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Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia

Michael J. Benton [a,*], Samir Bouaziz [b], Eric Buffetaut [c], David Martill [d], Mohamed Ouaja [e], Mohamed Soussi [f], Clive Trueman [a]

[a] *Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK*
[b] *École Nationale d'Ingenieurs de Sfax, Université de Sfax, B.P.W. 3038 Sfax, Tunisia*
[c] *Centre National de la Recherche Scientifiques (UMR 5561), 16 Cour du Liegat, 75013 Paris, France*
[d] *Department of Geology, University of Portsmouth, Burnaby Building, Burnaby Street, Portsmouth PO1 3QL, UK*
[e] *Office National des Mines, 24 rue 8601, 2035 La Charguia, Tunis, Tunisia*
[f] *Faculté de Sciences de Sfax, Université de Sfax, 3038 Sfax, Tunisia*

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Abstract

Remains of dinosaurs and other vertebrates (sharks, bony fishes, coelacanths, turtles, crocodilians, pterosaurs) are reported from the Chenini Formation of the Tataouine region in southern Tunisia. The Formation is part of the 'continental intercalaire', a succession of continental deposits of Early to Late Cretaceous age distributed over the whole of North Africa and the Sahara. It consists of bar and channel deposits of broad rivers that flowed NNW from the mid-Sahara region towards the southern shore of Tethys. Dinosaur-bearing units in the 'continental intercalaire' have been dated to the Hauterivian to Cenomanian, and the Chenini Formation is possibly Albian in age. Dinosaur fossils include abundant teeth of the theropods *Carcharodontosaurus* and *Spinosaurus*, as well as postcranial elements of theropods and a medium-sized sauropod. A tooth of an ornithocheirid is the first report of a pterosaur from the region. The dinosaur bones and teeth were transported some distance and deposited in a channel lag, associated with less damaged locally derived material such as fern fronds, coprolites, fish teeth and scales, and crocodilian scutes.

Keywords: Albian; Cretaceous; dinosaur; palaeoecology; sedimentology; vertebrate palaeontology

1. Introduction

The Cretaceous vertebrate faunas of Africa are of considerable importance in terms of palaeobiogeography and evolution. Africa was linked to South America and Euramerica during most of the Early Cretaceous, but these land connections were severed in the Late Cretaceous. Detailed faunal studies, and precise dating of faunas, show that African continental vertebrate faunas were essentially of cosmopolitan character until the Late Jurassic and earliest Cretaceous, but they developed ever more specialized features as land connections broke down (Buffetaut and Rage, 1993; Sereno et al., 1994, 1996; Russell, 1996; Sampson et al., 1998): Madagascar broke away from the main African landmass by 120 Ma, and South America finally separated from Africa by 100 Ma,

* Corresponding author. Tel.: +44-117-9545433; fax: +44-117-9253385.
E-mail address: mike.benton@bris.ac.uk (M. Benton)

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although those two land masses may have retained a connection with each other via Antarctica. A major transgression in the late Cenomanian then flooded most of North Africa and the Sahara, and a seaway extended from Algeria southwards across the Sahara, separating the northwestern portion of Africa from the rest of the continent

Dinosaurs and other vertebrates have been found extensively over North Africa and the Sahara, in Morocco, Algeria, Tunisia, Libya, Egypt, Sudan, Mali, and Niger in a sequence of rocks termed the ‘continental intercalaire’ by de Lapparent (1960). More recent work (e.g. Taquet, 1976; Bouaziz et al., 1989; Lefranc and Guiraud, 1990) has shown that the ‘continental intercalaire’ is a very loose term that includes rocks of latest Jurassic to Late Cretaceous (Cenomanian) age, and that there is a succession of faunas. These faunas show similarities with South America, especially in comparisons between Morocco and Brazil (Buffetaut and Rage, 1993; Sereno et al., 1994, 1998), and with Euramerican faunas (Buffetaut and Rage, 1993; Sereno et al., 1994, 1996). In the Late Cretaceous, the dinosaurs of Madagascar, India, and South America still retained resemblances, but those of Africa were somewhat different since Africa had become essentially an island by this time (Sampson et al., 1998).

Abundant bones of dinosaurs and other vertebrates have been reported from the mid-Cretaceous of the Tataouine region, southern Tunisia. The earlier reports were, however, either brief accounts that noted the presence of vertebrate remains as part of a broader-scale survey of the north African region (e.g. Pervinquière, 1912; de Lapparent, 1951, 1960) or reports of limited sampling operations (Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988). The bones were found in Tunisian

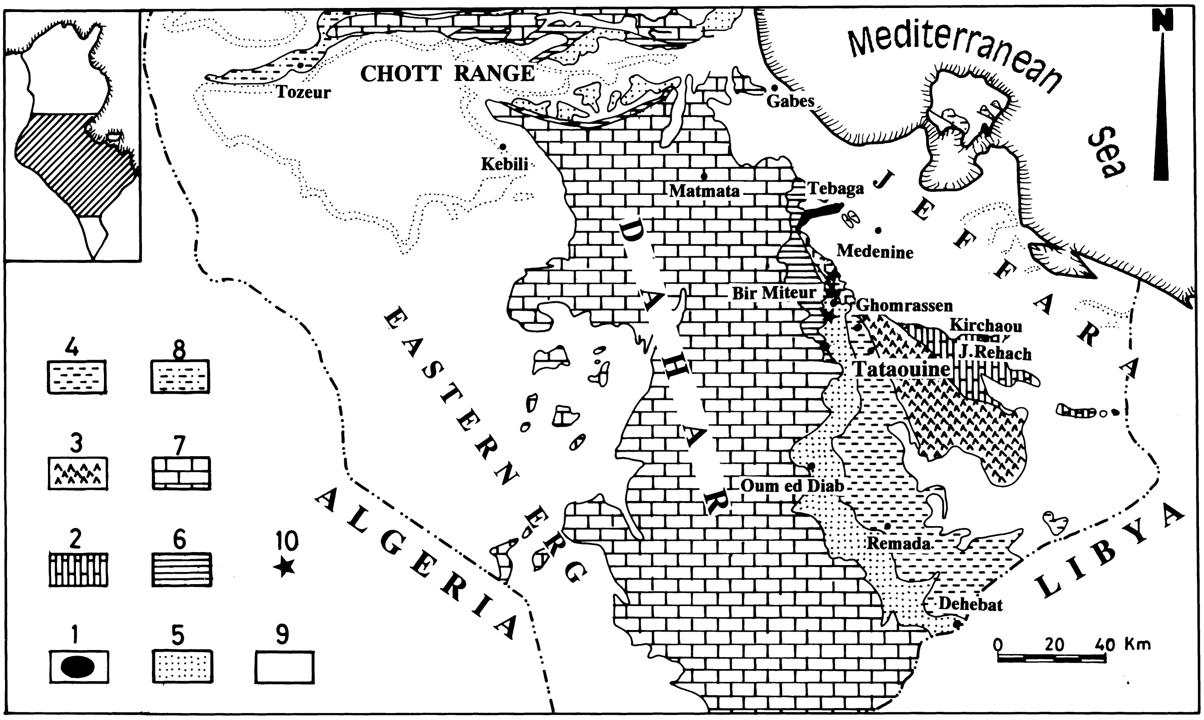

Fig. 1. Outline geological map of the south Tunisian area, showing the major geomorphological regions, the Jeffara, a low-lying coastal plain, the Dahar plateau, and the Saharan Erg Oriental. The main stratigraphic divisions are indicated. The location of southern Tunisia is indicated on the map of Tunisia, top left. Stratigraphic units: 1, Permian; 2, Triassic; 3, Lias; 4, Dogger; 5, Malm–Neocomian; 6, Vraconian (mid–late Albian); 7, Late Cretaceous; 8, Mio-Pliocene; 9, Pliocene–Quaternary; 10, dinosaur sites (modified from Zarbout et al., 1994).

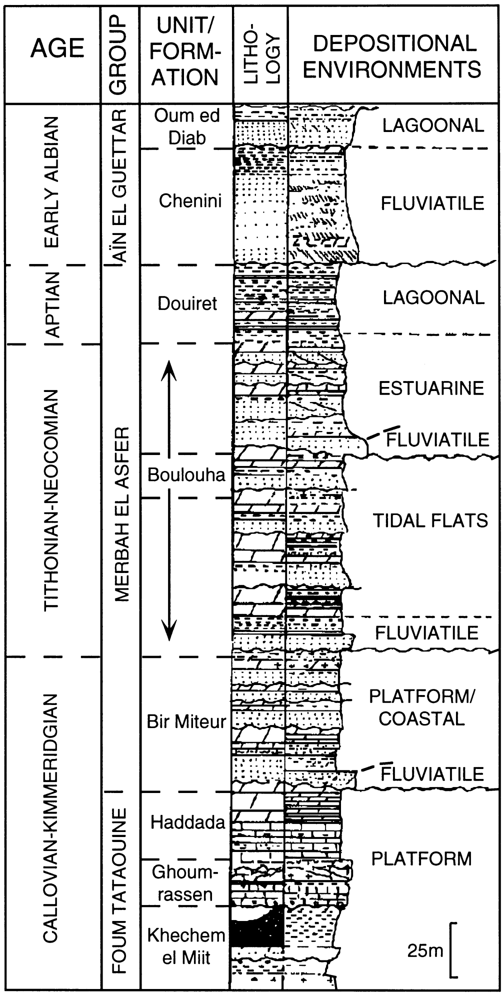

Fig. 2. Simplified stratigraphic column of the Late Jurassic to latest Early Cretaceous succession on the Dahar plateau in southern Tunisia, and the overlying Cenozoic rocks of the Jeffara plain (based on Zarbout et al., 1995).

equivalents of the continental intercalaire. Short Tunisian–British–French expeditions in 1997 and 1998 have provided additional information on the setting of the bone beds and on the vertebrate faunas. A new find, reported here, is the first evidence of a pterosaur, identified as an ornithocheirid.

The aims of this paper are to introduce the little-studied mid-Cretaceous vertebrate faunas of southern Tunisia, to describe the geological setting, dating, palaeogeography, and environment of the dinosaurs, and to provide comparisons with other North African and Saharan localities of similar age.

2. Geological setting

The fossil vertebrates occur in units of presumed early Albian age (latest Early Cretaceous, ca 100 Myr) within a succession of rocks dating from the Late Permian to latest Cretaceous (Figs. 1 and 2). These deposits are located on the northern edge of the Saharan platform, and south of the Atlas Mountains, the Chott Range, a fold belt that forms an east–west-trending structural unit across North Africa from Morocco to Tunisia. Southern Tunisia is divided into two domains, based on tectonics and geomorphology, the Jeffara coastal plain and the Dahar plateau (Fig. 1).

1. The Jeffara, the NW–SE-trending coastal plain, is a collapsed block formed during the Late Cretaceous and Cenozoic by extensional tectonic faulting. The basin was downthrown to the NE of the faults, and was filled with thick successions of Cenozoic sediments. The basin extends offshore NE beneath the Mediterranean Sea.
2. The Dahar plateau extends from the margin of the Jeffara plain to the Ergs of the Sahara in the west. It is a largely Mesozoic sedimentary sequence, capped by Late Cretaceous limestones. The beds of the Dahar plateau form a remarkable cliff line for some 300 km on their NE margin (Fig. 3), and they dip gently, at about 1° W and SW, beneath the dunes of the Saharan Erg Oriental. de Lapparent (1960) (p. 12) noted that “this long cliff … under the desert-like climate… is not particularly favourable to palaeontological research”, a rather odd statement in view of the excellent exposure and rich fossil discoveries.

The synthetic stratigraphic section of the Dahar domain consists of an almost complete sequence that ranges in age from Late Permian to Late Cretaceous (Figs. 2, 4 and 5) and represents the filling of a major subsiding basin, the Southern Tunisian Basin, or ‘Tataouine Basin’ of Busson (1967).

Late Permian marine units at the northern end of the basin grade up into nonmarine Triassic

Fig. 3. Photograph of the Dahar cliff line, opposite the main bonebed locality. The prominent ridges are sandstone units below and above the bone bed horizon, consisting of the Chenini Formation, capped by the Oum ed Diab Formation.

redbeds, a sequence of fluvio-deltaic and marginal marine units, overlain by the marine Mekraneb and Rehach formations (both early Carnian), and the evaporitic Mhira Formation (late Carnian to Norian). The Permian and Lower–Middle Triassic sequence was tectonically deformed in the early Carnian and in the Norian, and the beds now dip 20–30° to the south. They are capped by the transgression of the Messaoudi dolomite (Rhaetian), which rests unconformably on the older Triassic rocks, at the Sidi Stout unconformity (Busson, 1967; Bouaziz et al., 1987; Barrier et al., 1993).

Jurassic units are mainly marine. The basal Bhir evaporites begin the sequence E of Tataouine, while S and SE of Tataouine, the Zmilet Haber Formation (Pliensbachian) is a shallow to marginal marine unit. The succeeding Mestaoua Formation (Pliensbachian to Aalenian) is interpreted as a paralic sabkha, with hypersaline episodes. After the deposition of the Mestaoua Formation, a distinct north–south contrast developed. The northern area is marked mainly by platform carbonate facies, while sedimentary sequences south of Tataouine are thicker and more characteristic of deeper depositional environments (Fig. 5).

The overlying Krachoua Formation (Aalenian–Bajocian) is also interpreted as marine, with lagoonal episodes, indicating a widespread marine transgression which extended over the Saharan region of Algeria, Tunisia, and Libya. The Techout Formation (Bathonian) represents supratidal, sabkha, and intertidal environments. The shallow marine limestones and marls of the Tataouine Formation (Bathonian–Oxfordian) form much of the landscape around the town of Tataouine (Foum Tataouine), and extend from Tebaga de Medenine in the north to the Tunisian–Libyan border in the south.

The succeeding units, of Late Jurassic to Early Cretaceous age, are exposed in the cliffs of the Dahar, over a total distance of some 200 km, from Tebaga de Medenine in the north to the Tunisian–Libyan border in the south. These partly continental units, the 'continental intercalaire' of de Lapparent (1960), and the 'Purbecko–Wealdien' of Busson (1967), are dated over a long interval, from Oxfordian to Cenomanian (Ben Ismaïl et al., 1989; Bouaziz et al., 1989). They show considerable variations in both facies and thickness from north to south, and generally lack biostratigraphically useful fossils. They have been divided into two groups and five formations (Figs. 2 and 5), the Merbah el Asfer Group (Oxfordian to Neocomian), consisting of three formations, and the Aïn el Guettar Group, with two formations, the Chenini Formation (early Albian), and the Oum ed Diab Formation (mid-Albian to Cenomanian).

The Merbah el Asfer Group varies from a few metres thick in the north, to a maximum of 250 m at Merbah el Asfer itself. There are three sedi-

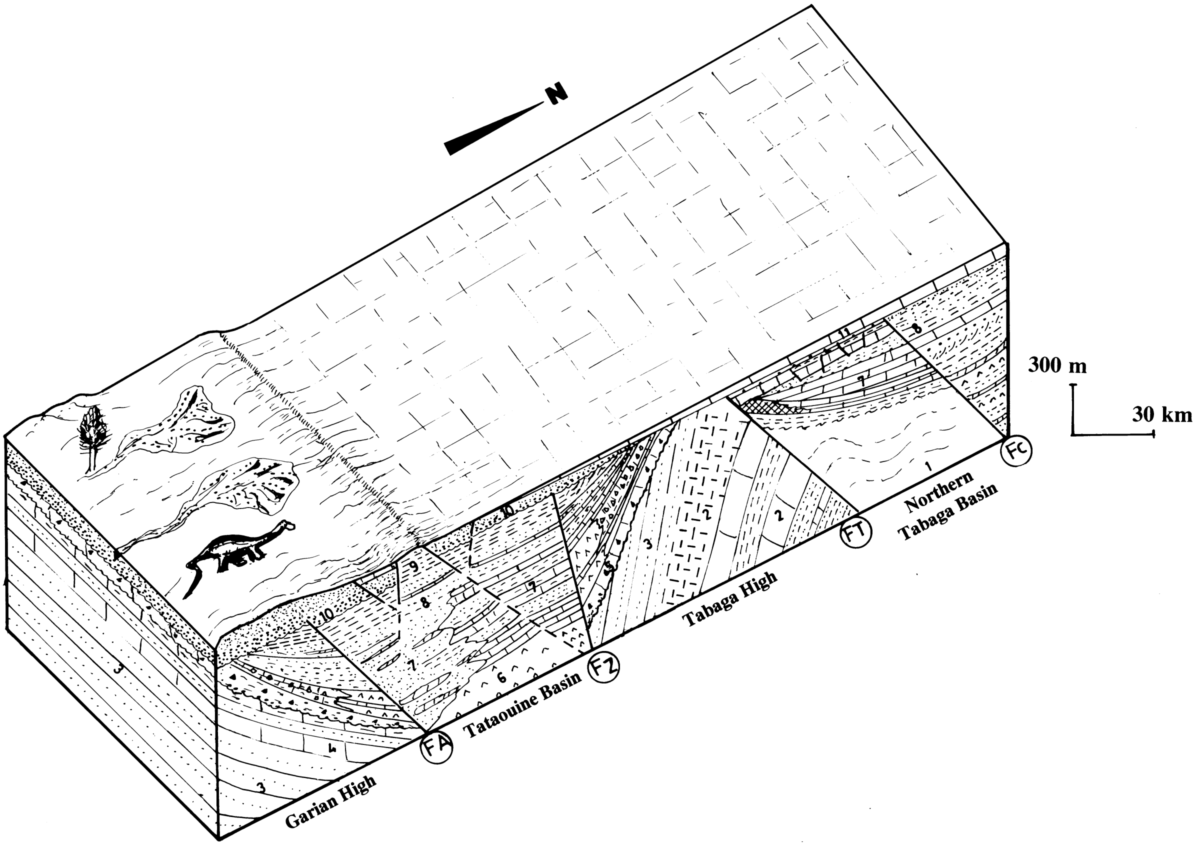

Fig. 4. Schematic block diagram of the southern Tunisian platform showing palaeogeographic evolution from the Late Permian to the Early Cretaceous (Albian). The structure of the basins is distinguished from the uplift zones. The diagram runs from the Garian High (Libya) in the south (bottom of diagram) to the Tebaga de Medenine region in the north (top). Stratigraphic divisions: 1, undifferentiated Permian; 2, Late Permian; 3, Early–Middle Triassic; 4, Carnian; 5, Rhaetian; 6, Lias; 7, Dogger; 8, Malm–Neocomian; 9, Aptian; 10, Albian–Vraconian; 11, Vraconian (mid–late Albian). Faults: FA, Azizia Fault; FC, Chotts Fault; FT, Tebaga Fault; FZ, Zemlet el Ghar Fault (based on Bouaziz, 1995).

mentary divisions, a 40 m thick unit of alternating green shales with gypsum, silts, sands, and dolomites near the base, the Bir Miteur Formation, late Oxfordian to Kimmeridgian in age, indicating lagoonal conditions. A marginal marine carbonate sequence of some 20 m follows, followed by alternating carbonates and mudstones some 50 m thick. This succession, the Boulouha Formation, ranges from Tithonian to Neocomian (? Barremian) in age. The third unit, the Douiret Formation, is composed mainly from mudstones, and it has been dated palynologically as early Aptian (Ben Ismaïl, 1991). An extensive flora has been noted from several horizons within the Merbah el Asfer Group (Barale et al., 1997, 1998).

The Chenini Formation consists of coarse sandstones with occasional conglomerates and breccias and mudstones, the last with insects and plant remains. The unit is remarkably laterally persistent, extending from Béni Kheddache in the north to the Libyan frontier, except in the Touil el Hira high (Fig. 5). Some of the coarse sandstone units contain vertebrate remains, the subject of this study. The basal unit is an indurated conglomerate bed, with wood debris and quartz pebbles, which forms an obvious marker bed along the length of

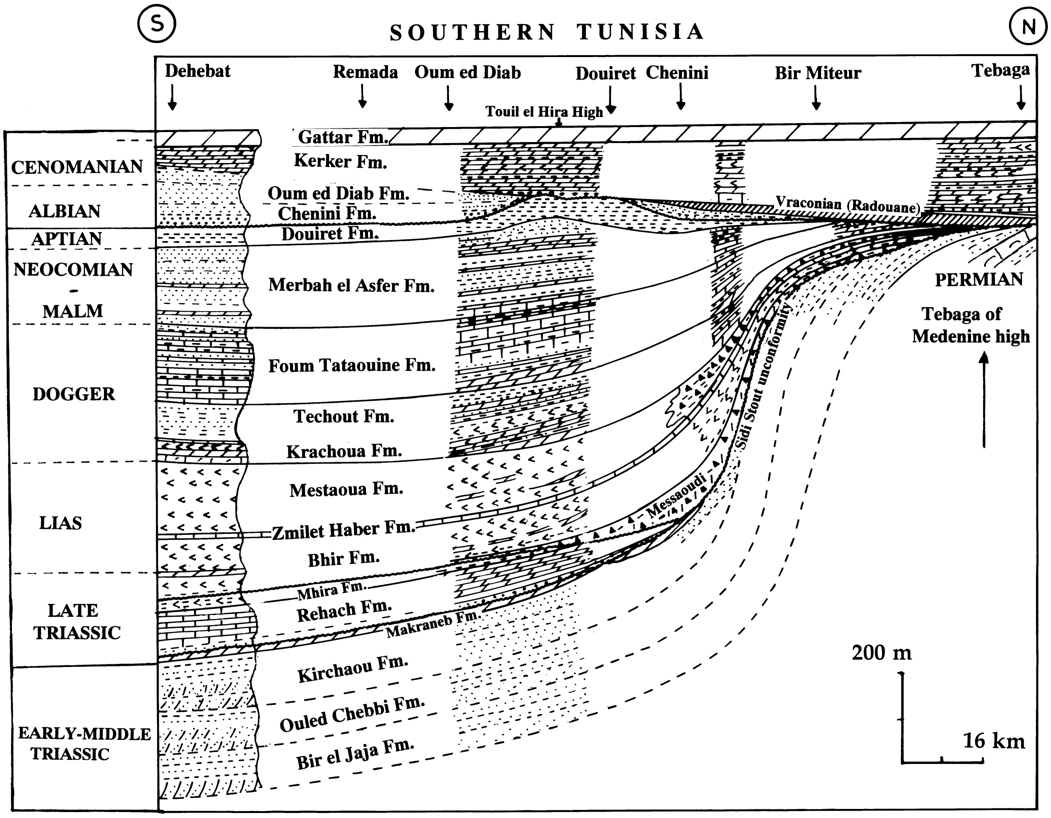

Fig. 5. Geological evolution of the south Tunisian basin, showing Triassic to Cenomanian basin fill from Dehebat (south) to Tebaga de Medenine (north) (based on Bouaziz, 1995).

the Dahar cliff, and thickens to the south. Above this unit, coarse sandstones with wood debris have produced abundant bones and teeth of fishes, turtles, crocodiles, and dinosaurs (de Lapparent, 1951, 1960; Burollet et al., 1983; Busson, 1967; Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988).

The Chenini Formation sandstones are overlain in the south by 15 m of alternating shales and sands, the Oum ed Diab beds (Figs. 2 and 5), which are dated as Albian to Cenomanian (Bouaziz et al., 1989). The Radouane Member, 10–15 m thick, which is a prominent feature in the Tataouine region, and northwards to Tebaga de Medenine, represents a major transgression. The unit rests directly on the Permian in the Tebaga de Medenine region, and more conformably on the Chenini sandstones in most of the Dahar (Figs. 2 and 5). This carbonate bar has yielded Albian ammonites, and at its base is a unit rich in fish remains, especially *Lepidotes* and pycnodonts, passing up into sandstone from the Douiret locality towards the south.

The overlying Late Cretaceous deposits are a 200–300 m thick succession of carbonates, representing a major marine transgression that extended further south in the Dahar region than the Aptian–Albian transgression, and which affected much of Africa from the Cenomanian onwards. The basal units are alternations of shale, gypsum, and dolomite that vary in thickness from 200 m at Tebaga in the north to 40 m in the south. The carbonate beds contain ammonites, echinoids, bivalves, and gastropods that indicate a mid- to late Cenomanian age. A 20–30 m thick dolomitic bed follows, dated as late Cenomanian to early

Turonian. Further west, these units are succeeded by up to 200 m of marls and limestones, dated as latest Turonian to early Coniacian, which disappear beneath the sands of the Erg Oriental (Fig. 1). Further south, younger marine bioclastic limestones are dated as early Campanian.

Cenozoic beds are absent over most of the Dahar. Sediments of this age are continental in origin, but they are scarce, occurring in the Chott Range and beneath the Jeffara coastal plain, which was subsiding during much of the Cenozoic (Fig. 1).

According to its location and sedimentary character, southern Tunisia is characterized by a major sedimentary basin, the Tataouine basin (Fig. 5). This basin is bordered by uplift zones, the Tebaga de Medenine high in central Tunisia and the Garian high in Libya. Palaeogeographic evolution in the region has been controlled by major unconformities of Carnian and Albian age and by major faults (Bouaziz, 1995) (Figs. 4 and 5).

3. Palaeogeography of North Africa in the mid-Cretaceous

During the Jurassic, Africa and South America were in close contact. The North Atlantic was opening southwards, and the South Atlantic northwards, as Africa and South America rotated apart. Sea levels were higher in much of the Late Jurassic, and North Africa and the Sahara were largely under shallow epicontinental seas, as indicated by the extensive deposition of marine units. In south Tunisia, a major marine transgression occurred in the Callovian, and this extended southwards to the Tunisian–Libyan border. Regressive episodes in the Late Jurassic gave mixed marginal marine and continental conditions.

During the early part of the Early Cretaceous, much of North Africa and the Sahara region were sites of continental deposition (Fig. 6A). Africa and South America continued to rotate apart, and the North Atlantic now extended well down the Moroccan coast, and the South Atlantic reached the Congo region (Reyment and Dingle, 1987). In Tunisia, a further marine transgression occurred in the early Aptian, removing upper parts of the Merbah el Asfer Formation in the northern part of the basin. By the late Aptian, the two branches of the Atlantic had extended further between the two continents, leaving a strip of land between Brazil and the Congo region only 200–300 km wide, but with extensive salt flats to the south.

In the early Albian, South America and Africa pulled further apart, and surface waters of the North and South Atlantic were intermittently exchanged (Reyment and Dingle, 1987). There

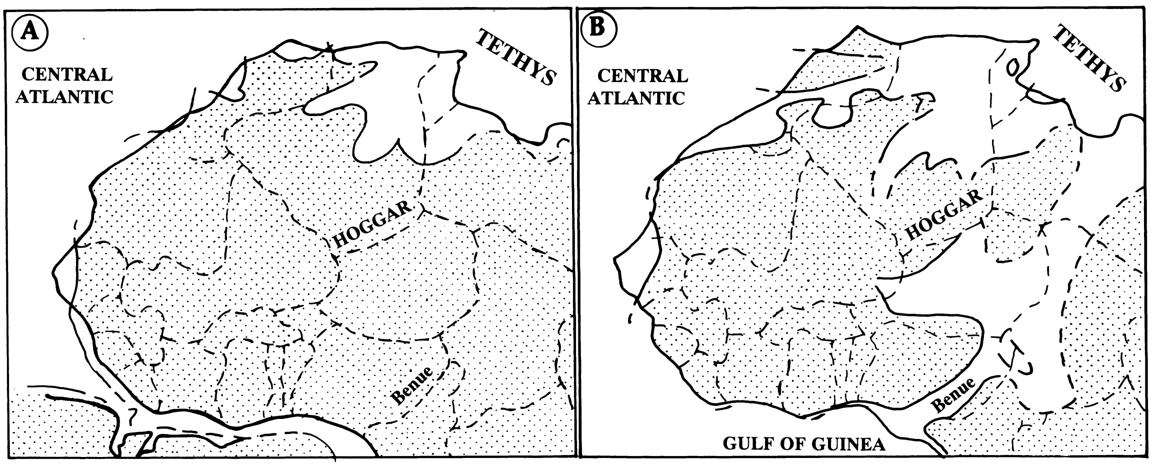

Fig. 6. North and West African palaeogeography, in the early Albian, at maximum regression (A) and in the late Cenomanian, after the major marine transgression (B). Stipple indicates main continental areas (based on maps in Reyment and Dingle, 1987).

was a regression during the early and mid-Albian in North Africa, when the sea withdrew north of Tebaga de Medenine. This was followed by a late Albian transgression over much of Africa, which triggered the beginning of exchange between the two halves of the Atlantic.

After a regression, the most notable of all transgressions occurred in the late Cenomanian (Fig. 6B), when marine incursions from north and south flooded North Africa and the Sahara (Furon, 1963; Reyment and Dingle, 1987). The beginning of the transgression is dated by the ammonite *Neolobites vibrayeanus* at the base of the Cenomanian–Turonian limestones that overlie the 'continental intercalaire', indicating the *Vibrayeanus* Zone, both in the west, in Morocco and Algeria (Busson and Cornée, 1989, 1991), and in the east, in Egypt (Luger and Gröschke, 1989). This transgression was coincident with a major rise in sea level world-wide, which marked the beginning of chalk deposition in Europe. Subsidence of the south Tunisian basin reversed at this time. Whereas the older sediments of Triassic to Aptian age are thicker in the south, and thin to nothing in the north, the Late Cenomanian limestones are thicker in the north (ca 400 m) and thinner in the S and SE (ca 40 m) (Fig. 5).

The regressive and transgressive cycles were caused by subsidence and sea level changes related to major N–S extensional tectonics caused by the pulling apart of the Eurasian and African plates (Barrier et al., 1993). The direction of extension rotated to ENE–WSW in the Cenomanian, and it was related to the opening of the South Atlantic, and the final separation of Africa and South America.

By the end of the Cenomanian, the transgression reached its maximum, when the northern oceanic incursion met a southern arm of the sea, and created a marine passage from Tethys to the South Atlantic. This marine passage closed off in the Turonian, but opened up again in the early Maastrichtian (Reyment and Dingle, 1987; Moody and Sutcliffe, 1991). By the Turonian, there was a definite break between Africa and South America, and exchange of terrestrial fauna between those two continents was reduced substantially.

4. Chenini Formation

4.1. Biostratigraphic setting

The Chenini Formation is generally dated as early Albian (Burollet et al., 1983; Bouaziz et al., 1988; Ben Ismaïl et al., 1989), a determination based partly on indirect evidence. The upper part of the underlying Merbah el Asfer Group, the Douiret Formation, has yielded palynomorphs that suggest an early Aptian age (Ben Ismaïl, 1991). Palynomorphs have suggested a late Aptian to early Albian age for the Aïn el Guettar Group, which includes the Chenini Formation (Pons, in Ben Ismaïl, 1991; Barale et al., 1998). The overlying prominent limestone bar, the Radouane Member, some 15 m above the Chenini sandstones in the Tataouine area, begins in the north (Fig. 5), with calcareous marls and bioclastic limestones rich in ammonites such as *Knemiceras syriacum* and *Knemiceras gracile*, determined as mid-Albian in age (Ben Youssef et al., 1985). The carbonate bar is assumed then to be Vraconian in age, that is mid- to late Albian.

Bouaziz et al. (1988) attempted to use evidence from the vertebrate fauna to confirm this date, but most of the taxa are stratigraphically long-ranging and indicate only a mid-Cretaceous age. The shark *Protolamna* is known only from the late Aptian and Albian (Cappetta, 1987). The dinosaur *Carcharodontosaurus* is not known before the Albian, being notably absent from the Aptian Gadoufaoua dinosaur fauna of Niger (Taquet, 1976). It is present in the Albian of Algeria (Depéret and Savornin, 1927), other Albian localities in the Sahara (de Lapparent, 1960; Taquet, 1976), and the early Cenomanian of Baharija, Egypt (Stromer, 1931). *Spinosaurus* was described from the early Cenomanian of Baharija (Stromer, 1915), but older spinosaurids have been noted from rocks of Barremian to Albian age in Africa, South America, and Europe. These include '*Spinosaurus*' from the Albian of Djoua, Niger (Stromer, 1915), *Cristatusaurus* (Taquet and Russell, 1998) or *Suchomimus* from the Elrhaz Formation (Aptian) of the Ténéré Desert, Niger (Taquet, 1984; Sereno et al., 1998), *Irritator* (Martill et al., 1996) and *Angaturma* (Kellner and

Campos, 1996) from the Santana Formation (Aptian–Cenomanian), and *Baryonyx* from lower units of the Wealden (Barremian–Aptian) of England (Charig and Milner, 1997). However, there is little independent evidence for the age of these units, except for the Wealden, and it is hard at present to determine the identity of all these spinosaurids, since most of the specimens are incomplete, and since the type specimen from Egypt was incomplete, and has now been destroyed.

4.2. Sedimentology

The Chenini Formation in the Tataouine area consists of cross-bedded buff-coloured and yellowish sandstones, containing large quartz grains, and showing in places breccias and conglomerates (Fig. 7). A basal conglomerate unit, indurated and cemented by iron oxide, contains wood fragments, isolated bones and teeth, and coarse quartz grains.

The succession at one of the main bone-bearing localities begins with major sandstone units at least 3 m thick near the base of the Chenini Formation (Fig. 7). The base of these sands was not seen at this locality. The sands are poorly sorted coarse-grained red sandstones with angular well-rounded clasts. They form large free-standing blocks, exposed in several discrete outcrops on the hill side (Figs. 3 and 8A). The lower sands are cross-bedded, the bedding often being indicated by lags of flattened clay intraclasts or phosphatic clasts (Fig. 8A). The dip directions of the foresets within this unit indicate a unidirectional current trending NW on a mean bearing of 330°.

The main bone-bearing units are found at the top of the lower sand. They are erosively based channel lag deposits, which clearly truncate cross-

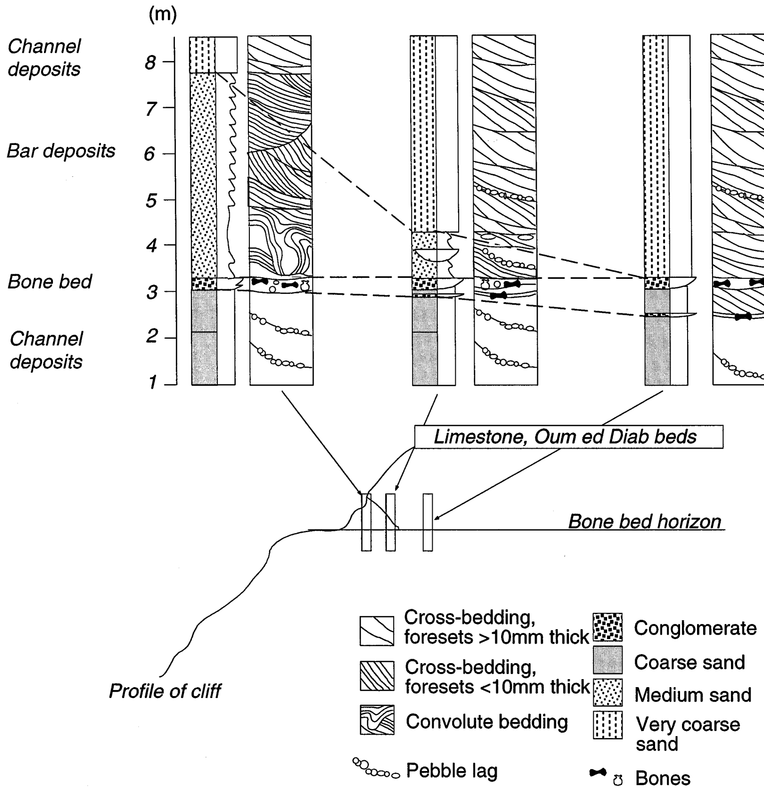

Fig. 7. Sedimentary logs through the sequence of the Chenini Formation at the major bone bed horizon (recorded by CT and DM in 1998).

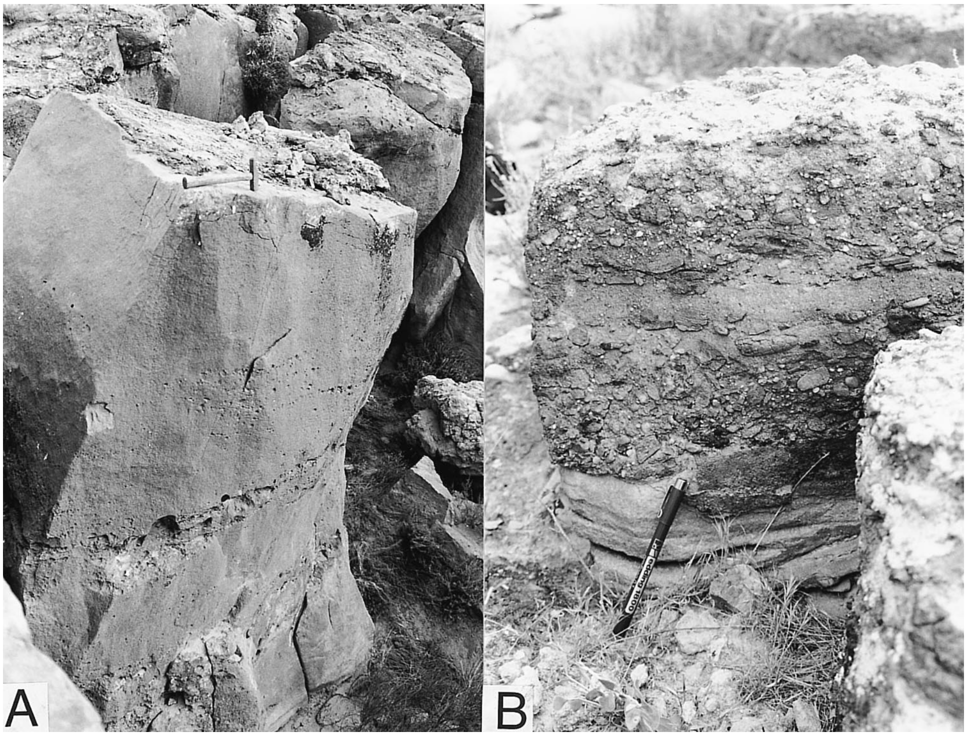

Fig. 8. Photographs of typical sedimentary features of the Chenini Formation: (A) the underlying cross-bedded sandstone, with occasional layers of phosphatic clasts; (B) the bone bed, consisting of two major coarse clastic phases separated by a thin band of sandstone, and showing an erosive base.

bedding in the lower sands (Fig. 8B). The erosive base of the bone bed is cut into the underlying sands to a depth of at least 0.5 m in places. In many outcrops, several individual bone-bearing horizons are present, separated by varying thicknesses of cross-bedded sand. These individual bone units converge laterally to form multi-phase single bone beds, with distinct differences in clastic composition (Figs. 8B, 9A and B). All bone-bearing units are themselves cross-bedded, showing low-angle planar cross-sets.

The bone-bearing units are conglomeratic, with clasts set in a poorly sorted coarse sand or gravel matrix (Figs. 8B and 9A–C). They are rich in bones and bone fragments, teeth, phosphatic pebbles, small quartz pebbles, and wood fragments. Quartz pebbles are typically small (50–100 mm diameter) and well rounded. Phosphatic pebbles are larger and also well rounded. Bone fragments are very variable in both size and shape (typically, clasts are 10–100 mm in length, although individual bones up to 300–400 mm are present in some localities). Bone clasts may be elongate, tabular, or irregular, and the margins of the bone clasts may be angular or rounded (Fig. 9A–F).

Wood may be either silicified or limonitized, and is also present in a range of sizes, from small fragments to logs >1 m in length (Fig. 10). Plants from the Chenini Formation include the ferns *Alstaettia* and *Weichselia* and the logs are from conifer trees (Barale et al., 1998). Associated fossils of these taxa include imprints of axes and leaves.

Within the bone bed, phosphatic clasts account for around 75% of all clastic material. In all areas, the deposit is clast-supported, most clasts being either flat-lying or showing imbrication (Figs. 8B and 9A–C). Individual foresets within the bone bed are separated by thin coarse sand or gravel layers, with very few clasts. These may represent fining-upwards units within the bone bed.

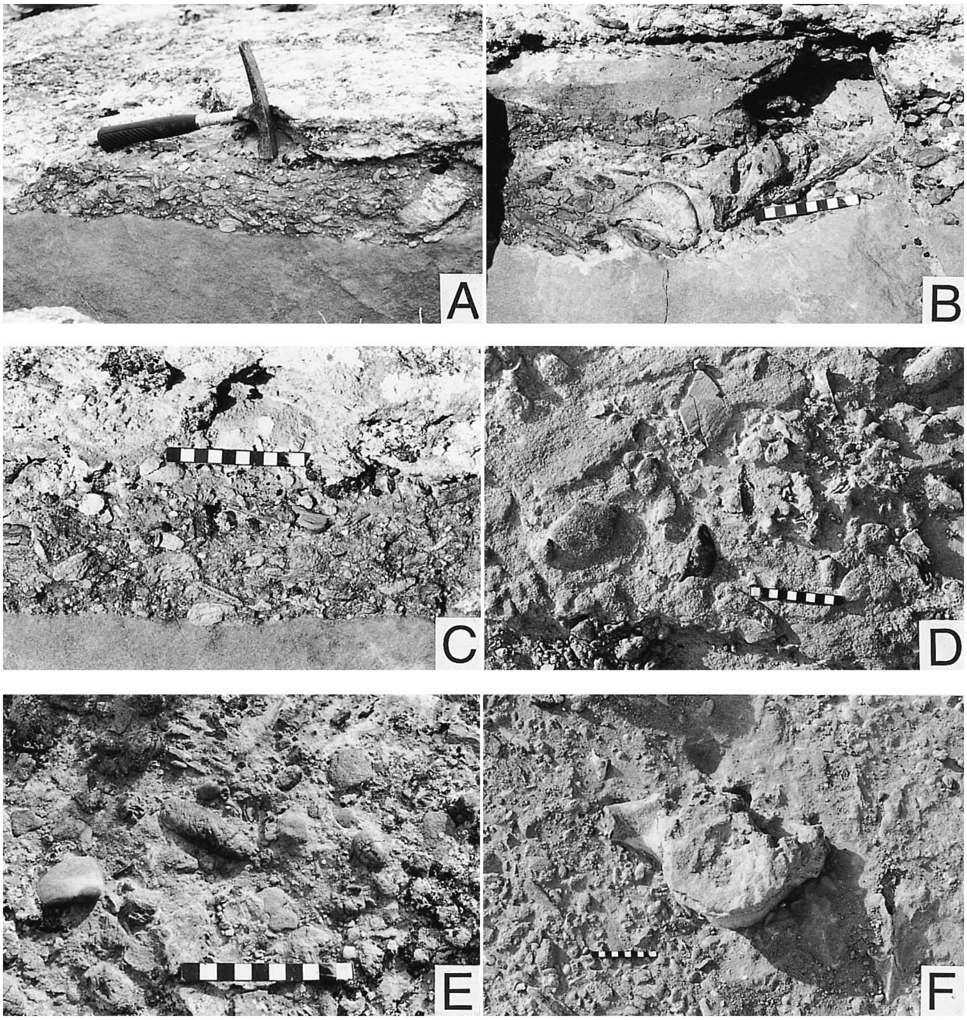

Fig. 9. Main Chenini Formation bonebed, seen in vertical section (A–C), and in plan view (D–F): (A–C) vertical sections through the bone bed, showing variable thickness, variation in clast size, shape, and orientation; (D) the bone bed with rounded bone fragments and a *Carcharodontosaurus* tooth to the left of the scale bar; (E) the bone bed with a coprolite just above centre; (F) a large sauropod vertebra sitting isolated on the bone bed surface. Scale bar is 100 mm.

In most exposures, the bone bed is immediately overlain by a coarse cross-bedded sandstone or grit (Fig. 7). The boundary between the coarse sandstone and the bone bed is sharp and erosive. Clasts from the bone bed are incorporated in the lowermost parts of foresets immediately overlying the bone bed. Occasional layers within the coarse sandstone contain small phosphatic and quartz pebbles, and these are also heavily iron-stained, like the bone bed. An isolated piece of turtle bone was white to blue–white in colour and quite different from the bone in the underlying bone bed. The pebble-rich units in the coarse sandstone are usually less than 30 mm thick, lenticular, and rarely extend further than 1–2 m laterally. Cross-bedding is pervasive throughout the lower (exposed) portions of the coarse sandstone. Cross-beds are tabular, with individual foresets typically 10–20 mm thick.

At one locality, the bone bed is immediately overlain by up to 4 m of medium- to fine-grained buff-coloured sands. These sands are clearly cross-

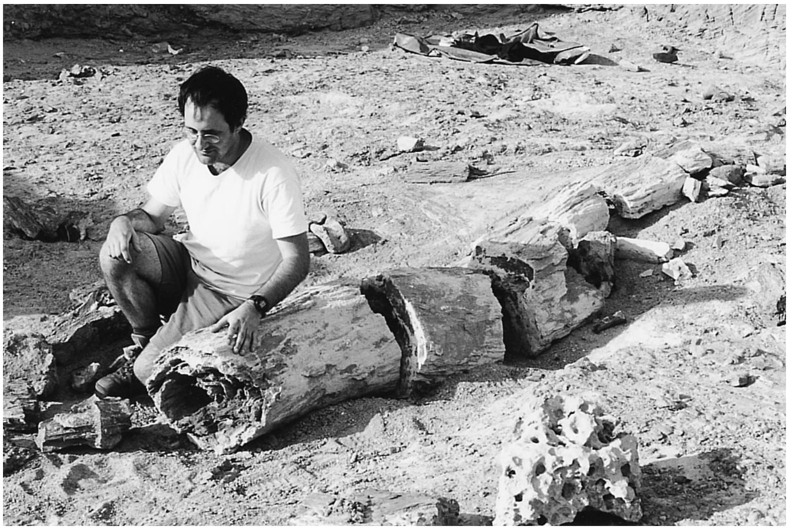

Fig. 10. Clive Trueman poses beside a broken log found on the main bone bed level. The log is some 4 m long.

bedded, and they display a range of sedimentary structures indicative of fluvial point-bar deposition. Individual cross-sets average 100 mm thick. Within these cross-sets, the individual foresets fine upwards from coarse sand to fine sand or silt. Individual foresets are typically 10–15 mm thick. In places, flaser bedding is clear, and in other areas, original sedimentary structures are obscured by soft-sediment deformation.

At the base of these sands, a prominent channel, approximately 3 m wide and 1 m deep, can be seen. Within the channel are coarse lags, consisting of gravels, with abundant flattened clay clasts up to 100 mm in length, and rarer wood and bone clasts. Soft-sediment deformation is apparent under the basal lags, and in places, clear flame structures can be seen. The channel is part of a larger sand body, which reaches a maximum thickness of 4–5 m, and pinches out rapidly laterally, extending for less than 20 m in all.

4.3. Taphonomy of the bonebeds

Bones and teeth in the Chenini Formation bonebeds are variable in size and degree of abrasion, and it seems clear that the fossils represent a mixed assemblage of materials brought together from different sources by the river systems. The size of elements ranges from tiny fish teeth and scales 1–2 mm in diameter (Fig. 9D and E) to sauropod vertebrae (Fig. 9F) and limb bones up to 1 m long. Fossil logs may be larger, up to 4 m in length (Fig. 10).

It seems probable that the fossil assemblage is mixed, with material derived from a range of locations, some local, and some very distant. This is especially indicated by the degree of abrasion of specimens, which ranges from entirely undamaged to heavily abraded (Fig. 9). At least four grades of material, assessed in terms of abrasion, may be identified. The best preserved specimens, such as coprolites and fern leaves, are presumably of local origin, while others, such as unabraded fish teeth and scales and crocodile scutes were transported only a short distance. Most of the dinosaur bones and teeth show slight abrasion, so they have probably been transported several kilometres. However, the close association of elements from specific theropod and sauropod taxa suggests that some of the transport happened while carcasses were still intact. More abraded specimens, including the logs, as well as some of the larger dinosaur bones, may have been rolled in from further away, or some may have been reworked. These are merely preliminary observations, and they require fuller testing.

4.4. Environment of deposition of the bone bed

The bone bed is clearly an attritional winnowed bone accumulation. This is demonstrated by the cross-bedded, clast-supported, and imbricated nature of the deposit, the mixed dissociated bone remains, and the well-rounded phosphatic pebbles. It seems likely that the bone remains were concentrated during periods of very low net sediment deposition, high rates of sediment reworking, and increased channel incision (e.g. relative drop in the water table). The final deposition of the bone-rich horizons occurred in at least two distinct events. This is clear as the bone bed is present as a single thick multi-storey unit in some localities, and as several distinct units, separated by up to 1 m of cross-bedded sands, in other localities. Evidently, where the bone bed units are separated by relatively thick sand or grit layers, background deposition was relatively rapid. Where multi-storey single bone beds are found, there was essentially no sediment deposition in the time period between the deposition of the two bone beds. Where single-storey bone beds are found, or the bone bed is absent, the original deposition of the bone bed may have occurred in areas experiencing net erosion.

The orientation of logs within the bone bed is fairly consistent (Fig. 11), and the mean trend of the logs is perpendicular to the flow direction (derived from the foreset dip direction). This further suggests that the logs were grounded in shallow water, rather than rapidly buried in a 'freezing' flow. The direction of flow in the vicinity of the dinosaur bone beds is 330°, essentially north-northwest, in line with the overall palaeogeographic reconstructions of the area (Fig. 6A and 12), which indicate enormous river systems running northwards from the Saharan region to the south shore of Tethys, some distance north of the study area. Busson and Cornée (1989, 1991) posited the same palaeocurrent distributions, but interpreted the sediments as deposited by sheet floods.

The bone bed clearly forms a lithological boundary, the sediments below and above the upper bone bed being very different in character. However, the palaeocurrent direction (derived from the foreset dip direction) is not significantly different above and below the bone bed, indicating that the driving mechanism responsible for concentration of the bone and wood clasts was not linked to a profound change in the direction of sediment supply. After deposition of the bone-rich horizons,

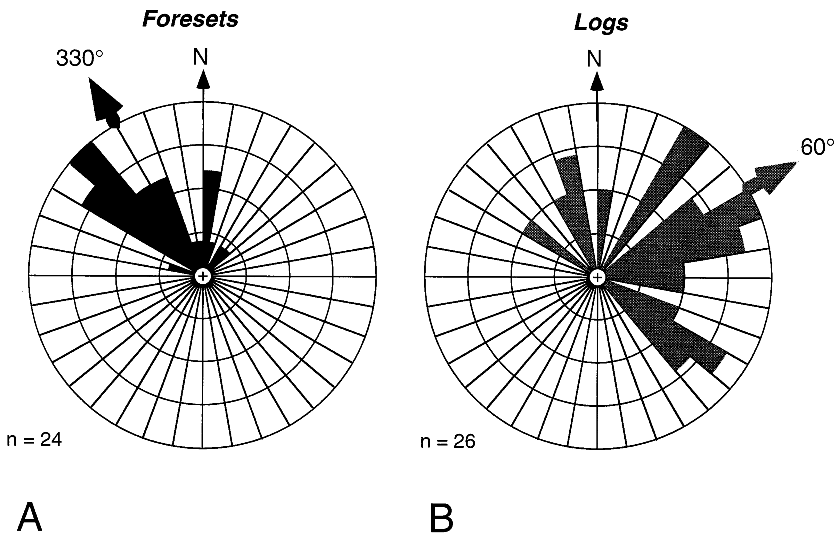

Fig. 11. Rose diagrams showing orientation of cross-bed foresets (A) and of long axes of logs (B). Note that the logs lie athwart the main current direction (NNW).

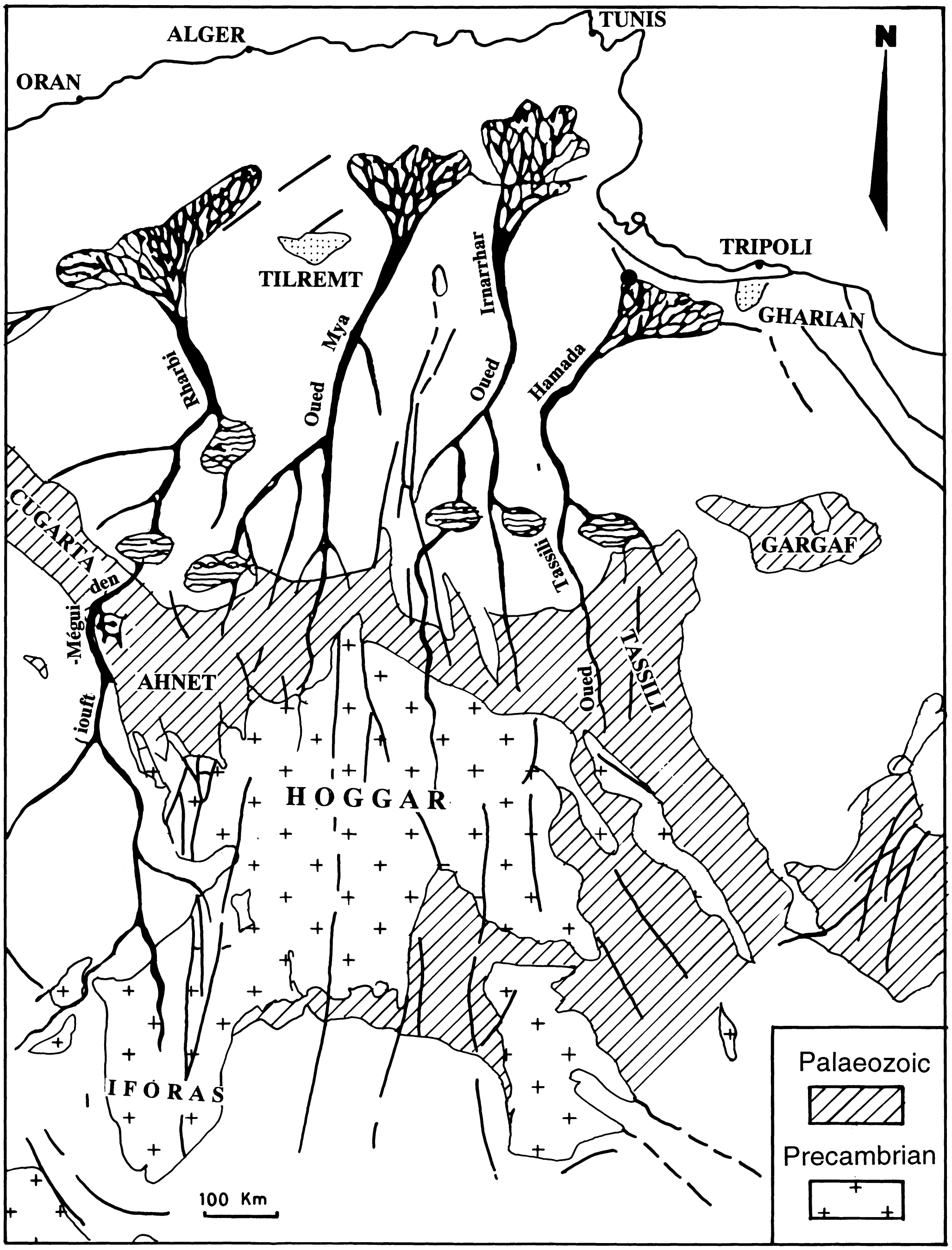

Fig. 12. Reconstructed palaeogeography of the Barremian–Aptian interval in central North Africa. The Chenini Formation (marked with black spot) lies in the delta region of the Oued Tassili–Hamada, a major drainage channel to the east (based on information in Lefranc and Guiraud, 1990).

the fluvial style changed from relatively massive cross-bedded sands to coarse cross-bedded grits and sands within channel systems, and large fine-grained sand bars, possibly suggesting a transition to lower total current energy, and greater channel sinuosity.

Earlier accounts of the environment of deposition of the Chenini Formation have pointed to either aeolian or marine conditions. Schlüter and Schwarzhans (1978) interpreted some of the cross-bedding in the yellow sand units overlying the bone bed as aeolian. There is no evidence for this view, either in the nature of the cross-beds, or in the characters of the sand grains, nor are there any other aeolian indicators. Bouaziz et al. (1988) suggested that there is evidence in the Chenini Formation for some marine conditions, based partly on the overall palaeogeographical situation and the common occurrence of shark teeth. However, the palaeogeographical reconstructions (Fig. 12) show that the coastline lay some 50 km to the north and north-east. Supposed herringbone cross-beds are simply adjacent sets of lateral accretion cross-beds indicating changes in the direction of channel migration. The shark teeth are from taxa, such as hybodonts, that are not exclusively marine, and which have been reported elsewhere from freshwater or estuarine units. The other fossils are terrestrially derived, and were presumably washed down the great Oued Tassili–Hamada river complex, with its deltaic region extending over the whole Dahar cliffline in southern Tunisia and westernmost Libya (Lefranc and Guiraud, 1990).

5. Vertebrate fauna

The vertebrate fauna of the Chenini sandstones has been reported by several authors (Pervinquière, 1912; de Lapparent, 1951, 1960; Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988). These authors noted the presence of teeth of sharks, teeth and scales of actinopterygian fishes, turtle carapace fragments, skull fragments, scutes, jaw elements, and teeth of crocodilians, bones and teeth of large theropod dinosaurs (including the teeth classically assigned to *Spinosaurus* and *Carcharodontosaurus*), a possible smaller theropod dinosaur, and large limb bones and vertebrae of a sauropod. Identifications given here are all tentative, and all these Tunisian vertebrates will be thoroughly revised after further collecting has taken place.

The first record of sharks from the Early Cretaceous of southern Tunisia was made by Tabaste (1963), who identified teeth of *Priohybodus arambourgi* and (?) *Asteracanthus* sp. Schlüter and Schwarzhans (1978) identified their shark teeth as *Odontaspis* sp., hybodontid indet., and a third unidentified shark. They also noted abundant shark coprolites. The indication of *Odontaspis* is unlikely since first records elsewhere are from the Campanian (Cappetta, 1987). Bouaziz et al. (1988) identified *Cretodus* ? (Fig. 13A and B) and *Protolamna* sp. (Fig. 13C and D). The actinopterygian remains include characteristic bulbous hemispherical crushing teeth of the semionotiform *Lepidotes* sp. (Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988) and pycnodonts, which occur abundantly and almost exclusively in some bonebed horizons. Other actinopterygian remains include similar crushing teeth of the pycnodontiform cf. *Anoemodus*, and smaller teeth of an unidentified pycnodontiform. The amiiform cf. *Caturus* is represented by caniniform teeth with a small enamel cap (Bouaziz et al., 1988). This identification is, however, uncertain since the teeth lack the typical carinae of *Caturus* (G. Cuny, pers. commun., 1999). Other rarer fish remains include tooth plates of the lungfish *Neoceratodus africanus* (Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988) and sculpted dermal bones of the coelacanth *Mawsonia* sp. (Schlüter and Schwarzhans, 1978). Similar remains were found on the 1998 expedition.

Reptilian remains include isolated elements of the carapace of turtles. Skull fragments, scutes, jaw elements, and teeth of crocodilians have also been reported. Schlüter and Schwarzhans (1978) noted teeth of cf. *Machimosaurus*, scutes and dermal skull bones of cf. *Steneosaurus*, and a crocodilian vertebra. However, the material on which these identifications were based was extremely fragmentary, and the occurrence of *Machimosaurus* and *Steneosaurus*, which are

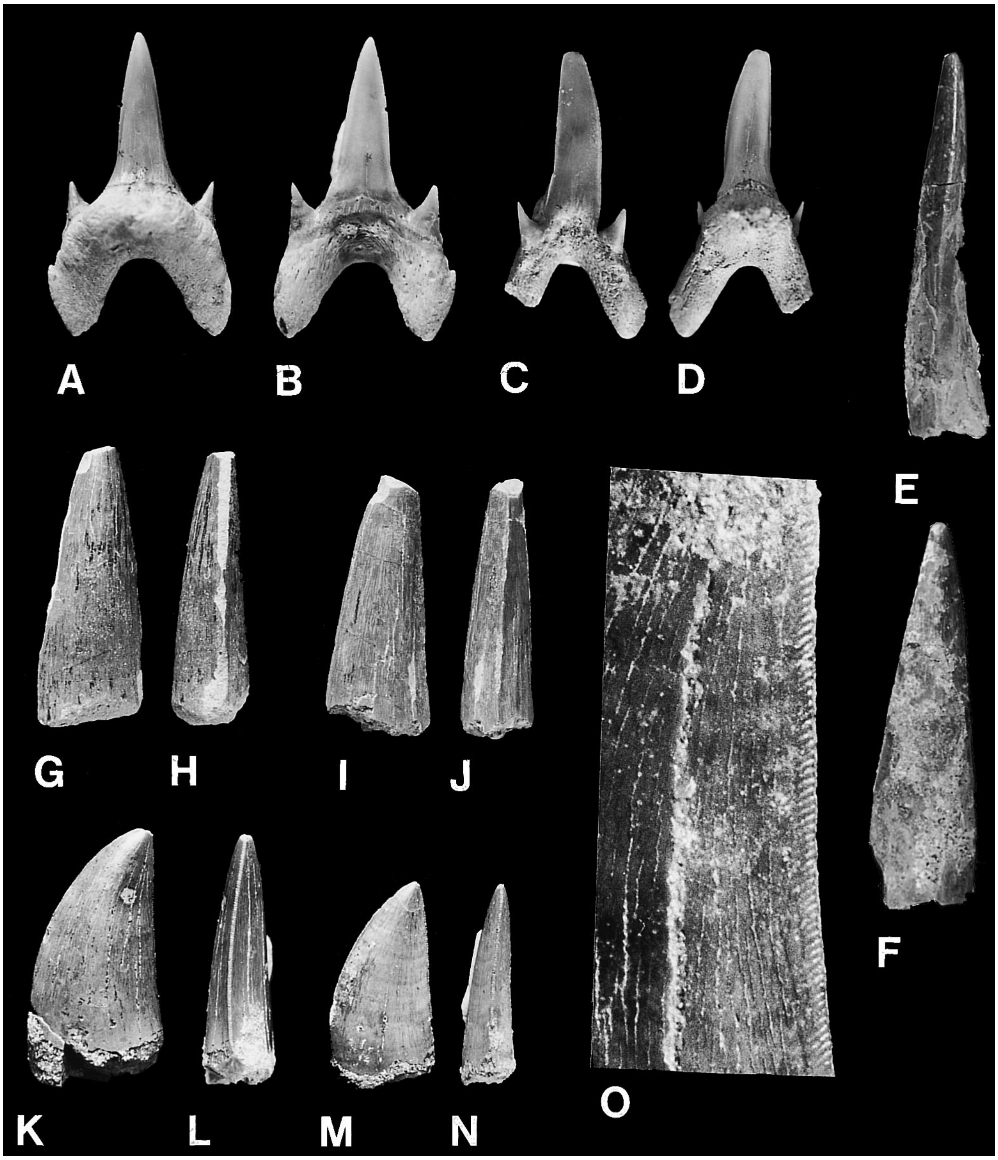

Fig. 13. Teeth of sharks (A–D), a pterosaur (E, F), and theropod dinosaurs (G–O) from the Chenini Formation. Teeth of the sharks *Cretodus*? (A, B) and *Protolamna* (C, D) in lingual (A, C) and labial (B, D) views. Tooth of an ornithocheirid pterosaur in lateral (E) and labial (F) views. Teeth of *Spinosaurus* (G–J) and *Carcharodontosaurus* (K–N) in lateral (G, I, K, M) and antero-posterior (H, J, L, N) views. The antero-posterior cutting edges of *Carcharodontosaurus* teeth are serrated (O), while those of *Spinosaurus* are not. Scales: A–F, ×2; G–N, ×1; O, ×5.

Jurassic marine crocodilians, is highly unlikely. Bouaziz et al. (1988) noted only conical teeth of crocodilians. The presence of such diverse crocodilian remains can be confirmed, and we found numerous dermal elements, teeth, and a dentary with teeth, representing several crocodilian taxa. The collection of the Geological Survey of Tunisia also includes a plesiosaur vertebra.

A previously unreported taxon is an ornithocheirid pterosaur, represented by an isolated tooth found during the 1998 expedition (Fig. 13E and F).

Dinosaurs from the Chenini Formation are the usual North African mid-Cretaceous taxa, the theropods *Carcharodontosaurus* and *Spinosaurus*, a sauropod, and an iguanodontid ornithopod (de Lapparent, 1951, 1960; Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988). The two theropods are identified generally by their teeth (Fig. 13G–O). The teeth assigned to *Spinosaurus* (Fig. 13G–J) are narrow, somewhat rounded in cross-section, and lack the anterior and posterior serrated edges characteristic of theropods and basal archosaurs. These teeth also frequently bear longitudinal facets. The teeth of *Carcharodontosaurus* (Fig. 13K–N) are flattened, recurved, and especially broad antero-posteriorly, with serrated anterior and posterior carinae. The enamel bears faint but distinct ridges or folds more or less perpendicular to the cutting edges (Fig. 13O). Among remains recovered during the 1998 expedition were numerous postcranial elements of theropods, some perhaps assignable to *Carcharodontosaurus*, others to *Spinosaurus*, and others perhaps to a smaller theropod.

The unidentified sauropod is represented by large bone fragments and a tooth (Schlüter and Schwarzhans, 1978; Bouaziz et al., 1988), as well as some more complete dorsal and caudal vertebrae (Fig. 9F), ribs, and limb bones. These indicate a sauropod of medium size, probably close to 10 m in length.

Ornithopods are represented by iguanodontid teeth, first reported by de Lapparent (1951, 1960). More recently, a number of typically leaf-shaped iguanodontid teeth, exhibiting various stages of wear, have been collected by the Geological Survey of Tunisia. Whether they should be referred to the genus *Iguanodon*, as suggested by de Lapparent (1960), or to another ignuanodontid, such as the African *Ouranosaurus*, is not easy to decide on the basis of the available material.

6. Biogeographical implications

The dinosaur beds of Saharan Africa range in age from Hauterivian or Barremian to Cenomanian. All these vertebrate-bearing units lie below the late Cenomanian marine transgression layer, represented in most regions by massive Cenomanian–Turonian limestones. The oldest dinosaur localities may be in the Tiourarén beds of In Gall in Niger, where Sereno et al. (1994) reported the theropod *Afrovenator* and a sauropod in units that lie stratigraphically below the ?Aptian Gadoufaoua beds. Associated fossils include the coelacanth *Mawsonia*, the dipnoan *Ceratodus*, and the semionotid *Lepidotes*, as well as turtle and crocodilian remains. Sereno et al. (1994) suggested a tentative Hauterivian–Barremian age for this unit, but presented no evidence.

The next assemblage of dinosaurs and other vertebrates, comes from the Elrhaz Formation (= assemblage GAD 5), a division of the Tégama Group of Gadoufaoua, Niger. This unit has been generally dated as Aptian (Taquet, 1970, 1976, 1980; Sereno et al., 1998), based on comparisons of the faunas with the Santana Formation of Brazil. For example, the crocodilian *Araripesuchus gomesii* from the Santana Formation is very much like *Araripesuchus wegeneri* from the Elrhaz Formation, and both units seemingly share the turtle *Araripemys* (Wellnhofer et al., 1983). Such a correlation depends, however, on certainty that the Santana Formation is Aptian, and that is debated. In particular, Pons et al. (1990) give a date no older than late Albian, and probably Cenomanian, for the fossiliferous nodule-bearing part of the Santana Formation (Martill, 1993; Tong and Buffetaut, 1994). Note that the hybodont shark *Tribodus* is found in the Santana Formation nodules, and also in the Cenomanian-age Baharija Beds of Egypt (P.N. Brito, pers. commun. to D.M.M., 1999).

A younger Cenomanian vertebrate-bearing unit in Egypt is more securely dated, and beds in Sudan and Morocco have been tentatively correlated. The Baharija beds of Egypt have always been assigned to the Cenomanian (Stromer, 1936; Allam, 1986), and a basal late Cenomanian age was confirmed by Luger and Gröschke (1989) on the basis of ammonites found in estuarine strata immediately overlying dinosaur-bearing sediments, and by Werner (1990), on the basis of comparative studies of the shark fauna. The Wadi Milk Formation of

Sudan might also be Cenomanian (Werner, 1994) since it shares remains of the shark *Asteracanthus aegyptiacus* with Baharija, and the remaining fauna of sharks, bony fishes, lungfishes, a gymnophionan, turtles, snakes, and crocodilians apparently confirm a Late Cretaceous age. Rauhut (1995), however, preferred an Albian age, based on comparisons of the dinosaur faunas. Both the Wadi Milk and Baharija formations share remains of *Carcharodontosaurus* and *Bahariasaurus*, but the Wadi Milk dinosaur fauna (titanosaurid indet., carcharodontosaurid indet., cf. *Ouranosaurus*, iguanodontid indet., ?hypsilophodontid) is more like that from the ?Aptian–Albian Gadoufaoua fauna of Niger.

The Kem Kem beds, a local manifestation of the 'grès rouge infracénomanien', a 200 m thick continental succession in SE Morocco, are probably also Cenomanian in age. These beds rest unconformably on Palaeozoic rocks, and they lie immediately below the Cenomanian–Turonian limestone, which contains the ammonite *Neolobites vibrayensis* at the base, thus setting an upper age limit of early late Cenomanian (Choubert, 1952). They were traditionally dated as Albian, but have been reassigned to the Cenomanian by Wellnhofer and Buffetaut (2000) on the basis of the vertebrate fossils. The fishes and reptiles from Kem Kem show the closest similarity to the Baharija forms, especially *Spinosaurus*, *Carcharodontosaurus*, and a titanosaurid sauropod, and the abundant giant freshwater fishes, *Hybodus*, *Lepidotes*, *Neoceratodus*, and *Mawsonia* (Russell, 1996). However, many of these fish and dinosaurian taxa are long-ranging, but the sharks are particularly useful in correlation (Wellnhofer and Buffetaut, 2000).

Variations in the vertebrate faunas of the North African 'continental intercalaire' may represent stratigraphic differentation, and it may be that it will be possible to distinguish Neocomian, Aptian, Albian, and Cenomanian faunas. However, the ages may in the end turn out to be more narrowly confined, and many of the differences may relate to local environmental variations, or larger-scale palaeogeographic effects (Russell, 1996). For example, the Gadoufaoua fauna of Niger, dominated by ornithopod dinosaurs, lay over 1000 km from any contemporary coastline (Reyment and Dingle, 1987; Moody and Sutcliffe, 1991), whereas the Chenini Formation of Tunisia and the Baharija Formation of Egypt, both yielding abundant fish remains, were within 100 km of the coastline, and the bonebeds are in a fluvio-deltaic environment.

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