All of them evoke warm climatic conditions with alternating dry and wet seasons, sometimes prolonged dry and short wet seasons and semi-arid conditions. Data obtained from animal remains have a similar significance: warm climate, variable wetness, depending on region. Continental sweet water fishes, dominate, associated with estuarine species including skates and sharks. Reptiles include tortoises, crocodiles, large snakes and many species of dinosaurs. The fossilized plants and animals of the CI indicate a wide variety of biotopes that evoke a vast and complex territory, comparable to the present African continent. One constant fact throughout the region, however, was a tropical

**Table 1.** Summary of the undifferentiated fossil floras of the Continental Intercalary and Nubian Sandstone formations (after Lefranc & Guiraud, 1990)

Order	Family	Triassic–Liassic (210–175 Ma)	Dogger–Mälm (175–136 Ma)
		Species	
<b>Fern Allies</b>			
	Equisetales	2	2
	Lycopodiales	1	1
<b>Ferns</b>			
	Filicales	6	
<b>Gymnosperms</b>			
	Bennettitales	1	3
	Caytoniales	1	1
	Coniferales	5	9
	Araucariaceae	2	1
	Cupressaceae*	1	1
	Ephedraceae		1
	Pinaceae†	1	
	Podocarpaceae	1	2
	Taxaceae		2
	Taxodiaceae		2
	Cordaitales	1	
	Cycadales	1	2
	Gingkoales		1
<b>Angiosperms</b>			
	Ebenaceae		1
	Lauraceae‡		2
	Nymphaeaceae		1

\*Subtribe Cupressineae.

†Subtribe Abietineae.

‡Includes Cinnamomaceae.

**Table 2.** Tentative sketch for correlating landmarks of the Upper Pleistocene and Holocene in the northern southern Sahara

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Years B.P.	Climatic fluctuations		Human activities and industries	Europe (Penck & Brückner, 1901, 1905, 1909; Blytt, 1876-1909; Sernander, 1908, 1910; Mangerud <i>et al.</i> , 1974)	Fauna	Flora and vegetation	Years B.P.
	S Sahara	N Sahara					
Present	Hyperarid	Hyperarid	Settlement of nomads, urbanization, man-made desertization		Extinction of large mammals	Increasing scarcity of trees and shrubs; Chenopodiaceae Amaranthaceae Mediterranean	Present
40 450				Little Ice Age	Presence of African large mammals		Forest remnants in the north and Highlands
2200 3000	Historic Period; aridity Arid to semi-arid		Cameline Period Equine Period	Sub-Atlantic Sub-Boreal Highlands; tropical		Mediterranean Forest in north and Highlands	2200 3000
3500	Climatic aridization		Bovine/pastoralists		Rich and diversified	Forest and savana in the south	3500
5500	Tafolian semi-arid	Rharbian semi-arid	Bovine/'Round Heads' Protomediterranean Cromagnoids	Atlantic	Afro-tropical	Gramineae and Cyperaceae	5500
6500	Nouakchottian optimum	Rharbian; semi-arid to sub-humid	Buffalo/Hunters			Mediterranean forest and tropical Savanna Gramineae and Cyperaceae	6500
8000	Short dry spell		Neolithic	Boreal	?	Chenopodiaceae	8000
10,500	Semi-arid to sub-humid Chadian		Capsian (Protoneolithic)	Pre-Boreal, Younger Dryas	Afro-tropical	Mediterranean forest and tropical savanna	10,500
12,500	Beginning of semi-arid build-up of Ogolian dune system	Beginning of semi-arid build-up of major sand seas	Iberomaussian (Epipaleolithic, Protomédit. Cromagn.) ( <i>Homo sapiens</i> )	Allerød Bölling	?	Chenopodiaceae, Amaranthaceae and <i>Artemisia</i>	12,500

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**Table 2.** *Continued*

Years B.P.	Climatic fluctuations		Human activities and industries	Europe (Penck & Brückner, 1901, 1905, 1909; Blytt, 1876–1909; Sernander, 1908, 1910; Mangerud et al., 1974)	Fauna	Flora and vegetation	Years B.P.
	S Sahara	N Sahara					
19,000	Hyperarid; Inchirian wet period	Hyperarid; Soltanian pluvial-erosion cycle	Aterian (Paleolithic) ( <i>H. neanderthalensis</i> ??)		? Afro-tropical	Mediterranean forest and tropical, savanna	19,000
40,000	Beginning of wet period			Wurm			40,000
70,000	Hyperarid; Symm. erosion sand ridges	Soltanian dry period; sand seas?	( <i>H. erectus</i> )		?	Chenopodiaceae, Amaranthaceae and <i>Artemisia</i>	70,000
125,000	Wet/warm	Tensiftian pluvial	(Levalloisian–Mousterian)	Eemian Inter- glacial Optimum	Afro-tropical	Mediterranean forest and tropical savanna	125,000
150,000	Hyperarid; leveled-down sand sheets	Hyperarid; sand seas?	Acheulean ( <i>H. habilis</i> ) (Paleolithic)	Riss	?	Chenopodiaceae, Amaranthaceae and <i>Artemisia</i>	150,000

CHANGES IN THE SAHARA

climate. The opening of the South Atlantic had only just begun during the mid-Cretaceous (120–100 Ma). The proximity of the American and African continents produced a 'continental effect' which accentuated the semi-arid character of northern Africa. Palaeomagnetic data, in good agreement with paleoclimatic and paleogeographic information, place the centre of the CI deposition directly under the probable trace of the palaeo-equator during the Jurassic and Lower Cretaceous'.

The Lower Cenozoic period (65–50 Ma) was characterized by a large marine transgression of a tropical sea that covered most of the Sahara and North Africa (Guiraud, 1978; Guiraud & Ousmane, 1980). The Continental Terminal (CT) is a formation of various ages from the mid Eocene (Lutetian) to the Quaternary epochs, but mostly Mio-Pliocene (26–1.7 Ma). It consists of unconsolidated sands, silts, conglomerates, clays and contains bauxite deposits, iron and lateritic hard pans (Siderolitic strata) (Guiraud, 1978; Guiraud & Ousmane, 1980; Lang *et al.*, 1990; Guiraud & Bellion, 1995). CT's bauxite, iron and lateritic hardpans occur up to 20–23° N (e.g. in the Umm Ruwaba formation of Kordofan). These sediments testify for a humid equatorial climate in these areas at the time of deposition since bauxite, iron and lateritic hardpans are nowadays only being laid down in Africa south of Lat. 8° N, i. e. in the Guinean eco-zone (Rognon, 1989a; Le Houérou *et al.*, 1993). At the same time, in the present north-western Sahara of Algeria and Morocco, there took place the deposition of thick lacustrine limestone, the Hammada formation, containing gasteropods (snails), Characeae and small mammals, all typical of a semi-arid to sub-humid climate.

The CT is the store formation of very important aquifers in the northern Sahara and arid zones of Algeria, Tunisia and western Libya. This CT aquifer discharges some  $21.5 \text{ m}^3 \text{ s}^{-1}$ , of which 8.5 is from 2000 boreholes and 13.5 from natural evaporation in the great salt lakes of the Algerian–Tunisian border (Gischler, 1979). The recharge is estimated to be  $18 \text{ m}^3 \text{ s}^{-1}$  from runoff on the Saharan Atlas.

The Sahara was at the present latitudes of the Sudanian ecozone (5–15° N) during the Upper Cretaceous and Eocene epochs (100–25 Ma). It reached its present latitudinal situation (16–32° N) during the Neogene, *c.* 10–20 Ma. The northward drift was then *c.*  $2.5 \text{ cm year}^{-1}$ ;  $4 \text{ cm year}^{-1}$  is currently being recorded in the Ethiopian rift.

### The Sahara during the Quaternary Period

During most of the Quaternary Period (1.6 M years), the Sahara had a number of dry-wet cycles, the causes of which are not clearly understood. There is, however, a consensus that these cycles relate to the strength and weakness of the Saharan anticyclonic pressure zone and, therefore, to advances and retreats of the Polar Front (PF) and the Intertropical Convergence Zone (ITCZ). Why the Saharan high pressure belt is alternately strong and weak is not clear. It may be connected with oceanic temperatures (Leroux, 1976, 1983; Kutzbach, 1981, 1987) and currents, and with the Pacific Ocean's Southern Oscillation that seems to control El Niño and drought phenomena around the world. It is now generally admitted that the 'forcing' of the earth's orbital processes, along with the Milankovitch theory (Milankovitch, 1930, 1941), plays a major role in the wet–dry cycles with a periodicity of 100,000, 41,000 and 21,000 years, perhaps in combination with shorter cycles of solar activity (Bernard, 1962, 1986; Lamb, 1977; Berger, 1978, 1981; Berger *et al.*, 1984; Lorius *et al.*, 1985; Lorius, 1989; Broecker & Denton, 1990).

There seems to have been at least eight to ten major dry-wet cycles since the Upper Pliocene. Thirty years ago, some scientists believed that European glaciations, related to the Penck & Brückner (1901, 1905, 1909) chronology for the Alps, were contemporary with the Saharan 'pluvial' periods and with the Blytt-Sernander

chronology (Blytt, 1909; Sernander, 1910) for the Upper Pleistocene and Holocene of Scandinavia. Then came the Dubief-Balout theory (Dubief, 1951; Balout, 1955) of the 'climatic swing of the Saharan edges'. According to this theory, there are periods when the Polar Front moves south, alternating with periods of a northward advance of the ITCZ. Consequently a dry period in the northern Sahara would have corresponded with a wet period in the south and *vice versa*. But there is now an increasing tendency to assume that the weakness of the Sahara anticyclone may produce a southward move of the Polar Front and, at the same time, a northward march of the ITCZ. The hyperarid nucleus of the Sahara, along the Tropic of Cancer, would therefore have alternately expanded and shrunk over a N-S distance of 1000–2000 km. The absolute dating chronology shows an almost perfect matching of the Saharan hyperarid periods with the higher latitude's glacials and the correspondence between a semi-arid Sahara and the interglacials (Fig. 5) for the Mid- and Upper Pleistocene and the Holocene. However, at present we are in a period that is both interglacial in the higher latitudes and hyperarid in the Sahara, thus contradicting the theory. Furthermore, fossil ergs expanded 400–600 km south of the present southernmost limit of drifting sands in the Sahel, whereas there is no fossil dune system of any substantial size north of the present limit of the Sahara. It follows that the limits of the Sahara do not seem to have shifted further north from their present position during the Quaternary, contrary to the southern limit which moved considerable distances southward (Fig. 4).

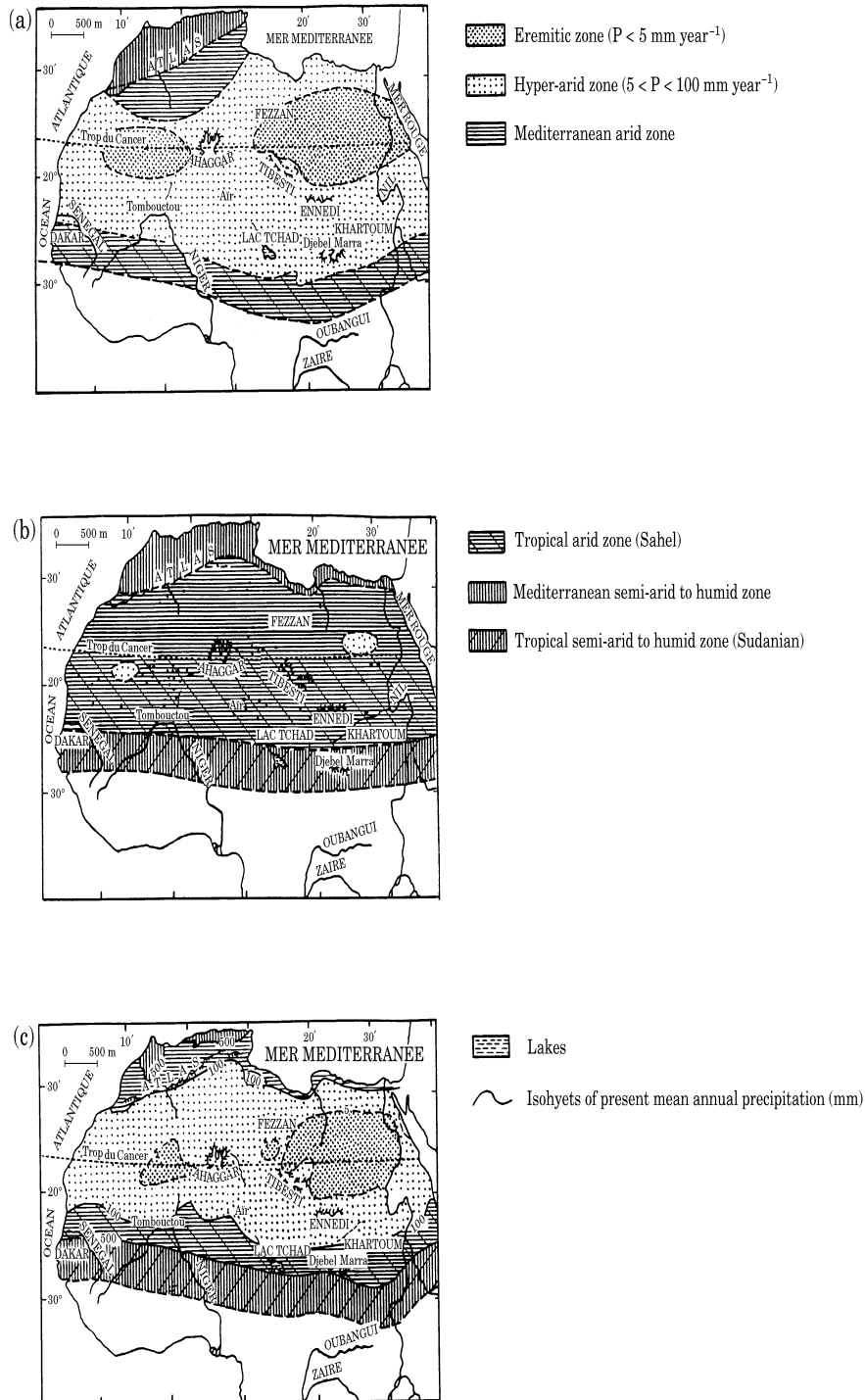
#### *The Pliocene, the Lower and Mid-Pleistocene*

The Sahara seems to have had a semi-arid to sub-humid tropical climate during the Cenozoic Epoch. Geological and palaeontologic data suggest a wet equatorial climate in the Lower Eocene, shifting in the Oligocene towards a Sudano-Guinean type of savanna, with a clear-cut dry season (Maley, 1980, 1981). The first evidence of aridity is known in the Mid-Upper Pliocene of the southern Sahara from aeolian deposits and fossils of xerophytic vegetation (*Retama* cf. *raetam*, *Tamarix* spp.). A period of aridity also occurred in North Africa during the Villafranchian, between the Pliocene and Pleistocene. This bore witness to deteriorating tropical conditions and the progressive disappearance of the archaic Neogene fauna (*Elephas africanus*, *Stylohipparion*, *Libytherium* and *Machairodus*). Some large tropical mammals (*Rhinoceros simus*, *Hyaena striata*, *Alcelaphus bubalis*, *Gorgon taurinus prognu*, *Taurotragus derbyanus*) together with present-day arid and semi-arid zone species still exist. The Villafranchian fauna of Ain Brimba, near Kebili, Tunisia, for instance, includes: *Gazella dorcas*, *Ctenodactylus gundi*, *Lepus kabilicus*, *Oryctolagus cuniculus*, *Canis aureus*, *Meriones cf shawi*, *Jaculus* sp., *Elephantulus rozetti*, *Hystix cristata*, *Struthio camelus*, *Acinonyx jubatus*, *Ammotragus lervia* (Joleaud, 1935; Arambourg, 1949, 1952; Arambourg & Coque, 1958). Most of these were part of the Saharan fauna less than 100 years ago and a few are still to be found in the desert today. But the presence of a few species (*Ursus arctos*, *Rhinoceros mercki*, *Bos primigenius*) suggests that conditions were somewhat colder than now.

The Villafranchian flora of northern Tunisia shows a shift from tropical Pliocene (21%) to Mediterranean species (52%) and boreal elements (21%). Some 47% of this flora is still present (*Quercus faginea*, *Q. suber*, *Q. ilex*, *Olea europaea*, *Cetonia siliqua*, *Laurus nobilis*) along with some boreal species which no longer exist in North Africa (*Fagus sylvatica*, *Ulmus scabra*).

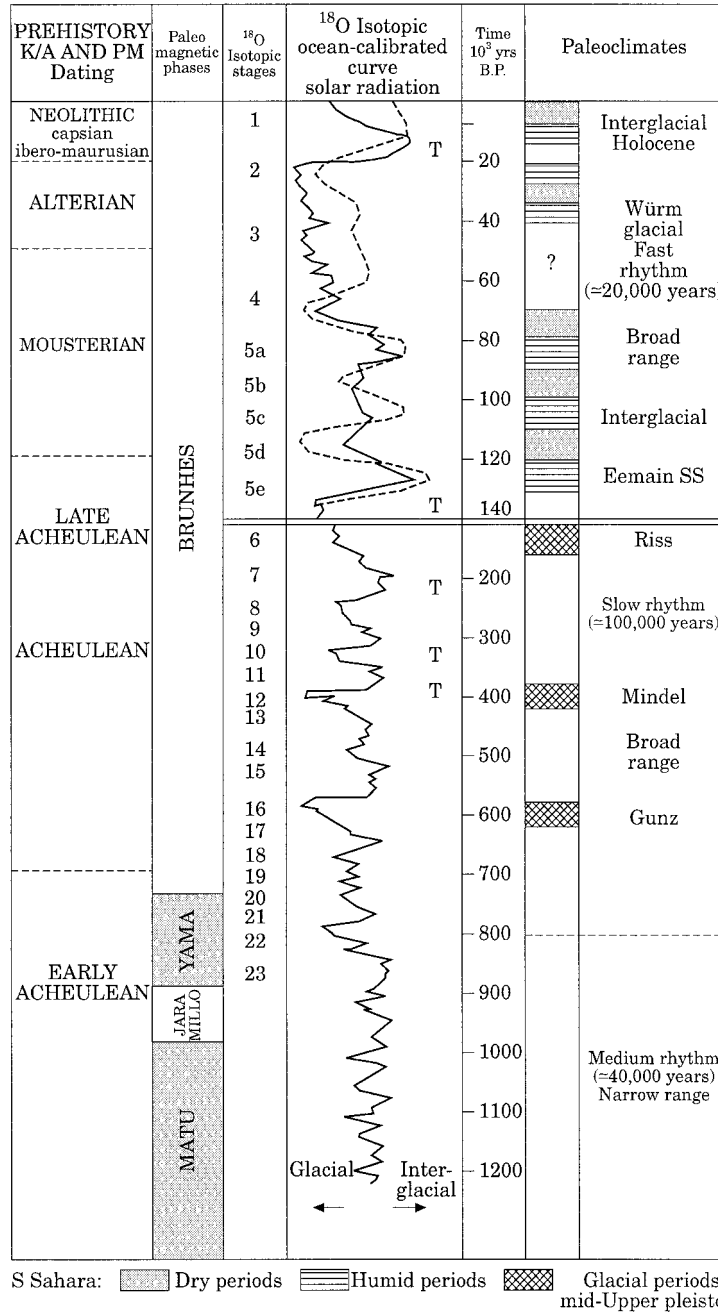
It is probable that the major sand seas of the Sahara began to be established at that time.

It also corresponded with a thick generalized limecrust north of the tropics, the Villafranchian or Moulouyan limecrust, also called the 'Salmon crust of Helicidae' (because of its colour and the frequent presence of snails within it) (Durand, 1953;



**Figure 4.** Climatic and biogeographic variation in the Sahara and neighbouring zones over the past 20,000 years (in part from Duplessy *et al.*, 1989*a, b*): (a) The Sahara 18,000 years B.P.; (b) The Sahara 8000 years B.P.; (c) The Sahara today.

Choubert *et al.*, 1956; Coque, 1962). Limecrust and gypsum crust formations seem to correspond with transition periods between pluvial and arid conditions (Coque, 1962). It was at one time believed that the erosion period of each sedimentary cycle corresponded with arid to semi-arid climatic conditions, whereas the deposition part



**Figure 5.** Tentative palaeoclimatic chronology of the Pleistocene and Holocene in the Sahara (after Rognon, 1989b).

corresponded with pluvial periods (Alimen, 1955; Biberson, 1961; Coque, 1962; Chavaillon, 1964; Rognon, 1967; Conrad, 1969; Camps, 1974). The times of deposition in these cycles were thought to be contemporaneous with the alpine glaciations of Penck & Brückner (1901, 1905, 1909), while the periods of arid erosion were equated with interglacial periods. These views are being strongly challenged. Most specialists now consider that glacial is equivalent to dry and interglacial to humid.

The Lower Pleistocene period is characterized by the Pebble Culture of Australopithecinae and of *Homo habilis*. The long period of Acheulean industries, the Gunz-Riss interval (1,000,000–150,000 B.P.), is little known, although Acheulean industries are widespread, even in the most arid parts of the Libyan and Egyptian Deserts (McCauley *et al.*, 1982, 1986; Petit-Maire, 1982). At least three cycles of erosion and sedimentation took place during this period. These were the Moulouyan, Saletian and Tensiftian, with two or more limecrust formations in the Moulouyan and Tensiftian, and two or more formations of gypsum crust (Choubert *et al.*, 1956; Coque, 1962). *Homo erectus*, known from East Africa, has not so far been reported from the Sahara. Levalloisian and Mousterian artefacts (80,000–50,000 B.P.) are very rare, unlike the Acheulean (500,000–100,000 B.P.) and Aterian (40,000–20,000 B.P.) industries.

The fauna and flora do not seem to have changed much in respect to the Upper Villafranchian. Among the animals present were: *Loxodonta africana*, *Rhinoceros simus*, *Equus mauritanicus*, *Hippopotamus amphibius*, *Homoïceras antiquus* (= *Alcelaphus bubalis* = *Bubalis antiquus*), *Alcelaphus buselaphus*, *Bos primigenius*, *B. ibericus*, *Gazella dorcas*, *G. cuvieri*, *G. rufifrons*, *G. atlantica*, *Ammotragus lervia*, *Papio* sp., *Arvicanthis* sp., *Meriones shawi*, *Gerbillus campestris*, *Hystrix cristata*, *Serengetilagus* sp., *Canis aureus*, *Crocuta crocuta*, *Hyaena stritata*, *Phacochoerus aethiopicus*, *Sus scrofa*, and *Camelus dromedarius*. Most of these belong to the Afro-tropical fauna, suggesting a dry tropical climate.

The flora was predominantly Mediterranean with a number of tropical and temperate elements which, again, did not change very much after the Upper Villafranchian and continued throughout the rainy periods of the Pleistocene and Holocene. Of course, there were differences according to latitude and altitude; the Sahara mountains showed a more temperate climate flora (*Tilia*, *Alnus*, *Acer*, *Betula*, *Quercus* spp.). Throughout the Pleistocene rainy periods some of the most common species were: *Ephedra* sp., *Cedrus atlantica*, *Pinus halepensis*, *P. laricio*, *Cupressus* sp., *Juniperus oxycedrus*, *Taxus* sp., *Platanus* sp., *Salix* spp., *Corylus* sp., *Alnus* spp., *Betula* sp., *Quercus afares*, *Q. ilex*, *Q. coccifera*, *Q. mirbecki* (= *Q. faginea*), *Q. suber*, *Juglans regia*, *Tilia* spp., *Sapindus* sp., *Argania* sp., *Pistacia atlantica*, *P. lentiscus*, *Rhus* sp., *Tamarix* sp., *Acacia tortilis* subsp. *raddiana*, *Ziziphus lotus*, *Helianthemum* spp., *Cassia* spp., *Erica arborea*, *Olea europaea*, and *Fraxinus* spp. (Pons & Quézel, 1958; Quézel, 1960; Van Campo, 1975; Beucher, 1971; Cour & Duzer, 1976; Brun, 1979, 1983, 1985, 1987, 1989; Maley, 1981; Van Zinderen Bakker & Maley, 1979). This suggests a vegetation similar to that of the present humid Mediterranean climate of North Africa, with somewhat cooler temperatures (*Alnus*, *Corylus*, *Tilia*, *Juglans*, *Betula*, *Taxus*, *Cedrus*) on the mountains, and remnants of the Pliocene tropical flora (*Sapindus*, *Argania*) in the lowlands. Vegetation seems to have remained semi-arid to arid in the plains during the pluvials; it was probably comparable to the present-day arid steppes of North Africa, to the north of the Tropic of Cancer, and to that of the Sahel to the south of the Tropic (*Acacia tortilis* subsp. *raddiana*, *Ziziphus lotus*, *Helianthemum* spp., Combretaceae, *Cassia* spp.). There is, however, little data on the dry and hyperarid periods because ecological conditions were not conducive to conservation of plant and animal remains; but arid and hyperarid periods are demonstrated by the interstratification of aeolian deposits between the lake and organic deposits of the wet periods.

*The Upper Pleistocene and the Holocene (Table 2)*

The Mid- and Upper Pleistocene correspond roughly with the two last alpine glaciations of the Riss, Würm and post-Würm age (Fig. 5). In North African chronology, these are referred to as Soltanian and Rharbian erosion-sedimentation cycles (Choubert *et al.*, 1956). In terms of human artefacts they correspond to Acheulean, Mousterian and Aterian (Mid-to Upper Palaeolithic). The post-Würm ages (12,500 B.P. onwards) correspond with Aterian, Ibero-Maurusian (Epipalaeolithic), Caspian (Protoneolithic) and Neolithic civilisations. These civilisations are known from many sites throughout the Sahara (Balout, 1955; Camps, 1974; Hugot, 1974), including Neolithic rock paintings and engravings (Fröbenius & Obermeier, 1925; Fröbenius, 1937; Lhote, 1958; Mori, 1965; Hugot, 1974). Palaeontological data are particularly numerous from 12,500 B.P. onwards (Butzer, 1966; Faure, 1966; Butzer *et al.*, 1972; Van Campo, 1975; Cour & Duzer, 1976; Rognon, 1976*a, b*; Brun, 1979, 1983, 1985, 1987, 1989; Petit-Maire, 1979, 1986, 1989; Maley, 1981; Dutour, 1984, 1988; Fontes *et al.*, 1985; Faure *et al.*, 1986; Petit-Maire & Dutour, 1987; Fontes & Gasse, 1989; Wendorf *et al.*, 1990). This situation is in part due to the older limit of reliable <sup>14</sup>C dating. It is well established that in the southern Sahara and the Sahel, at least eight to ten arid and wet periods occurred over the past 125,000 years. The older dune system (150,000 B.P.?) is composed of levelled sands. The second system (125,000–70,000 B.P.) forms longitudinal, symmetrical (NE–SW), erosion sand ridges (Michel, 1973; Mainguet, 1976, 1982, 1983, 1984; Rognon, 1989*a, b*). The third 'Ogolian' or 'Kanemian' system (12,000–20,000 B.P.) is made up of transverse (NW–SE) asymmetrical, depositional dunes, extending some 400–600 km further south than the present drifting sands (Hunting Technical Services, 1964; Chamard, 1973*a, b*; Michel, 1973; Servant, 1973; Wickens, 1975; Rognon, 1976*a, b*, 1980; Mainguet, 1976, 1982, 1983, 1984; Servant & Servant-Vildary, 1980; Maley, 1981). The fourth dune system of barchans and barchanoids dates back to 3000 years B.P. onwards; it is a reshuffling of the two former, the third being a reshuffling of the second and so forth.

Pollen analysis from sea sediments has shown there has been a dry period in the northern Sahara between 18,000 and 24,000 B.P. (i.e. slightly older than the 'Ogolian' transverse sand dunes of the Sahel) (Brun, 1979, 1983, 1985, 1987, 1989; Brun & Rouvillois-Brigol, 1985). Then an optimum pluvial, during the Neolithic (10,000–4000 B.P.) was followed by a return to arid, then hyperarid conditions from 3000 B.P. onwards (Faure, 1966; Petit-Maire, 1979, 1982, 1986, 1987, 1988). Semi-arid to sub-humid climatic conditions prevailed throughout the Holocene in the lowlands, along the Tropic of Cancer until c. 3000 B.P. These facts are established by sedimentation studies and lake levels. The Mid-Holocene Sahara, including the present most arid areas, contained a large number of lakes [Lower Saoura Valley (Touat, Ahnet), Taoudeni, Araouane, the Fezzan (Shati, Murzuk and Wadi al Ajial Basins)] (Chavaillon, 1964; Faure, 1966; Conrad, 1969; Hebrard, 1972; Elouard, 1973; Servant-Vildary, 1977; Sarnthein, 1978; Rodhenburg & Sabelberg, 1980; Petit-Maire, 1982; Petit-Maire & Riser, 1983; Callot, 1984, 1987; Stein & Sarnthein, 1984; Faure *et al.*, 1986; Pachur & Kröpelin, 1987; Fabre & Petit-Maire, 1988).

Other evidence is afforded by ubiquitous rock paintings and engravings (Fröbenius & Obemeier, 1925; Fröbenius, 1937; Lhote, 1958; Camps, 1961, 1974, 1980; Mori, 1965; Hugot, 1974). Five Neolithic periods have been recognized: (a) the Buffalo [*Homoïceras (Bubalus antiquus)*] or Hunter's period c. 9000–6000 B.P.; (b) the Bovine period (6500–2500 B.P.), subdivided into three sub-periods—Round Headed (6500–4500 B.P.), Bovine proper (5000–4000 B.P.), and Horsemen sub-period (3500–2000 B.P.); and finally (c) the Cameline Period (2200 B.P., onwards). The Hunters' period and early Bovine period are characterized by melanodermic people similar to the Fulani and to East African pastoralists, while the late Bovine (Horsemen

**Table 3.** Floristic richness of various parts of the Sahara and neighbouring areas

Region	No. of species	Surface area ( $\times 10^3$ km <sup>2</sup> )	Sp. per 10 <sup>4</sup> km <sup>2</sup>	Log species numbers		References
				Log area (km <sup>2</sup> )		
Northern Sahara	1100	1000	11.0	0.50		Le Houérou (1990)
Southern Sahara	850	1500	5.7	0.47		Le Houérou (1990)
Central Saharan Lowlands	500	3000	1.7	0.42		Le Houérou (1990)
Saharan Highlands	830	500	16.6	0.51		Le Houérou (1990)
Western Sahara	870	3700	2.4	0.45		Le Houérou (1990)
Oceanic Sahara	450	70	64.3	0.55		Le Houérou (1990)
Eastern Sahara	1700	3600	4.7	0.49		Le Houérou (1990)
Sahara (overall)	2800	8000	3.5	0.50		Le Houérou (1990)
Fezzan	230	600	3.8	0.49		Corti (1942)
Mountains	850	500	17.0	0.51		Quézel (1954, 1957, 1958), Kassas (1956), Bruneau de Miré & Gillet (1956), Gillet (1968), Hassan (1974)
Djourab (1)	50	150	3.3	0.33		Quézel (1965)
Ténéré (2)	20	200	1.1	0.25		Quézel (1960)
Majabat (3)	7	150	0.5	0.16		Monod (1958)
Tunisian Sahara	480	100	48.0	0.54		Le Houérou (1959)
NW Sahara of Algeria (Beni-Abbes)	380	12	31.7	0.63		Guinet (1958)
Ahaggar	350	150	23.3	0.49		Quézel (1954)
Tibesti	568	200	28.4	0.52		Quézel (1958)
Tassili	340	90	38.4	0.51		Leredde (1957)
Moroccan Sahara	350	350	10.0	0.46		Guinea (1949), Guinet & Sauvage (1954), Mathez & Sauvage (1974), Birouk <i>et al.</i> (1991)
Air	410	85	48.2	0.53		Bruneau de Mire & Gillet (1956)
Egyptian Sahara 1000 (without Sinai)	1000	950	10.5	0.50		Täckholm (1974), Boulos (1975, 1995)



**Table 3.** *Continued*

Region	No. of species	Surface area ( $\times 10^3$ km <sup>2</sup> )	Sp. per 10 <sup>4</sup> km <sup>2</sup>	Log species numbers		References
				Log area (km <sup>2</sup> )		
Ennedi	528	70	75.4	0.56		Gillet (1968)
N African Steppes	2220	628	35.4	0.58		Le Hou��rou (1990, 1995)
Mauritania	1000	800	13.0	0.51		Monod (1940), Lebrun (1977), Barry & Celles (1991)
Libya	1800	1760	10.2	0.52		Boulos (1975), Le Hou��rou (1975, 1988, 1990, 1995)

and Cameleers) represent leucodermic people 'the People of the Sea', invaders from Libya-Egypt and probable ancestors of the Kel Tamasheq (Tuareg). Leucodermic protomediterranean cromagnoids, closely related to the makers of the Epi-palaeolithic Ibero-Maurusian and Capsian industries of the Maghrib, survived until proto-historic times in the central, western and southern Sahara and in the Nile Valley; physical anthropology data suggest that these same Cro-Magnoids might have been the ancestors of the Guanches, aboriginal (now extinct) inhabitants of the Canary Islands (Petit-Maire, 1979; Dutour, 1984, 1988; Petit-Maire & Dutour, 1987; Wendorf *et al.*, 1990).

In the northern Sahara, wet periods corresponded with the extension of a Mediterranean-type of vegetation characterized by the dominance of pollen from Mediterranean trees and shrubs (e.g. *Quercus ilex*, *Q. coccifera*, *Quercus suber*, *Pistacia lentiscus*, *Pinus halepensis*, *Cedrus atlantica*, *Olea europaea*, *Phillyrea* sp., *Myrtus communis*, *Abies* sp., *Ceratonia siliqua*, *Laurus nobilis*, *Rhus coriaria*, *Juniperus oxycedrus*, *Tetraclinis articulata*, *Cupressus* sp., etc.) These are species of the present vegetation in the semi-arid and sub-humid zones of northern Africa (Libya, Tunisia, Algeria, Morocco) (Van Campo, 1957; Leroi-Gourhan, 1958; Gruet, 1960; Santa, 1960; Van Campo & Coque, 1960; Brun, 1979, 1983, 1985, 1987, 1989; Brun & Rouvillois-Brigol, 1985). The arid and hyperarid periods corresponded with vegetation dominated by *Artemisia* and Chenopodiaceae/Amaranthaceae-Poaceae steppes, respectively (Beucher, 1971; Maley, 1973; Van Campo, 1975; Cour & Duzer, 1976; Van Zinderen Bakker & Maley, 1979; Van Zeist & Bottema, 1982; Brun, 1985, 1987, 1989).

The situation was similar in the highlands of the Central Sahara, but with a stronger contribution of temperate climate species in the higher altitudes (*Abies*, *Cedrus*, *Corylus*, *Fagus*, *Ulmus*, *Erica arborea*, *Alnus*, *Daphne*, *Fraxinus*, *Quercus mirbecki*, *Q. afares*, *Juglans* and *Tilia*).

During the arid and hyper-arid periods, a flora similar to that presently known in similar zones developed: *Ziziphus lotus*, *Acacia* spp., *Retama*, *Tamarix*, *Ephedra*, Chenopodiaceae, *Artemisia* spp., Compositae, Brassicaceae, Cistaceae, Zygophyllaceae, Cyperaceae, *Maerua*, *Balanites*, etc. (Pons & Quézel, 1957a, b, 1958; Quézel & Martínez, 1958, 1960; Maley, 1973, 1980, 1981; Van Campo, 1975; Cour & Duzer, 1976; Petit-Maire & Riser, 1983; Ritchie *et al.*, 1985; Neuman, 1987; Neuman & Schulz, 1987; Schulz, 1987, 1988).

Most of our knowledge relates to the southern Sahara. The humid periods supported a flora that included many strong Mediterranean influences (*Quercus*, *Pinus*, *Fraxinus*, *Platanus*, Cupressaceae, *Alnus*, *Tilia*, etc.), mixed with Sahelian and Sudanian elements (Combretaceae, *Grewia*, *Acacia* spp., *Hyphaene*, *Commiphora*, *Maerua*, *Balanites*, *Bauhinia*, *Celtis integrifolia*, *Hymenocardia*, *Salvadora*, *Cadaba*, *Capparis*, *Diospyros*, *Uapaca*, *Olea hochstetteri*, *O. europaea* subsp. *cuspidata* (syn. *O. africana*, *O. chrysophylla*) and subsp. *laperrinei* (syn. *O. laperrinei*), *Syzygium*, *Tamarindus*, *Lannea*, *Alchornea cordifolia*, etc. (Maley, 1981). Conversely the arid and hyperarid periods were dominated by Sahelian and Saharo-Arabian elements, respectively. The latter included *Tamarix*, *Cornulaca*, *Cleome*, *Zygophyllum*, *Artemisia*, *Pentzia*, *Tribulus*, *Launaea*, *Plantago*, *Aerva*, *Euphorbia*, *Chrozophora* and *Polycarphaea* (Maley, 1981).

### Present-day flora, vegetation and fauna

#### *Flora and vegetation (Figs 1-3, 6; Table 3)*

The flora and vegetation of the Sahara may be subdivided into five main entities: the northern Sahara with a flora and vegetation belonging to the Mediterranean region and

closely correlated with an extreme form of the Mediterranean climate. The southern Sahara, conversely, belongs to the Sudano-Deccanian region and the Palaeotropical floristic and ecoclimatic zone, closely tied, in turn, to an extreme form of the tropical climate. The central Sahara plains are characterized by intense aridity without any defined rainfall regime. The flora and vegetation are strictly Saharo-Arabian, i.e. a mixture of Holarctic and Palaeotropical elements showing a high degree of adaptation to aridity. Perennial plant communities are restricted to runoff or to the presence of ground-water. The Saharan highlands and mountains bear many similarities with both the northern and the southern Sahara. Mediterranean elements are, however, dominant above 1000–2000 m, mixed with tropical species and representatives of the archaic pan-African Rand flora. The Atlantic Sahara is an attenuated form of coastal desert including both Mediterranean and tropical species and a remarkable degree of endemism.

### *Fauna*

The situation is more complex than that for the flora, relationships depending, to a large degree, on the taxonomic groups considered. Large mammals, ungulates and carnivores are predominantly of tropical origin; they belong to the so-called 'Afrotropical fauna', formerly called 'Ethiopian fauna'. This has been the situation throughout the Quaternary; they therefore represent a continuation of the Mid-Pliocene fauna (see below). Conversely, small mammals, particularly rodents, are essentially of Mediterranean origin. The same is true for birds: 80% are Palearctic (Heim de Balsac, 1936; Dekeyser & Derivot, 1959; Casselton, 1984; Le Berre, 1989). Reptiles are derived almost equally from Palearctic and Palaeotropical elements. The same applies to fishes (Lambert, 1984).

Coleoptera are predominantly Mediterranean, whereas Palaeotropical elements predominate in ants and termites (Bernard, 1954). Arachnids, spiders, Solifugae and scorpions show a predominantly Mediterranean affinity (Cloudsley-Thompson, 1984*a, b*).

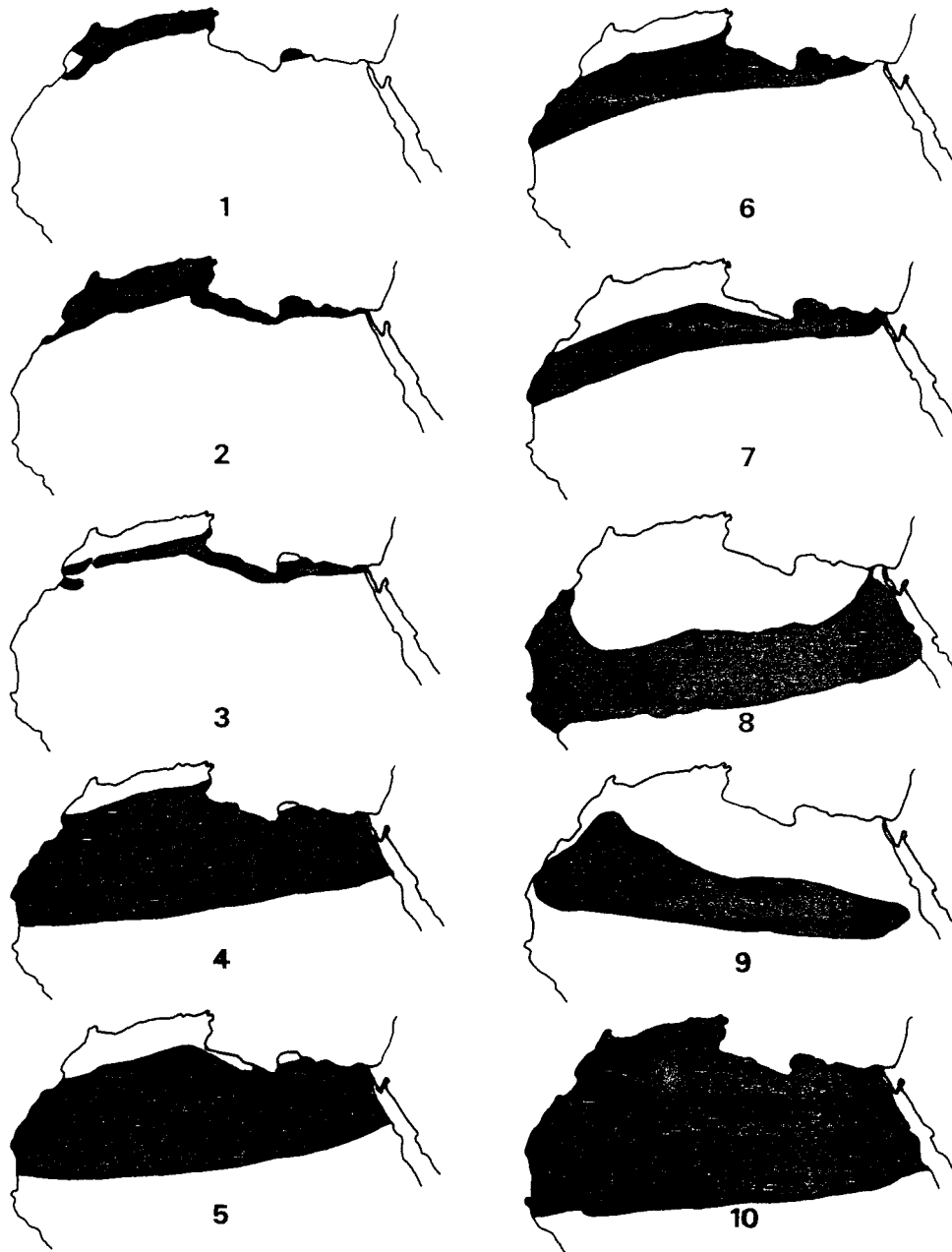
Tropical elements of both plants and animals reach higher latitudes along the Atlantic and Red Sea shores. Many species reach 30° N and beyond in southern Morocco and eastern Egypt (and further north-east along the Rift Valley as far as the Dead Sea). This is probably due to the milder temperatures in these regions as compared with the central Sahara (Le Houérou, 1989*b*, 1990). Winter temperatures play a role at least as important as seasonal rainfall patterns in the distribution of both plants and animals. Mediterranean species and communities tend to dominate under low winter temperatures, even with summer rains, in elevations above 1500 m between the latitudes 18 and 28° N. This occurs in the Tibesti, Aïr and Gourgueil. Conversely tropical species tend to dominate in areas with mild winter temperatures, despite a Mediterranean rainfall regime, as in south-west Morocco, on the shores of the Red Sea and the Arabian Gulf. In all these areas the mean daily minimum temperature of January ('m') is above 7°C: the distribution of Saharan *Acacia* and tropical grasses corresponds to the 'm' isotherm of 5°C and above; virtually all tropical species disappear when 'm' drops to 3°C or below (Le Houérou, 1959).

(For further information on the present day flora and fauna, see Le Houérou, 1992, pp. 8–12, and Le Houérou, 1995*a, b*).

### **Conclusions**

The biological history of the Sahara appears throughout the Pleistocene and Holocene to have been a series of wet-dry periods corresponding with alternating expansion and

shrinking of a more or less permanent arid to semi-arid nucleus in the lowlands along the Tropic of Cancer. The wet periods are much better documented than the dry spells because organic remains are better preserved during sedimentation cycles than during erosion phases. For the same reasons the later wet periods of the Neolithic are better documented since previous sediments have often been eroded. The advent of Th/U isotopic dating techniques in the 1980s showed, however, that many lake deposits were much older than previously thought (80,000–120,000 B.P. vs. 30,000–40,000 B.P.), on the basis of erroneous  $^{14}\text{C}$  dating (Fontes *et al.*, 1985; Causse *et al.*, 1988; Fontes & Gasse, 1989; Gasse *et al.*, 1990). There are, however, a few striking facts, some of



which seem paradoxical. The fauna changed little from the Lower Pleistocene until about 100 years ago. The Afro-tropical fauna of large mammals, elephant, hippopotamus, giraffe, addax, oryx, gazelle, lion, cheetah, leopard, hyaena, white rhino, hartebeest, wildebeest were common until c. 2000 years ago and quite a few species managed to survive until 80–100 years ago. These include the ostrich and the crocodile. In early historic times, this fauna extended to Mediterranean northern Africa (lion, elephant, oryx, addax, hartebeest, leopard, etc.). It is probable that these animals were reduced in numbers during the dry or hyperarid periods, but they managed to survive in refuges and thrive again when favourable conditions returned. The situation has now drastically changed since a large number of species have become extinct, or are at the verge of extinction in the Sahel and East Africa. This is a result of the impact of an exponentially growing human population and extensive hunting. So far few protective measures have been enforced. Most protected areas exist only on paper and wildlife is often persecuted by those who are supposed to protect it (Le Houérou & Gillet, 1985). Somewhat paradoxically, the flora and vegetation did not follow the pattern of the fauna. Mediterranean and temperate species were in existence in the northern Sahara and the highlands throughout the Pleistocene and Holocene, with periods of expansion during the wet phases and retreat during the dry periods. This contrasts again with the situation in the Pliocene, when relicts from the tropical climate of the Oligocene and Miocene remained dominant. In the southern Saharan lowlands tropical elements seem to have dominated throughout the Pleistocene and Holocene. The situation thus seems to have been analogous to the present: a northern Mediterranean flora and vegetation opposed to a Palaeotropical flora and vegetation to the south; along the lowlands bordering the Tropic of Cancer, a nucleus of more or less permanently arid or hyperarid conditions in which both Mediterranean and tropical influences played an alternating role, thus developing throughout the Quaternary, the Saharo-Arabian phytogeographic entity. This explains why the Saharo-Arabian element lacks taxonomic individuality. It contains elements from both Mediterranean (65%) and tropical (35%) floras. Perhaps also time was too short (2 million years) for an original flora, with endemic tribes and families, to develop.

**Figure 6.** (facing page). Some typical patterns of distribution of plants and animals in the Sahara and adjacent areas (Le Houérou, 1990). **(1) Mediterranean zone:** semi-arid to hyper-humid. Flora: *Quercus ilex*, *Juniperus oxycedrus*, *Pistacia lentiscus*. Fauna: *Macaca sylvana*, *Cervus elaphus barbarus*, *Sus scrofa barbarus*, *Ciconia ciconia*, *Erithacus rubecula*, *Pica pica*, *Lacerta lepida*, *Acanthodactylus vulgaris*. **(2) Mediterranean and steppic zones.** Flora: *Juniperus phoenicea*. Fauna: *Gazella cuvieri*, *Pterocles orientalis*, *Passer hispaniolensis*, *Passer domesticus*, *Carduelis carduelis*, *Prinia gracilis*, *Parus caeruleus*, *Tarentola mauritanica*, *Chamaeleo chamaeleon*, *Coluber florentulus*, *Ophiops elegans*, *Vipera libetina*. **(3) Arid steppic zone.** Flora: *Stipa tenacissima*, *Lygeum spartum*, *Artemisia campestris* var. *glutinosa*, *Artemisia campestris* var. *cinera*, *Seriphidium herba-alba* = *Artemisia herba-alba*, *Helianthemum lippii*, *H. sessiliflorum*. Fauna: *Cursorius cursor*, *Emberiza calandra*, *Naja haje*, *Echis melanogaster*. **(4) Saharan and steppic zones.** Flora: *Stipagrostis pungens*, *Retama raetam*. Fauna: *Zorilla libyca*, *Gazella dorcas*, *Hyaena hyaena barbara*, *Meriones* spp., *Gerbillus* spp., *Psammomys obesus*, *Uromastix acanthinurus*, *Varanus griseus*, *Agama agama*, *Cerastes cerastes*, *Chlamidotys undulata*. **(5) Saharan zone, sensu stricto.** Flora: *Calligonum crinitum* subsp. *comosum*, *C. azel*, *C. arich*. Fauna: *Fennecus zerda*, *Felis margarita*, *Vulpes rueppelli*, *V. pallida*, *Passer simplex*, *Oenanthe leucopyga*, *Ammomanes cincturus*, *Corvus ruficollis*, *Stenodactylus sthenodactylus*, *S. petrei*, *Cerastes vipera* *Psammophis schockari*, *Phenops sepioides*. **(6) Northern Sahara and steppe zones.** Flora: *Hammada schmittiana*, *Anabasis articulata*. Fauna: *Ctenodactylus gundi*, *Ammomanes deserti*, *Oenanthe deserti*, *Emberiza striolata*, *Acanthodactylus pardalis*, *Lythorhynchus diadema*. **(7) Northern Sahara.** Flora: *Anthyllis sericea* subsp. *henoniana*. Fauna: *Ctenodactylus vali*, *Ramphocorys clot-bey*, *Scotocera inquieta*, *Oenanthe lugens*, *Coluber choumovitchii*. **(8) Southern Sahara.** Flora: *Schouwia thebaica*, *Balanites aegyptiaca*. Fauna: *Lycanorhynchus pictus*, *Gazella rufifrons*, *Hirundo obsoleta*, *Bitis arietans*. **(9) Central and southern Sahara.** Flora: *Maerua crassifolia*. Fauna: *Oryx dammah*, *Addax nasomaculatus*, *Gazella dama mohor*, *Procapra capensis*, *Corvus albus*, *Streptopelia senegalensis*. **(10) Mediterranean, Saharan and Sahelian zones.** Flora: *Tamarix aphylla*. Fauna: *Ammotragus lervia*, *Capra ibex*, *Canis aureus*, *Lanius minor*.

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