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Paleontological studies of Cretaceous vertebrate fossil beds in the Tataouine Basin (southern Tunisia)

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ABSTRACT

Cretaceous fossil vertebrate remains from Northern Africa are known in the literature from the beginning of 1900's, when several Lower Cretaceous beds with fragmented material of fish, turtles, crocodiles and non-avian dinosaurs were discovered. In particular, the '*Continental Intercalaire*' deposits of the Tataouine basin of southern Tunisia preserve one of the most diverse Lower Cretaceous vertebrate fauna from Africa. This alternation of Late Jurassic – Late Cretaceous shallow-marine, littoral and non-marine deposits extends from Algeria to Egypt and provides important data for the comprehension of Mesozoic faunas end ecosystems. This research project focuses on a detailed revision of the stratigraphic distribution of mid-Cretaceous fossil beds in the Tataouine Basin, and include the description of four, newly discovered vertebrate tracksites.

A detailed, basin-scale revision of the stratigraphic occurrence and lateral variability of fossil-bearing strata based on accurate sampling, description, and comparison of different faunal assemblages, indicates 1. a strong, lateral facies variability within the context of a low gradient, circalittoral to coastal-plain environment, and 2. multiple and diachronous fossil beds which include elasmobranchs, actinopterygians, sarcopterygians, turtles, crocodyliforms, pterosaurs, and non-avian dinosaurs remains. In the Tataouine region, macro- and microvertebrate remains are recovered from three distinct stratigraphic intervals: the lower Douiret Formation (Barremian), the Chenini (rare) and Oum ed Diab members of the Aïn El Guettar Formation (Albian). The Douiret Formation is characterized by mainly siliciclastic deposits in coastal environments (foreshore to coastal sabkha facies): fossils recovered from this interval are essentially representative of freshwater taxa. In addition, the Chenini sandstones, known in the literature as the richest fossil-bearing unit in southern Tunisia, are barren of fossils: fossil beds are instead referred to the overlying, Oum ed Diab Member.

Four vertebrate tracksites have been discovered in the study area: the Middle Jurassic Beni Ghedir site, the late Albian Chenini site, the Cenomanian Ksar Ayaat locality and the upper Cenomanian Boulouha site. Depositional settings of each tracksite have been defined on stratigraphic and sedimentologic data, and tracks are ascribed to different ichnocoenoses in relation to their paleoenvironments. In order to have a more objective representation of the vertebrate tracks, digitalisation techniques, such as laser scanning, has been used to generate three-dimensional models of the tracks.

Callovian beds exposed at the Beni Ghedir site preserve approximately 130 tridactyl footprints distributed over an area of 200 square meters, and represent the oldest evidence of a dinosaur fauna in Tunisia. The Chenini tracksite includes poorly preserved crocodilian tracks and the dinosaur ichnospecies *Apulosauripus federicianus*, whereas footprints assigned to a pleurodiran turtle are exposed at the Ksar Ayaat locality. The J. Boulouha tracksite presents almost 100 well-preserved tridactyl tracks referred to small-sized theropods, fossil bird tracks - ichnogenus *Koreanaorins* – and tracks referred to a mammalian trackmaker: these discoveries represent the first report of fossil bird and mammal from the Cretaceous of continental Africa and Tunisia respectively. The occurrence, in Tunisia, of the ichnospecies *A. federicianus*, originally described from the Santonian of the Apulian platform, provide additional data on the controversial framework of vertebrate faunal distribution in the mid-Cretaceous Mediterranean carbonate platforms context. In particular, data collected from the Tunisian tracksites have been compared with those of Italy and Croatia, showing important analogies in overall morphology and paleoenvironmental setting of dinosaur ichnoassociations. Data presented here suggest that similar vertebrate faunas might have inhabited "extreme" environments, such as arid carbonatic platform, supporting the hypothesized subaerial connection between the northern African margin and the Mediterranean platforms during the mid-Cretaceous.

RIASSUNTO

Sin dall`inizio del secolo scorso, quando i primi fossili di pesci, coccodrilli, tartarughe e dinosauri furono scoperti in nord Africa, diversi studi si sono susseguiti descrivendo i depositi giurassico-cretacei, a prevalenza continentale, che si estendono dal Marocco all'Egitto, noti successivamente in letteratura col nome di "*Continental intercalaire*". In particolare, nel Bacino di Tataouine nel Sud tunisino affiora l'intera successione del "*Continental intercalaire*", facendo di questa regione una località ideale per la comprensione delle faune e degli ecosistemi mesozoici. Questo progetto di ricerca si propone di fornire la prima dettagliata revisione stratigrafica dei siti fossiliferi cretacei del Bacino di Tataouine e di descrivere quattro nuovi siti a impronte fossili di vertebrati recentemente scoperti.

Il campionamento, la descrizione e revisione stratigrafica dei livelli fossiliferi del Bacino di Tataouine indica una forte variazione laterale delle facies, all'interno di un contesto circa-litorale o di piana costiera. I resti di macro- e microvertebrati comprendono elasmobranchi, attinopterigi, sarcopterigi, tartarughe, croccodiliformi, pterosauri e dinosauri non-aviani e provengono da tre distinti intervalli stratigrafici: la base della Formazione di Douiret, il Membro di Chenini (rari) e quello di Oum ed Diab della Formazione Aïn el Guettar. La Formazione di Douiret è caratterizzata da depositi silicoclastici di ambiente costiero, simile alle attuali sabke, in cui l`associazione faunistica presenta una prevalenza di taxa d'acqua dolce. Le sabbie fluviali del Membro di Chenini, a cui in precedenza venivano attribuiti gli intervalli fossiliferi, sono qui considerate sterili, i resti di vertebrati sono invece interpretati come conglomerati transgressivi, marker del sovrastante Membro di Oum ed Diab.

Per quanto riguarda le impronte di vertebrati, quattro siti sono stati scoperti e descritti: il sito Giurassico Medio nella valle di Beni Ghedir, il sito Albiano superiore di Chenini, il sito Cenomaniano di Ksar Ayaat e il sito Cenomaniano superiore di Boulouha. In ogni località si sono studiate le caratteristiche sedimentologiche del livello a impronte e le tracce sono state riferite a diverse icnocenosi, in relazione al loro paleoambiente. Inoltre, per avere un`oggettiva rappresentazione delle impronte, i calchi, realizzati in silicone, sono stati scansionati tramite l`utilizzo di un laser scanner, ottenendo modelli tridimensionali digitali fedeli all`originale.

Un centinaio d'impronte tridattili sono state scoperte in depositi Calloviani nella valle di Beni Ghedir, sebbene la scarsa preservazione limiti l`attribuzione delle tracce a un generico teropode, questa scoperta rappresenta la più antica testimonianza di dinosauri in Tunisia. Il sito di Chenini è invece caratterizzato da tracce attribuibili a coccodrilli e da ben conservate impronte attribuite all`icnospecie di dinosauro quadrupede *Apulosauripus federicianus*. Questa icnospecie, originalmente descritta in depositi santoniani della piattaforma Apula (Bari, Italia), rappresenta la prima segnalazione di *A. federicianus* in Africa. Il sito di Ksrar Ayaat presenta numerose impronte di tartaruga, le prime rinvenute in Tunisia. Infine, la maggior concentrazione d'impronte meglio conservate è stata trovata nel sito di J. Boulouha, dove sono state scoperte quasi un centinaio d'impronte tridattili, attribuite a un generico teropode di medie dimensioni, piccole impronte attribuite all`icnogenere di uccelli *Koreanaornis* e tracce riferite a un generico piccolo mammifero. Questi ultimi due ritrovamenti, in particolare, rappresentano la prima testimonianza di uccelli e mammiferi nel Cretaceo rispettivamente dell'Africa continentale e della Tunisia. La presenza dell'icnospecie *A. federicianus* in Tunisia, suggerisce una possibile connessione tra le icnofaune tunisine e quelle delle coeve piattaforme carbonatiche dell'area mediterranea. Dal confronto tra le impronte di vertebrati trovate nel Cretaceo medio del Bacino di Tataouine e quelle scoperte nelle coeve piattaforme carbonatiche dell'area mediterranea, emerge una certa somiglianza nella morfologia, dimensione e paleoambiente delle icnofaune a teropodi: la presenza di animali di forme e dimensioni simili, in analoghi ambienti "estremi", come possono essere le aride piattaforme carbonatiche, aggiunge nuovi dati a supporto della tesi che suppone un collegamento, tipo ponte di terra, tra le piattaforme mediterranee e il margine nord africano nel Cretaceo medio.

GENERAL INTRODUCTION

Premise

One of the key tasks in vertebrate paleontology has always been the understanding of paleoecology and paleobiogeography through the geological eras. In this context, Cretaceous has always been regarded as a turning point, not only because dinosaurs and other reptiles become extinct at the end of Cretaceous, but also because it was a period of big modification in the paleogeography of present day continents. The transition from Lower to Upper Cretaceous marks an important change in the distribution of land faunas. It was during Lower Cretaceous that the opening of southern Atlantic Ocean separated America from Africa, creating a natural barrier that isolated the faunas of the two continents (Foster, 1999; Gheerbrant and Rage, 2006). In addition, a major transgressive event in the Turonian submerged most of the present day North Africa, separating the continent from Europe. As a result, two different phases are distinguished between Lower and Upper Cretaceous faunas in Europe, Africa and America (Le Loeuff, 1991; Gheerbrant and Rage, 2006; Ősi et al., 2010). During Lower Cretaceous, taxa have trans-Tethyan affinities and they were not well differentiated, as land bridges connected the major continents allowing animal dispersal. Examples of common taxa between dinosaurs were Dryosauridae, Iguanodontidae, Rebbachisauridae and Abelisauridae (Sereno et al., 1998; Grigorescu, 2003; Sereno et al., 2004; Sànchez-Hernàndez et al., 2007). On the other hand, during Upper Cretaceous Africa was isolated and experienced a change in climate towards more dry and extreme environments, such as arid tidal flats and stormy weathers, which forced animals to develop peculiar adaptions, like structures that increased the bodily surface area, resulting in a lower faunal diversity (Russel and Paesler, 2003; Gheerbrant and Rage, 2006). Similarly, in the Upper Cretaceous, endemic small-bodied taxa evolved in isolated platforms of Europe (Dalla Vecchia, 2003; Fejfar et al., 2005; Vullo et al., 2007), in the Adriatic–Dinaric Carbonate Platforms (Dalla Vecchia, 2009) and western Romania (Nopcsa, 1902, 1923; Weishampel et al., 1991; Jianu and Weishampel, 1999; Csiki and Grigorescu, 2007). For all these reasons the study of Cretaceous African faunas has always been of great importance, as it brings information on land vertebrates dispersal routes and affinities between African, European and South American faunas.

Restricting the investigation field to the Mediterranean area, which is the bulk of this study, there is a huge debate on the possible African provenance of the dinosaurs from the carbonate platforms in the Mediterranean area, and on the existence of land bridges between the Italian and Croatian platforms, which might have lasted up to the Upper Cretaceous (Bosellini, 2002; Conti et al., 2005; Sacchi et al., 2009; Zarcone et al., 2010). This Ph.D. project aims to investigate this topic, focusing on the study of Cretaceous Tunisian vertebrate faunas and their interaction in the peri-mediterranean framework.

The study area is located in southern Tunisia, in the Tataouine region (Fig.1 intro). Deposits cropping out in the area include the whole Permian to Upper Cretaceous succession, resulting from the infilling of a major subsiding structure, known as the Tataouine basin (Busson, 1967). This basin is delimited to the North by the Medenine high, and to the Southwest by the Garian high, in Libya (Bouaziz, 1995) (Fig.1B intro.). Cretaceous sediments in the study area range from the Lower Cretaceous to the Turonian, when a major transgressive event submerged all present days Tunisia, sealing the Tataouine basin (Buson, 1967; Bouaziz, 1995). The alternations of continental and nearshore sediments that characterize the Cretaceous interval are also known in the literature as *Continental Intercalaire* (Kilain, 1931). This informal name refers to the continental deposits cropping out extensively in North Africa from Morocco to Libya and from Niger to Sudan, that are famous for having yield numerous vertebrate remains (Bouaziz et al., 1988; Zarbout et al., 1994; Benton et al., 2000; Bodin et al., 2010).

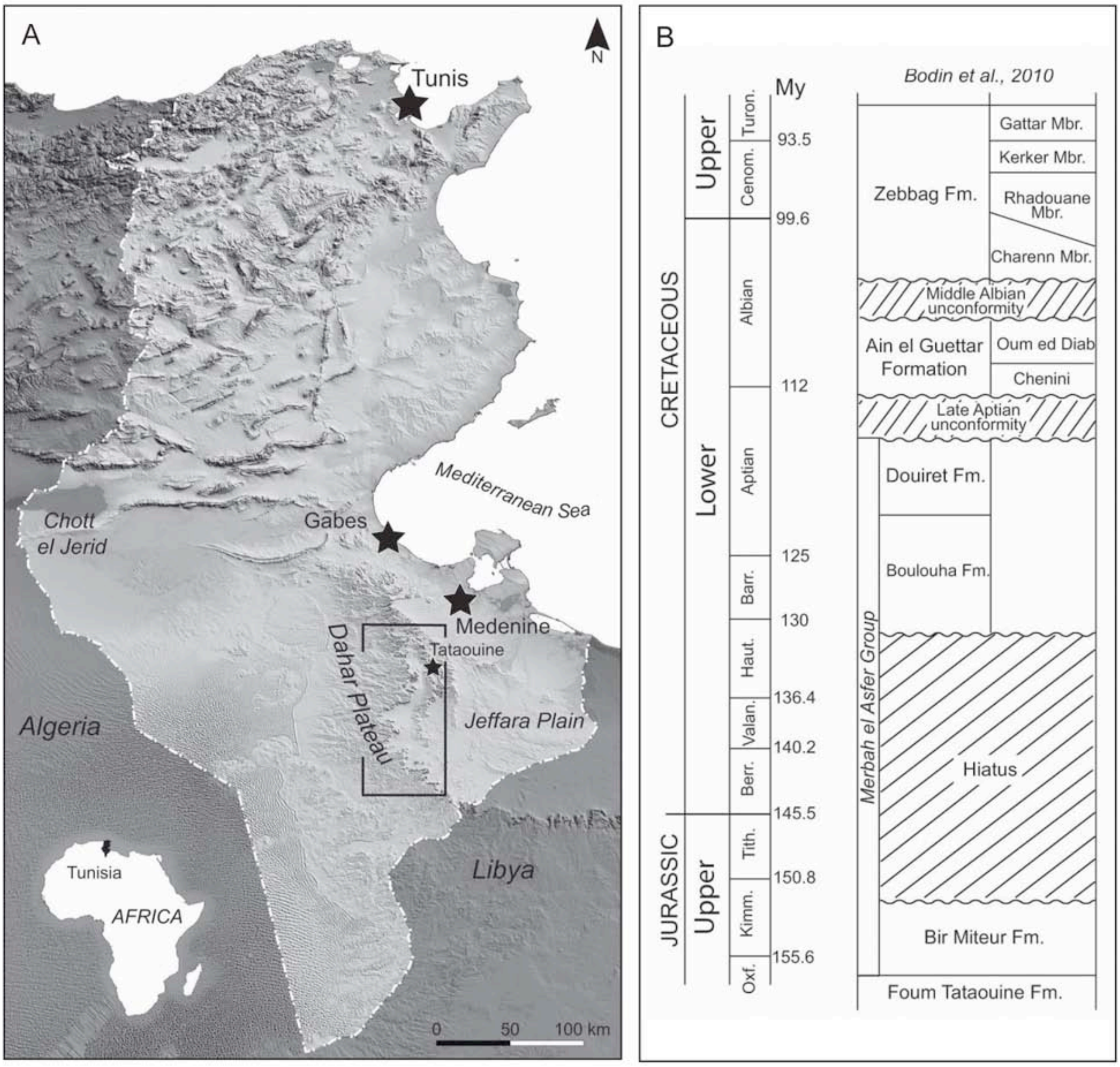

Figure Intro. 1 – Study area. A) Map of Tunisia showing the location of the Tataouine region. B) Stratigraphic nomenclature for the Upper Jurassic – Upper Cretaceous of the Tataouine Basin (after Bodin et al., 2010).

Historically, Cretaceous deposits in southern Tunisia have been divided into three formations: Douiret, Aïn el Guettar and Zebbag (Bouaziz et al., 1988; Zarbout et al., 1994). Vertebrate fossils are found in the conglomeratic beds from the Douiret and Aïn el Guettar formations, which have been tentatively dated as Aptian and Albian, respectively, on the basis of the correlation with marine deposits in central Tunisia (Bouaziz et al., 1988; Zarbout et al., 1994; Benton et al., 2000; Bodin et al., 2010). Vertebrate remains in the study area are mostly disarticulated and poorly preserved, although a varied fauna is represented, including fishes

(*Lepidotes* sp., *Hybodus* sp., *Ceratodus* sp. and pycnodontiformes), turtles, crocodiles and dinosaurs (*Spinosaurus* sp., *Carcharodontosaurus* sp., allosauridea and ornithischian) (De Lapparent, 1960; Benton et al., 2000; Ouaja, 2003; Cuny et al., 2004). Present studies on vertebrate sites in the Tataouine basin limit the sampling to few historically well-known localities: Oued el Kihl, Bir Miteur, el Hmaima and Om ed Diab. Abrasion stages and rare earth elements compositions on vertebrate remains have been use to differentiate the depositional environments, resulting in a terrestrial provenance of faunal assemblages from the Douiret Fm. and a more controversial mixed marine/continental environment for the Aïn el Guettar Fm. (Anderson et al., 2007). The fossiliferous layers are interpreted as fluvial conglomerates within the Chenini Member, and dinosaur and other fossils remains are believed to be transported, possibly as far as present day Niger (Benton et al., 2000; Ouaja, 2003).

In 2004 a Tunisian student discovered, in the Cretaceous deposits near Tataouine, a vertebrate tracksite dominated by tridactyl footprints, presumably of dinosaurian origin. During fieldworks, carried out during this Ph.D. research project, three more vertebrate tracksites have been recovered in the Mesozoic deposits of the Tataouine basin. In this Ph.D. research project tracksites will be investigated in detail for the first time.

Aim of the work

Although fossil beds cropping out in the Tataouine basin are well known to the scientific community, two major deficiencies arise from the literature. Firstly, the majority of specimens are described from few, well-known and geographically confined localities. Secondly, there is no detailed study of fossil associations within the context of the stratigraphic successions nor depositional facies. This research project, aims to present a paleontological and sedimentologic revision of southern Tunisia fossil-bearing beds and to discuss their implication in paleoecological reconstructions. Secondly, it targets to describe previously unreported vertebrate tracksites and their significance in the Tunisian mid-Cretaceous paleobiogeographic context. In addition, a comparison is carried out by comparing the Tunisian, Croatian and Italian track record in order to investigate the hypothesis of a land connection linking the mid-Cretaceous Mediterranean carbonate platforms and the northern African margin that could have served as a dinosaurs dispersal route (Bosellini, 2002; Conti et al., 2005; Zarcone et al., 2010).

In order to achieve these goals, several aspects of the geology and paleontology of the area are taken into account:

- Sedimentologic and stratigraphic aspects of the bone- and track-bearing layers;
- Description of tracksites, focusing on the sedimentologic characteristics of the track-bearing layers, and relation between footprints and paleoenvironments;
- Taxonomy of both vertebrate remains and tracks, tentatively referring the latter to possible trackmakers;
- Analysis of the faunal diversity and implication for the paleoecology of the area.

In addition, modern techniques, such as laser scanning and isotope analysis are also used. The first is used to produce three-dimensional digital models of the footprints, in order to give a more objective representation of the tracks. Analysis on stable isotopes, such as O^{16}, are tested on fossil enamel to obtain more precise dating, as no direct dating of the fossiliferous beds in the Tataouine Basin are available so far.

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CHAPTER 1 - The "*Continental Intercalaire*" of southern Tunisia: stratigraphy, paleontology, and paleoecology.

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ABSTRACT

The "*Continental Intercalaire*" deposits of southern Tunisia preserve one of the most diverse Early Cretaceous vertebrate fauna from Africa, consisting of elasmobranchs, actinopterygians, sarcopterygians, turtles, crocodyliforms, pterosaurs, and non-avian dinosaurs. Vertebrate remains representative of both marine and fluvial environments have been historically referred to a specific bonebed within the Chenini Member, which crops out extensively in the Tataouine region. A stratigraphic revision of the mainly siliciclastic deposits of the Douiret and the Aïn El Guettar formations in the area based on new sedimentological and paleontological data is presented. Data collected indicate the presence of multiple fossil-bearing strata encompassing the stratigraphic interval from the Berriasian to the Albian and document faunal variation through time as well as major environmental and climatic changes. Detailed sedimentological analysis combined with biostratigraphic correlation performed at a basin scale indicate lateral facies variability within each formation as a result of tectonically and climatically driven zonations within the Tataouine Basin in the Early Cretaceous. Furthermore, proposed stratigraphic correlations indicate that vertebrate remains previously referred to the fluvial Chenini Member (and in particular theropod and sauropod dinosaurs) are instead representative of a transgressive deposit which mark the base of the overlying Oum ed Diab Member.

1.1. Introduction

Since 1912, when L. Pervinquière first reported fossil vertebrate remains from the Early Cretaceous beds of the Tataouine region in southern Tunisia (Fig. 1), tens of scientific expeditions have dealt with the thick sequence of rocks termed the "*Continental Intercalaire*" by Kilian in 1931. This alternation of Late Jurassic – Early Cretaceous shallow-marine, littoral and non-marine deposits extends over much of northern Africa, from Algeria to Egypt and from Sudan to Niger (Bouaziz et al., 1988; Lefranc and Guiraud, 1990; Zarbout et al., 1994; Benton et al., 2000; Courel et al., 2003; Anderson et al., 2007; Khalifa and Catuneanu, 2008; Cavin et al., 2010). Fossils collected from these beds consist primarily of incomplete elements, but the combination of a diverse palaeontological record (both marine and non-marine taxa, and megaplant remains) as well as continuous exposures of the sedimentary successions provides a unique database for the comprehension of the evolution of this sector of southern Tethys during the Early Cretaceous. Thus, a steady succession of studies have treated the potential of the area from different perspectives, including geodynamic evolution (Bouaziz et al., 1989, 2002; Bodin et al., 2010), stratigraphy (Aubert, 1891; Joly, 1909; Robaux and Chobert, 1941; Burollet and Magnier, 1963; Busson, 1967; Abdallah, 1989; Lefranc and Guiraud, 1990; Zarbout et al., 1994; Abdallah et al., 1995, 2000; Courel et al., 2003; Marzouk and Youssef, 2008), palaeontology and paleoecology (Lapparent, 1951, 1960; Gorce, 1960; Tabaste, 1963; Schlüter and Schwarzhans, 1978; Taquet, 1980; Bouaziz et al., 1988; Benton et al., 2000; Buffetaut and Ouaja, 2002; Ouaja, 2003; Russell and Paesler, 2003; Cuny et al., 2004; Durand, 2005; Anderson et al., 2007; Amiot et al., 2010; Cuny et al., 2010; Contessi et al., 2011a, b), and paleobotany (Barale et al., 1998; Ben Ismaïl, 1991; Barale and Ouaja, 2001, 2002; Ouaja et al., 2004).

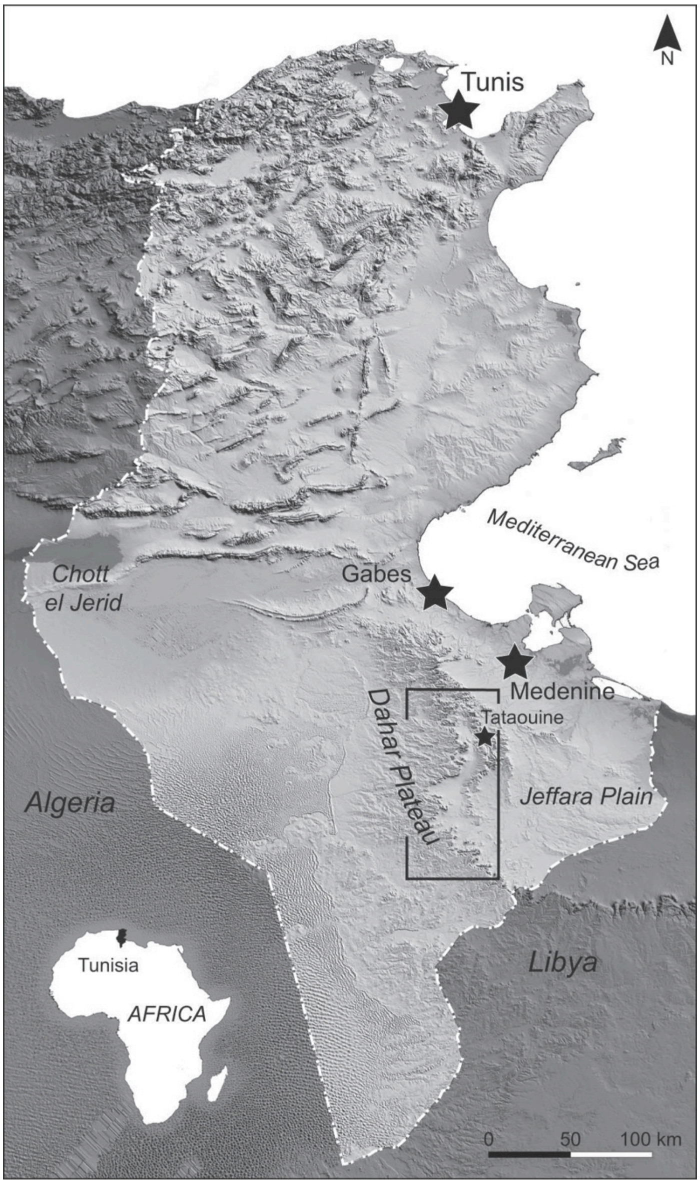

Figure 1 - Reference map and digital elevation model of Tunisia showing the position of the Tataouine region. The study area is located along the prominent Jeffara escarpment that separates the Dahar Plateau in the west from the Jeffara Plain.

In these and other studies, macro- and microfossil vertebrate remains (which include sharks, bony fishes, turtles, crocodylians, dinosaurs and pterosaurs) have been referred to the Aptian-Albian Douiret and Aïn El Guettar formations, which consist in alternating shallow marine, coastal and fluvial deposits (Bouaziz et al., 1988; Ben Ismaïl, 1991; Benton et al., 2000; Ouaja et al., 2002, 2004). However, it is important to notice two substantial methodological weaknesses in the paleontological data available in the literature. First of all, much of the specimens described and used for paleoecological interpretations are representative of just few well-known and heavily sampled fossil localities confined in the northern section of the Tataouine basin. Second, with the exception of specimens described by Benton et al. (2000), there are no references to specific beds within a stratigraphic column, but only generic attributions to a formation or a member. Furthermore, such studied lack of data on lateral variations of both faunal assemblages and associated depositional facies, limiting the overall accuracy and comprehension of paleontological and stratigraphic interpretations. In this study we introduce a stratigraphic and paleontological revision of the "*Continental Intercalaire*" exposed in the Tataouine basin of southern Tunisia (Fig.

1). Results presented here are articulated in order to provide 1) a description of boundaries, age, and sedimentological signatures of each stratigraphic unit; 2) a statement of the diversity of the vertebrate assemblage recovered; and 3) a discussion on the implication of this database for the paleoecological reconstruction of southern Tunisia during the Early Cretaceous. In so doing, particular attention was given to the nature and lateral variation of units boundaries and depositional facies, as well as to specific faunal assemblages associated to marker beds. Finally, we integrate our data with those available in the literature from coeval strata of northern Africa, introducing a palaeogeographic reconstruction of southern Tunisia during the deposition of the "*Continental Intercalaire*".

1.2. Study area and stratigraphic nomenclature.

Data for this study have been collected in the Tataouine basin along a 120 km long, north-south oriented section of the Dahar cliff from the Oued El Khil locality in the north to the El Asfer section (approximately 10 km southwest of Remada) in the south (Fig. 2). The Late Jurassic (Oxfordian-Kimmeridgian) to Early Cretaceous (Albian), mainly siliciclastic deposits are divided in two groups and five formations: in ascending order, the Merbah el Asfer Group (Bir Miteur, Boulouha, and Douiret formations), and the Aïn El Guettar Formation (Chenini and Oum ed Diab members) (Peybernès et al., 1985, 1996; Bouaziz et al., 1988; Ben Ismaïl, 1991; Chandoul et al., 1993; Zarbout et al., 1994; Barale and Ouaja, 2002; Bodin et al., 2010). Data from this stratigraphic interval, and in particular from the Douiret and Aïn El Guettar formations represent the bulk of this study. The overlying Cenomanian and Turonian carbonate-dominated successions are represented by the Zebbag Formation (Rhadouane, Kerker, and Gattar members) (Burollet, 1956; Busson, 1967; Ben Youssef et al., 1985; Bouaziz et al., 1989; Razgallah et al., 1994; Abdallah and Meister, 1997; Robaszynski et al., 2010). Recently, Bodin et al. (2010) proposed the introduction of a new lithostratigraphic unit confined to the northern section of the Tataouine basin, named the Charenn Member, at the base of the Zebbag Formation based on lithological evidences (Fig. 3).

The largely tectonically controlled deposition in the Tataouine basin during the Early Cretaceous resulted in major variations in terms of subsidence, facies distribution and fossil preservation. To the north, the basin is bounded by the Tebaga de Medenine, a unique outcropping marine Permian sequence overlain by spectacular angular unconformities related to the complex Mesozoic tectono-sedimentary events. Overall, the Tataouine basin is interpreted as a large, tilted block controlled by east-west oriented fault systems (Aziza fault system of the Ghadames Basin, Underdown et al., 2007; Lazzez et al., 2008; Bodin et al., 2010; Raulin et al., 2011). Relevant to this study, the Douiret Formation and both the Chenini and Oum ed Diab members are bounded by regional, angular, subaerial unconformities which represent significant but undetermined gaps in the deposition (Ouaja et al., 2004; Underdown et al., 2007; Bodin et al., 2010). Underdown et al. (2007) resume a series of data to support the influence of large scale tectonic events on the timing of depositional events within the Tataouine basin. In particular, they indicate two major unconformities bounding the "*Continental Intercalaire*" deposits, the lower "basal Cretaceous" and the upper "Austrian" unconformities. The stratigraphic resolution of data presented in Underdown et al. (2007), however, does not allow to refer such unconformities to any of the Cretaceous formations discussed herein.

The strong asymmetry of the Tataounie basin along its north-south axis is also marked by the presence of a relevant west-dipping (>30°) anticline named the "Touil el Hira" (Busson, 1967, Bouaziz et al., 1989, Bodin et al., 2010) responsible for the formation of two major late Lower Cretaceous depocenters, as well as for the juxtaposing of Cenomanian carbonates (Kerker member of the Zebbag Formation) on top of early Aptian clays (upper Douiret Formation).

Furthermore, the chronostratigraphic framework of the Tataouine basin is still primarily based on indirect evidences. In fact, with the exception of few fossil-bearing beds, much of the deposits are barren of fossils and those recovered provide environmental rather than biostratigraphic information. Thus, the entire succession has been primarily dated on correlation with marine-equivalent deposits to the north and by correlations far east with their Libyan counterparts (Ben Youssef et al., 1985; Abdallah and Memmi, 1994; Bouaziz, 1995; Duffin, 2001; Bodin et al., 2010; Le Loeuff et al., 2010). As a consequence, the age of fossil-bearing strata based on indirect evidences can result very inaccurate. Best attempts to asses an age to these deposits came from palynological studies carried out on megaplants remains as well as from pollens recovered from discontinuous paleosoils (Ben Ismaïl, 1991; Barale et al., 1998; Barale and Ouaja, 2002).

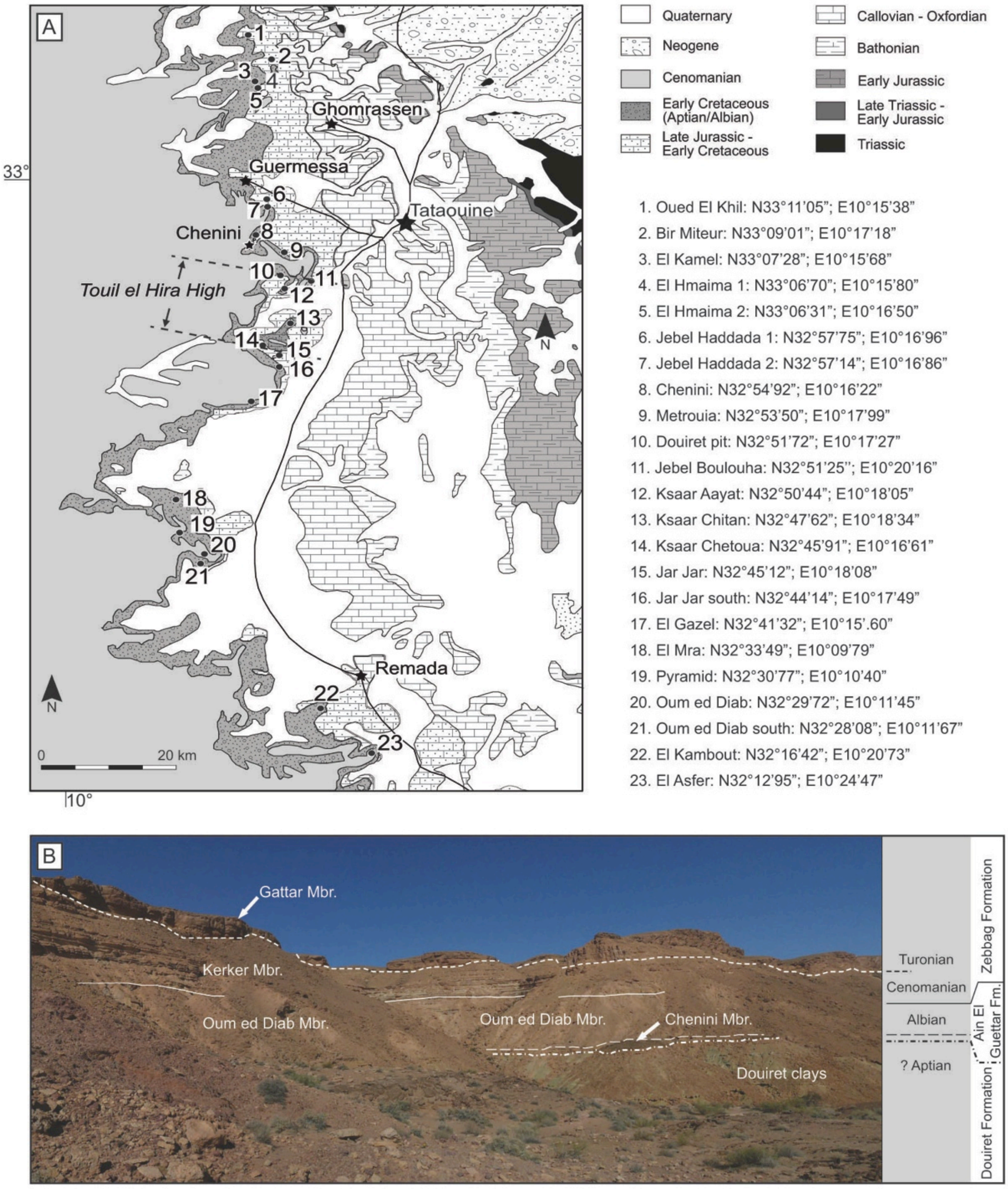

Figure 2 - (A) Geological map of the Tataouine region showing the location of the studied sections. (B) Field photograph at the El Gazel locality showing the principal features of the Early Cretaceous deposits along the Jeffara escarpment and their stratigraphic occurrence.

1.3. Materials, methods, and institutional abbreviations

This study is the result of four field-seasons undertaken in the Tataouine region between 2009 and 2011 by a team of the University of Bologna (Italy) with the support of the Office National des Mines (Tunis). During the early stages of field activities, the development of a robust stratigraphic scheme based on major unconformities, marker beds, and fossil-bearing intervals, was initiated to provide a framework within which more localized observations could be placed (Fig. 4). In so doing, seventeen reference sections were measured and six locations were prospected and included in the GPS database in order to document lateral variations of reference beds and major stratigraphic contacts. Each lithostratigraphic unit was described in terms of overall architecture and geometry, sedimentology, and palaeontological characteristics. All data sets were ultimately combined to document facies distribution and palaeontological signature for the entire succession. GPS coordinates of measured sections are given in Fig. 2. Palaeocurrent directions were measured from various sedimentary features (predominantly tabular and trough cross-bedding structures) as well as from *in situ* fossilized logs, and plotted as rose diagrams. Thin sections were obtained from 75 rock samples (sandstone, limestone, and dolostone) representative of the entire succession. A total of 21 samples were collected from clay and silt deposits for micropaleontological analyses: approximately 150 gr. of sediment were dried in an oven for 8 hrs at 50°C and then washed with water plus hydrogen peroxide (15% volume) through sieves of 63 μm an then dried again for 24 hrs before quantitative analysis at the microscope.

In addition, sandy sediments of the Oum ed Diab member were collected for screen washing at different stratigraphic level of the El Mra and Oum ed Diab sections. Those samples yielded 363 and 393 identifiable specimens respectively. Surface collection yielded a total of 2574 identifiable elements from the lower Douiret Formation (Sandy Member) and 2888 from the Oum ed Diab member providing a robust database for palaeontological interpretation (see Table 1). Vertebrate remains were compared with taxa described in the literature, in particular from Tunisia (Bouaziz et al., 1988; Benton et al., 2000; Buffetaut and Ouaja, 2002; Cuny et al., 2004, 2010), Libya (Duffin, 2001; Smith and Dalla Vecchia, 2006; Le Loeuff et al., 2010; Smith et al., 2010), Egypt (Smith et al., 2001) , Niger (Taquet, 1976; Broin, 1980; Taquet and Russell, 1999; Sereno et al., 1999, 2001; Sereno and Brusatte, 2008) and Morocco (Russell, 1998; Cavin et al., 2010).

Terminology for theropod teeth description follows Currie et al. (1990), Smith and Dodson (2003), and Fanti and Therrien (2007), and their identification is based on the following parameters: basal compression ratio (CR, as the ratio between fore-aft basal length and basal width), elongation ratio (ER, as the ratio between fore-aft basal length and the tooth crown height), number of denticles per millimeter on both anterior (DPMa) and posterior carinae (DPMp), presence/absence of blood grooves.

Specimens studied in this work will be deposited in the collection of the Office National des Mines in Tunis.

Institutional abbreviations

IGRG, Integrated Geoscience Research Group, Ravenna, Italy; MGGC, Museo Geologico Giovanni Capellini, Bologna, Italy; MNSV, Museum of Natural Sciences of Venice, Venice, Italy; ONM, Office National des Mines, Tunis.

Other Abbreviations

CR, tooth basal compression ratio; DPM, denticles per millimetre measured from the anterior (a) and posterior (p) carinae. BW, tooth basal width; ER, tooth elongation ratio.

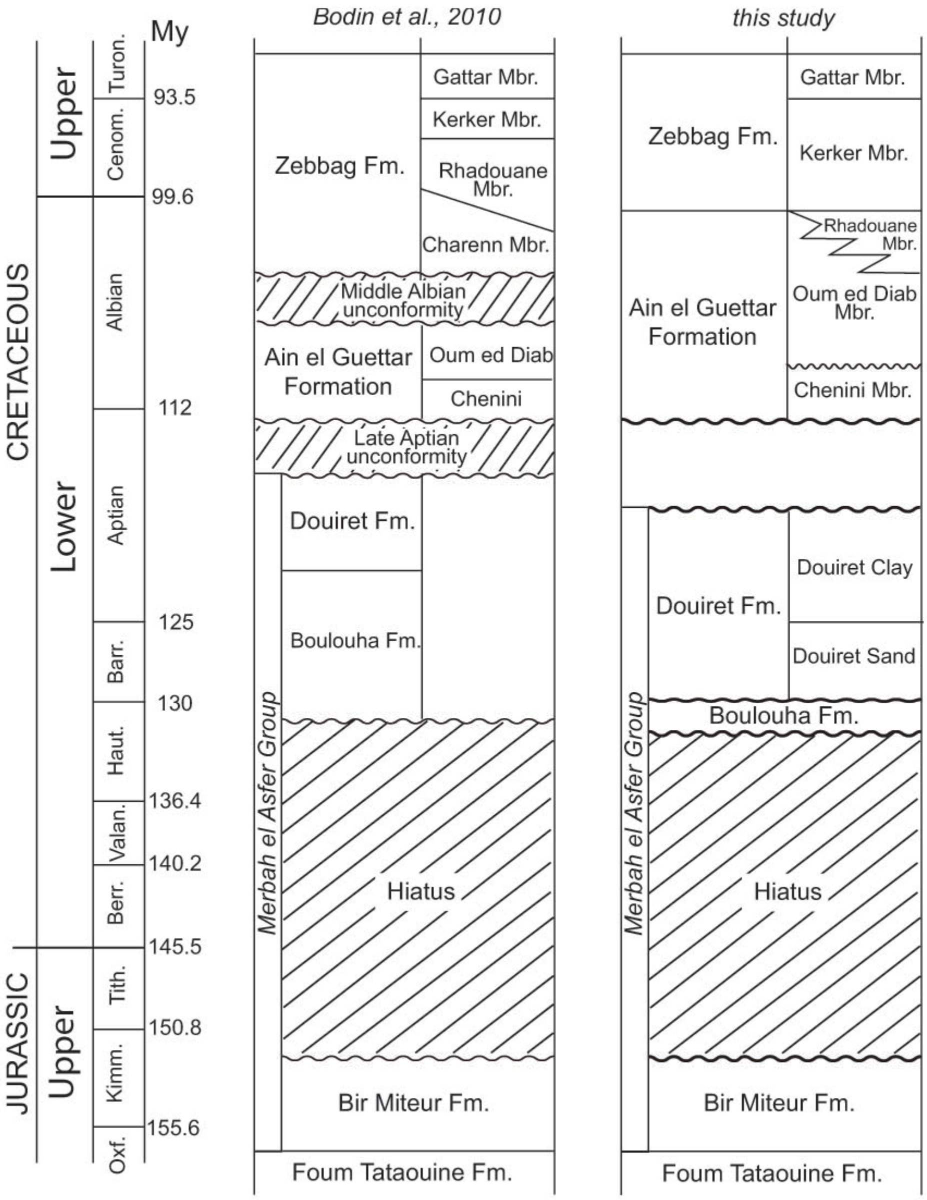

Figure 3 - Stratigraphic nomenclature for the Upper Jurassic – Upper Cretaceous of southern Tunisia showing the proposed litho- and chrono-stratigraphic subdivision of the "*Continental Intercalaire*".

1.4. Biostratigraphy and age

1.4.1 Douiret Formation

Early studies on the Douiret Formation by Ben Youssef et al. (1985) and Bouaziz et al. (1989) indicate a lower Aptian age for the upper clay member based on lateral correlation with the Bédoulien (Barremian- lower Aptian) carbonates that crop out in the Tebaga de Medenine area. Bein Ismaïl (1991) reports of palynomorphs that suggest an early Aptian age for the upper deposits of the Douiret Formation. More recently, the occurrence of the rhynchonellid brachiopod *Loriolithyris russillensis* and the stratigraphic position above the Hauterivian-Barremian levels of the Boulouha Formation led to consider the Douiret Formation as Barremian-early Aptian in age (Peybernès et al. 1996; Ouaja, 2003). However, biostratigraphic data from microfossil assemblages

(Cuny et al., 2010) do not fully support this interpretation, suggesting a Barremian age. Similarly, recent studies on coeval deposits and fossil assemblages in Libya support a Barremian age for the Douiret Formation (Le Loeuff et al., 2010). Data presented in this study indicate the occurrence of the hibodontid *Egertenodus* and *Gyrodus* in the sandy deposits of the Douiret Formation. Rees and Underwood (2008) indicate the latest ascertain record of *Egertenodus* in the Barremian of Spain, and Kriwet and Schmitz (2005) note the youngest record of *Gyrodus* in the Hauterivian of Germany. Therefore, we assess an ?Hauterivian-Barremian age to the lower Douiret deposits (sandy unit) and a Barremian-Aptian age to the upper Douiret strata (clay-dominated interval) (Fig. 3).

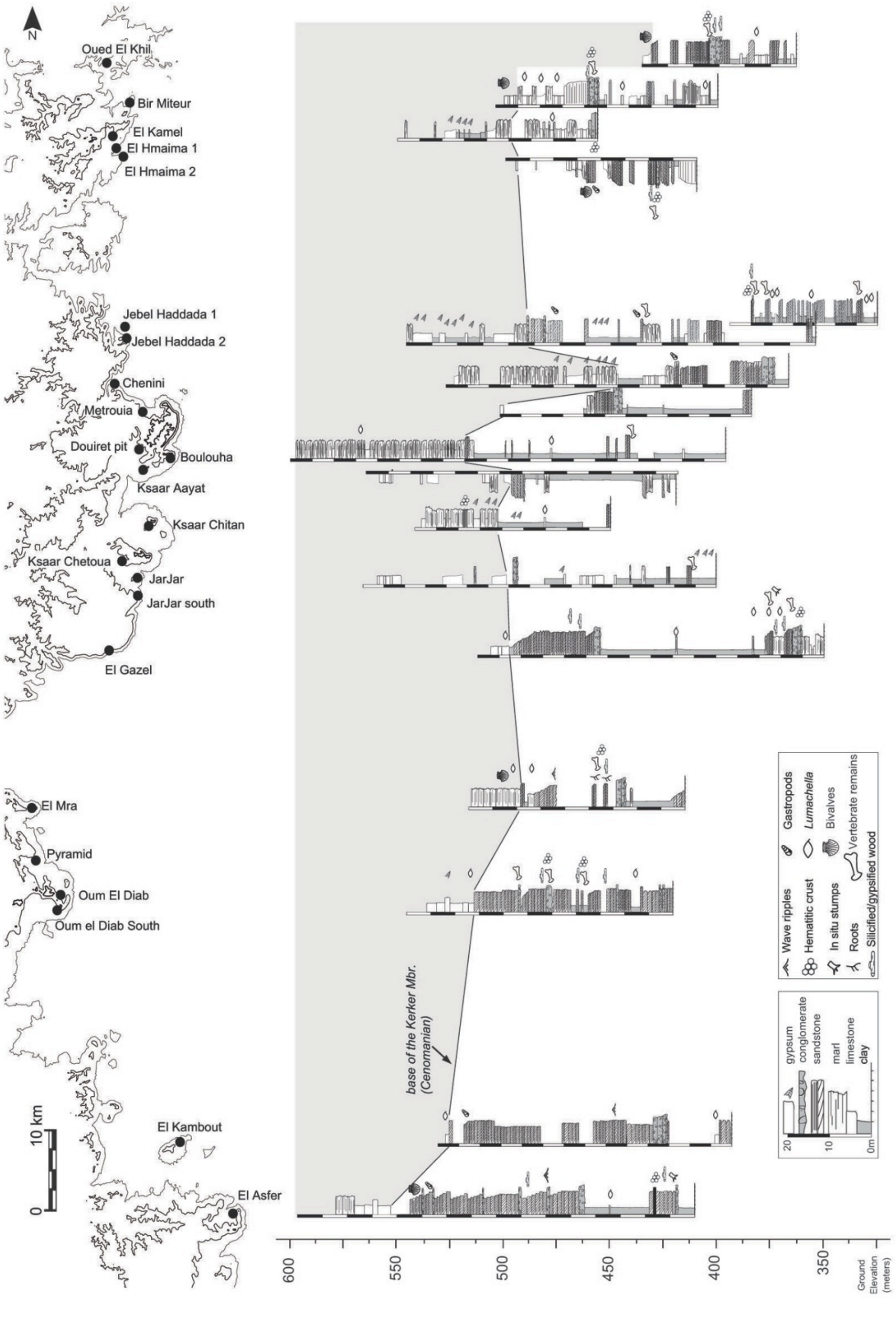

Figure 4 - Key stratigraphic field-log and their geographic distribution along the Jeffara escarpment represented by using ground elevation. The base of the Kerker Member (Zebbag Formation) has been used as lithostratigraphic marker for field correlation.

1.4.2 Aïn El Guettar and Zebbag formations

Robaux and Choubert (1941), and Robaux et al. (1941) firstly referred the Aïn El Guettar deposits to the Albian by correlation with similar siliciclastic successions cropping out in the northern saharian regions and Algeria. Similarly, Busson (1967) considered this stratigraphic interval as Barremian-Aptian in age. Bouaziz et al (1988) dated the coarse deposits of the Chenini member to the lower Albian based on the discovery of a rich fossiliferous bed and associated vertebrate fauna. However, data presented in Ben Ismaïl (1991) and in this study indicate that the fossil bearing strata were erroneously referred to the Chenini sandstone and should be referred to the Oum ed Diab Member. The sole direct evidence to constrain the age of this interval are represented by palynomoprhs reported in Ben Ismaïl (1991) and Barale et al. (1998) that suggest an upper Aptian-lower Albian age for the Aïn El Guettar Formation. More recently, a number of studies supported an Aptian-Albian age (Burollet and Magnier, 1963; Bouaziz et al., 1988; Benton et al., 2000; Bodin et al., 2010), a determination based nearly exclusively on data presented in previous studies or from indirect evidences. In addition, the Chenini sandstones have been tentatively correlated with the upper deposits of the Aptian-Albian Libyan Cabao Formation (Le Loeuff, 2010): however, a recent revision of this formation based on stratigraphic and paleontological evidences, does not support this interpretation, indicating a Hauterivian to Barremian age for the Cabao Formation (Rubino et al., 2010; Tawadros, 2011, pag. 335). It is also important to notice that none of previous studies provided data to constrain the temporal gap represented by the major tectonic unconformity that marks the base of the Aïn El Guettar Formation, nor identified the unconformity (transgressive lag deposits) that separates the Chenini and the Oum ed Diab members. On the light of new data presented in this study, and in particular the chronostratigraphic constrains provided for the Oum ed Diab Member, we refer the Chenini Member to the lower Albian.

The upper limit of the Aïn El Guettar Formation has been placed in concomitance with a distinctive, tabular, carbonatic bed that crops out extensively north of the Boulouha section known in Tunisian geological studies as the “Barre Vraconnienne” of the Rhadouane Member (Bouaziz et al., 1989; Robaszynski et al., 1994; Amédro, 2008; Raulin et al., 2011). The age of this marker bed has been largely debated, because its age is inferred from indirect evidences. Busson (1967) suggested a late Aptian age based on lateral correlation with orbitolinides faunas found in carbonatic deposits on the north flank of the Jebel Tebaga de Medenine. Ben Youssef et al. (1985) indicated a Vraconnian (late Albian) age based on the occurrence of the Albian ammonite *Knemiceras* (see also Avnimelech et al., 1954; Abdallah and Memmi, 1994; Abu-Zied, 2008; Robaszynsky et al., 2008; Krassilov and Schrank, 2011). This age is also supported by other studies on coeval deposits in central Tunisia (Moreno-Bedmar et al., 2008; Pons et al., 2010) where the “*Knemiceras* beds” are strictly Albian in age. In this study the “Barre Vraconnienne” is considered as late Albian in age: therefore, the Oum ed Diab member and the vertebrate fauna recovered in this unit (see detailed discussion below) is middle Albian in age (Fig. 3).

Finally, the carbonatic Kerker Member, which is used as *Zero datum* in stratigraphic correlations proposed in this study, is Cenomanian in age. The Cenomanian transgression resulted in the deposition of carbonaceous marls, mudstones and evaporites over large sections of Algeria, Tunisia, and Libya, grading upward into shallow marine carbonates (Hammuda, 1980; Yahi et al., 2001; Underdown et al., 2007).

1.5. The Douiret Formation

The Douiret Formation (upper Merbah el Asfer Group) crops out discontinuously in the Tataouine region from the Oued el Khil locality in the north, to the southern Tunisian border, and extends further south and east in Algeria and Libya (Busson, 1967; Bodin et al., 2010, and references therein). Overall, this formation consists of approximately 80 meters of interbedded sandstones and greenish clays, with frequent intercalation of dolomitic beds. In the study area a gradual transition from the lower, sand-dominated deposits and the overlying clay-dolomitic beds has been largely documented in the field (Busson, 1967; Bouaziz et al., 1989; this study). Thus, in the literature the formation has been informally divided in two lithological members: the Douiret sands, rich in vertebrate remains as well as pollens and megaplants, and the Douiret clays which are essentially barren of fossils with the exception of dolomitic, tabular beds showing a typical *lumachella* fabric. Bouaziz et al. (1989) also reported the occurrence of rare marine ostracods. The lower boundary of this unit is a regional, erosive unconformity that juxtaposes fine-grained, lagoonal to shallow-marine deposits of the Boulouha Formation with a coarse, fossil-rich conglomerate that marks the base of the Douiret Formation (Fig. 5A). Best exposures of these deposits are located in the southern sector of the Tataouine basin, in particular at the El Gazel and El Kambout sections. Fossils display evidences of intense pre-burial transportation, with no preferential orientation and systematic disarticulation of elements indicating a high-energy hydraulic regime. Samples collected indicate that fossil remains form up to the 60% of the conglomerate components (Fig. 5B). The overlying sandy member is characterized by repeating, fining-up sequences of sand, clay, and dolomite. Sandstones are cross-bedded, medium to coarse grained with angular to sub-angular clasts and grade into horizontally bedded silt deposits (Fig. 5C). These deposits are also particularly rich in plant and megaplant remains, including large gypsified and sporadic hematized trunks up to 4 meter long. Clay lenses on top of the sandstone beds are commonly rich in gypsum and, in some cases, some gypsified fossils have been documented. Fining up sequences are systematically capped by an alternation of clay and dolostone or dolomitized sandstone composed of quartz, and abundant bivalves remains. The abundance of tree-trunks combined with trough cross-bedding structures, provide excellent data for paleocurrent measurements. A total of 140 measurements from clinoforms in the lowermost deposits indicate an almost westward-directed flow (average N280E). Differently, the orientation of tree-trunks (n=25) recovered in the finer upper Douiret sands is nearly normal to this trend suggesting a wave-driven orientation (Fig. 5D). The top of the Douiret sands is marked by a fossil-rich, coarse-grained sandstone. Best exposures of this marker bed are located in the north of the study area, and in particular between the Jebel Haddada and Oued el Khil localities. At Bir Miteur and Oued el Khil, this layer is cut by the basal, fossil rich deposits of the Oum ed Diab member.

The transition to the overlying Douiret clays member is overall conformable and indicated by an increasing number of dolomitic beds (Fig. 6). This unit consists of approximately 50 meters of distinctive green, planar stratified clays with subordinate sandstone lags and dolostone, the latter showing a distinctive *lumachella* fabric (Fig. 6C-D). Best exposures of these strata are at the Boulouha and El Gazel sections. The basal contact of dolostones is sharp and erosive; in thin section this lithofacies appears as a dolomitized wackestone and grainstone with dolomite cement and oriented, millimetric shells. The quartz component systematically exceeds the 50%, and abundant matrix has been observed. Occasionally, clays are also interbedded with light-colored marls or cut by coarse, high-energy, gravel deposits (Fig. 6B). The clay interval yielded a diverse floral assemblage dominated by well-preserved pteridophytes and gymnosperms (Ben Ismaïl, 1991; Ouaja et al., 2004); the lack of angiosperms from this interval (Barale and Ouaja, 2002) supports a lower Aptian age of the Douiret clays. No vertebrate remains have been recovered in this interval to date.

1.5.1. Fossil vertebrate of the Douiret Formation, and their paleogeographic distributions

Vertebrate remains from the Douiret Formation (sandy member) pertain to freshwater, brackish and subordinate marine taxa, and include elasmobranchs, actinopterygians, and crocodyliforms (Figs. 7 and 8). Bivalves are also common in these deposits, although the poor preservation due to high calcite recrystallization does not allow for an accurate taxonomic classification. Specimens described here support the presence of iguanodontid in the Douiret sands member; teeth of pterosaurs are the first reported from this formation.

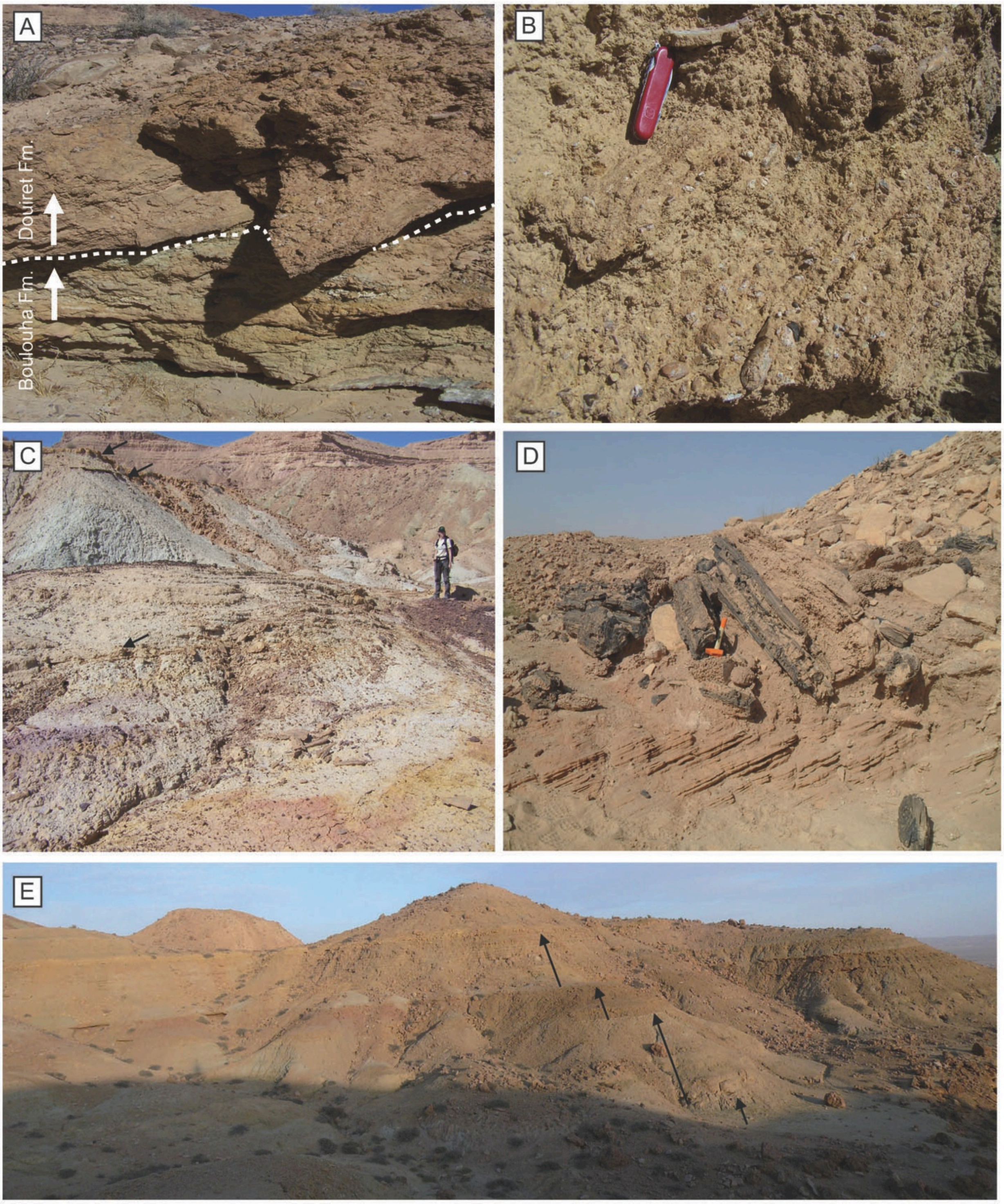

Figure 5 - Field photographs of the sandy member of the Douiret Formation. (A) The sharp contact between the lagoonal deposits of the Boulouha Formation and the overlying high-energy, coarse grained beds of the Douiret Formation. (B) Detail of the fossil-rich conglomerate marking the base of the Douiret Formation. (C) The fine grained upper sandy member exposed at the El Gazel locality. (D) Example of in situ tree stump from the upper Douiret sands: note that the orientation is nearly normal to the underlying foreset suggesting a wave-driven orientation; (E) The upper section of the sandy member is characterized by repeating, fining-up sequences of sand, clay, and dolomite (black arrows). A-C, El Gazel section; D, El Asfer section; E, Boulouha section.

1.5.1.1. Fishes

Elasmobranchs are represented by teeth and fragmentary dorsal fin spines of the Hybodontid *Priohybodus arambourgi*, previously reported in the Douiret deposits by Cuny et al. (2004) (Fig. 7A-E). *Priohybodus* teeth are labio-lingually compressed, have a high and triangular main cusp flanked by two pairs of diverging cusps, and possesses serrated edges (Duffin, 2001). This taxon has been previously reported from Late Jurassic deposits of Somalia, Ethiopia, Yemen, and Uruguay, as well as from the Early Cretaceous of Libya (Duffin, 2001; Perea et al., 2001, Cuny et al., 2004; Le Loeuff et al., 2010; Soto et al., 2012). In this study we consider this taxon as a biostratigraphic marker for the lower Douiret Formation.

Two isolated specimens present previously unreported morphologies within the shark record of southern Tunisia. The first morphotype (represented by a single fragmentary tooth collected at the Jer Jer locality) displays a triangular cusp 12 mm high and 9 mm wide, characterized by longitudinal striation and serrated edges (DPM=4.5). The tooth curves lingually toward the apex of the crown and is labio-lingually compressed at its base (Fig. 7F-G). Unfortunately, laterals cusps have not been preserved. A second morphotype is represented by a small tooth with preserved main and an accessory cusp collected at El Hmaima. Both cusps are complete and measure 8 and 3 mm respectively and curve slightly toward the apex of the crown. The enamel presents a clear longitudinal ornamentation and edges are unserrated (Fig. 7H-I). Pending the discovery of more teeth referable to these morphotypes, both specimens are tentatively referred to *Hybodus* sp. based on the high main cusp, pattern of enamel ornamentation and cross-section.

Fossils of actinopterygians are among the most common fish remains found in the Douiret sands member. They are represented in particular by abundant teeth and scales of the semionotiform *Lepidotes* and by fragmentary teleostean remains (Fig. 7J-R). Scales of *Lepidotes* vary in shape and size with respect to their position along the body, and range between 5 mm to 4 cm in length. Teeth are hemispherical with a maximum diameter of 14 mm (apical view) and a maximum height (including preserved ganoine-covered base) of 6 mm. Overall, it is possible to divide such teeth in three different morphotypes: 1. hemispherical, with flat crown surface; 2. hemispherical, flat crown surface with a small, circular pit in the center (apical view); 3. elongated, slightly compressed in cross-section with conical crown surface. Teeth referred to the latter morphotype are commonly 40% smaller than other teeth. Sarcopterygian remains are represented by cranial elements (parietals and postparietals fragments) and a small tooth plate referred to the coelacanthiform *Mawsonia* (Fig. 7S-T), a genus known from Early and mid-Cretaceous beds of Brazil, Egypt, Algeria, Morocco, Niger, and Democratic Republic of Congo (Maisey, 2000; Churcher and De Iuliis, 2001; Grandstaff et al., 2002; Yoshitaka, 2002; Carvalho and Maisey, 2008; Candeiro et al, 2011). *Mawsonia* has been previously reported from the Chenini beds of southern Tunisia (Benton et al., 2000) and Libya (Le Loeuff et al., 2010), but this is the first record of this genus from the Douiret Formation.

1.5.1.2. Turtles

The record of chelonid from the Early and mid-Cretaceous of northern Africa is extremely poor and fragmentary. Broin (1980) and Lapparent (2000) referred several remains (shell fragments and postcranial elements) to an undetermined pleurodiran and reports the occurrence of *Taquetochelys* sp. and "*Pelomedusoides*" from the Douiret Formation. Pleurodiran chelonids have been also reported from coeval deposits of Libya (Cabao Formation, El-Zouki, 1980, Le Loeuff et al., 2010; Rubino et al., 2010) and from the Gadofaoua site in Niger (Broin, 1980; Rauhut and Lopez-Arbarello, 2009). Similarly, indeterminate pleurodiran remains have been reported from the Early Cretaceous of northern Brazil (Candeiro et al., 2011), whereas Cenomanian representatives of four groups of Pleomedusoides have been recognized in the Kem Kem beds of Morocco (see Torices et al., in press). In the study area, turtles remains are more frequent in clay-dominated beds, where shell fragments, vertebras, and other postcranial elements are found. With the exception of fragments recovered in sand-dominated deposits, carapace elements and isolated vertebrae are partially or entirely gypsified.

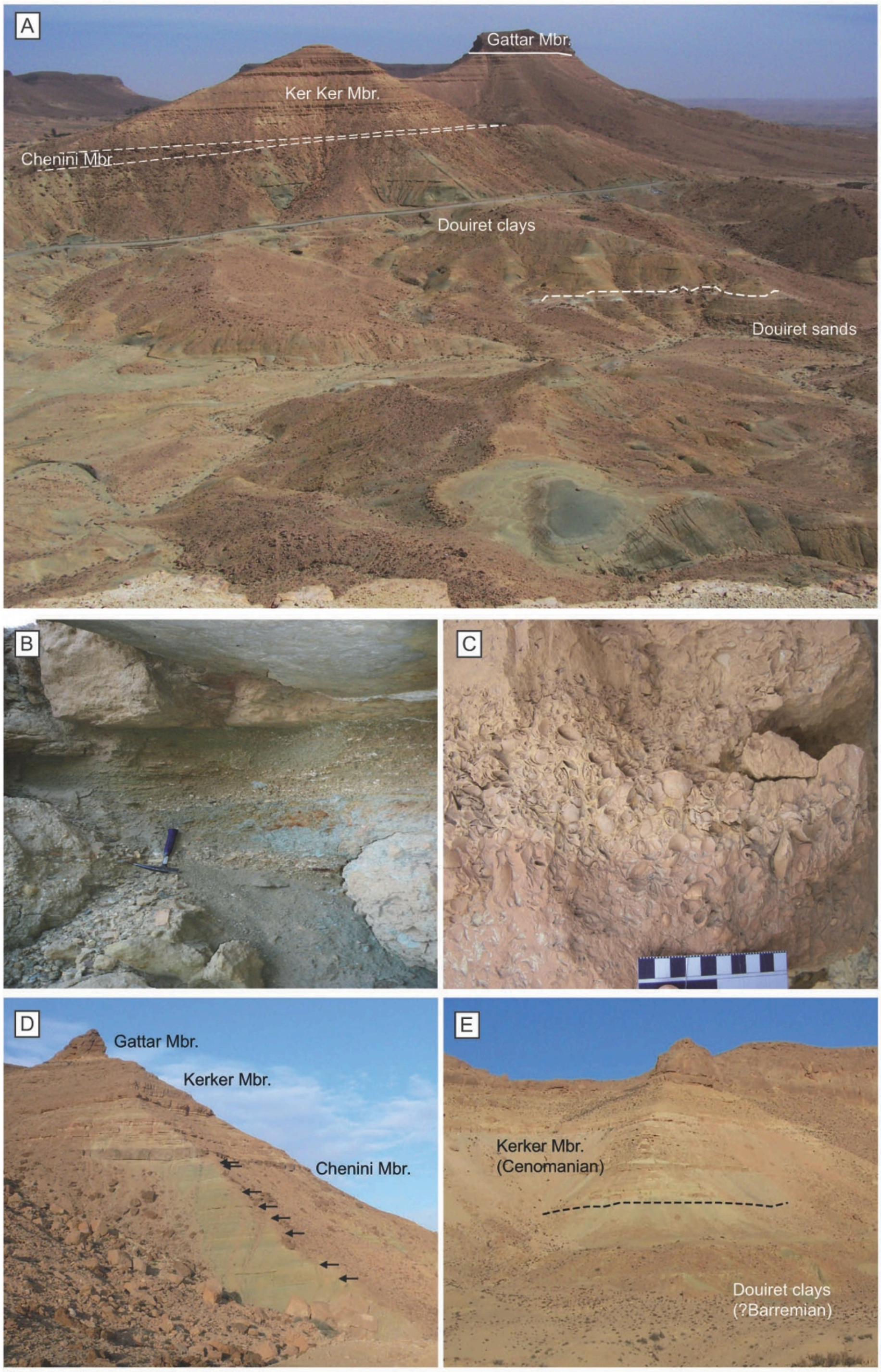

Figure 6 - Field photographs of the clay member of the Douiret Formation. (A) Panorama from the Ksar Ayat locality, looking northeast. The Chenini Member that overlies the greenish clay of the Douiret Formation is pinching out to the east on the southern edge of the Touil el Hira High. (B) Example of the coarse, high-energy gravel deposits interbedded with the Douiret clays. (C) *In situ* dolostone layer showing the typical *lumachella* association. (D) The Douiret clay member at the Jebel Boulouha section; arrows indicate tabular, sharp-based dolostone layers. (E) The juxtaposing of the Barremian upper Douiret Formation and Cenomanian Kerker Member (Zebbag Formation) are a direct consequence of the Aptian-Albian development of the Touil el Hira anticline. B-D; Boulouha section; E, Ksaar Chitan section.

1.5.1.3. Crocodyliforms

Crocodylian remains, and in particular teeth and osteoderms are very abundant in the Douiret sands. Pending the discovery of diagnostic cranial and postcranial elements, three teeth morphotypes are identified. Teeth included in the first morphotype (Fig. 8A-C) are conical, lingually recurved, with striated enamel, and range between 10 and 25 mm in height; the second is represented by relatively large teeth (average crown height 35 mm), with longitudinally striated enamel and prominent, unserrated carinae (Fig. 8D); finally, the third morphotype is represented by a fragment of a large, conical tooth with fine longitudinal ridges on the enamel (Fig. 8E-F).

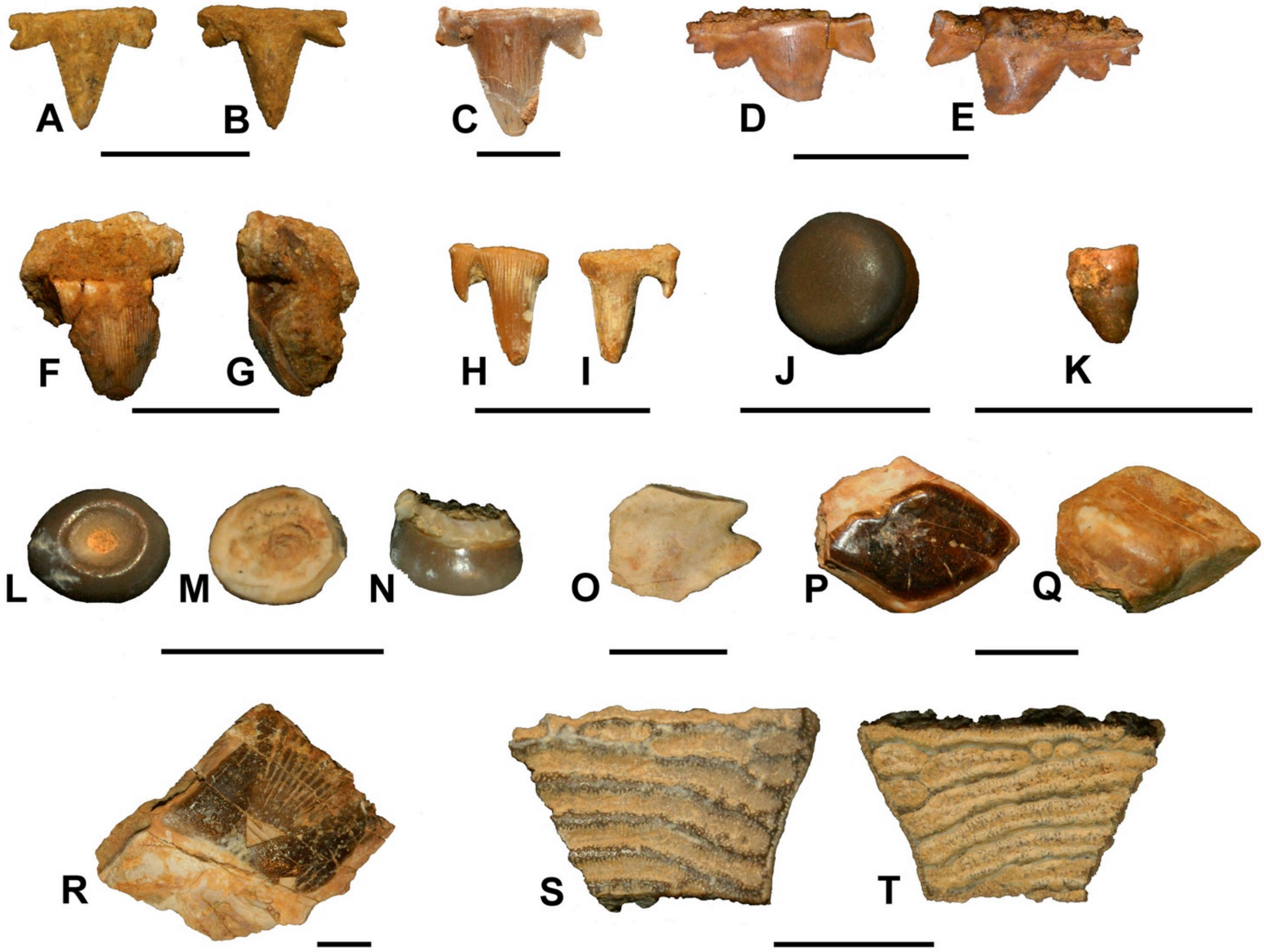

Figure 7 - Representative fossil from the sandy member of the Douiret Formation. (A-E) *Priohybodus arambourgi*. (F-G) *Hybodus* sp., new morphotype 1. (H-I) *Hybodus* sp., new morphotype 2. (J) *Lepidotes* tooth, morphotype 1. (K) *Lepidotes* tooth, morphotype 2. (L-N) *Lepidotes* tooth, morphotype 3. (P-R) *Lepidotes* scale. (S-T) *Mawsonia* sp. tooth. Scale bar 1 cm.

1.5.1.4. Pterosaurs

A previously unreported taxon from the Douiret sand member is a possible ornithocheirid pterosaur, represented by several isolated teeth (Fig. 8G-N). The crown is long, narrow and uniformly curved toward the apex: fine, longitudinal lines are present on the enamel, no carinae are visible. Teeth show a slightly asymmetrical, triangular basal cross-section. The best preserved tooth is only 17 mm high and 5 mm wide at its base; the largest tooth collected from the Douiret sands member is not completely freed from the matrix, and is 4 cm high and 11 mm wide.

1.5.1.5. Dinosaurs

Dinosaur remains from the Douiret Formation are represented by a single, poorly preserved tooth referable to an iguanodontid ornithopod (Fig. 8O-P). Srarfi et al. (2004) also reports a *Carcharodontosaurus* sp. tooth and fragmentary postcranial remains from an undetermined layer at the El Gazel locality.

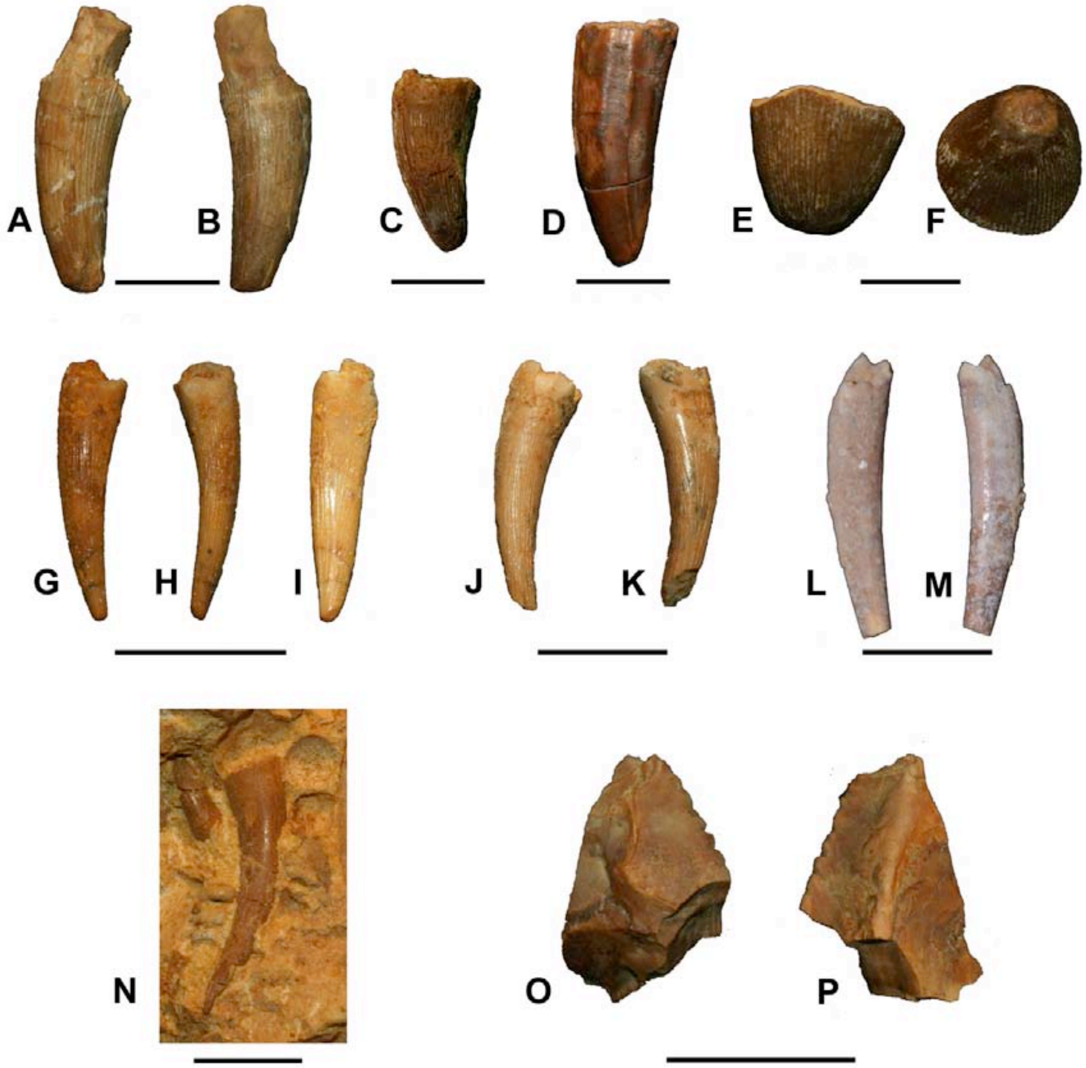

Figure 8 - Representative fossil from the sandy member of the Douiret Formation. (A-C) crocodilian tooth, morphotype 1. (D) crocodilian tooth, morphotype 2. (E-F) crocodilian tooth, morphotype 3. (G-N) possible ornithocheirid teeth. (O-P) iguanodontian tooth fragment. Scale bar 1 cm.

1.6. The Aïn El Guettar Formation: Chenini member

Chenini beds crop out extensively in the southern section of the Tataouine basin where they locally reach an overall thickness of 50 meters; to the north, strata pinch out in correspondence of both the southern (near the Jar Jar locality) and northern (Ksaar Ayat) shoulders of the “Touil el Hira” high (see also Fig. 6A).

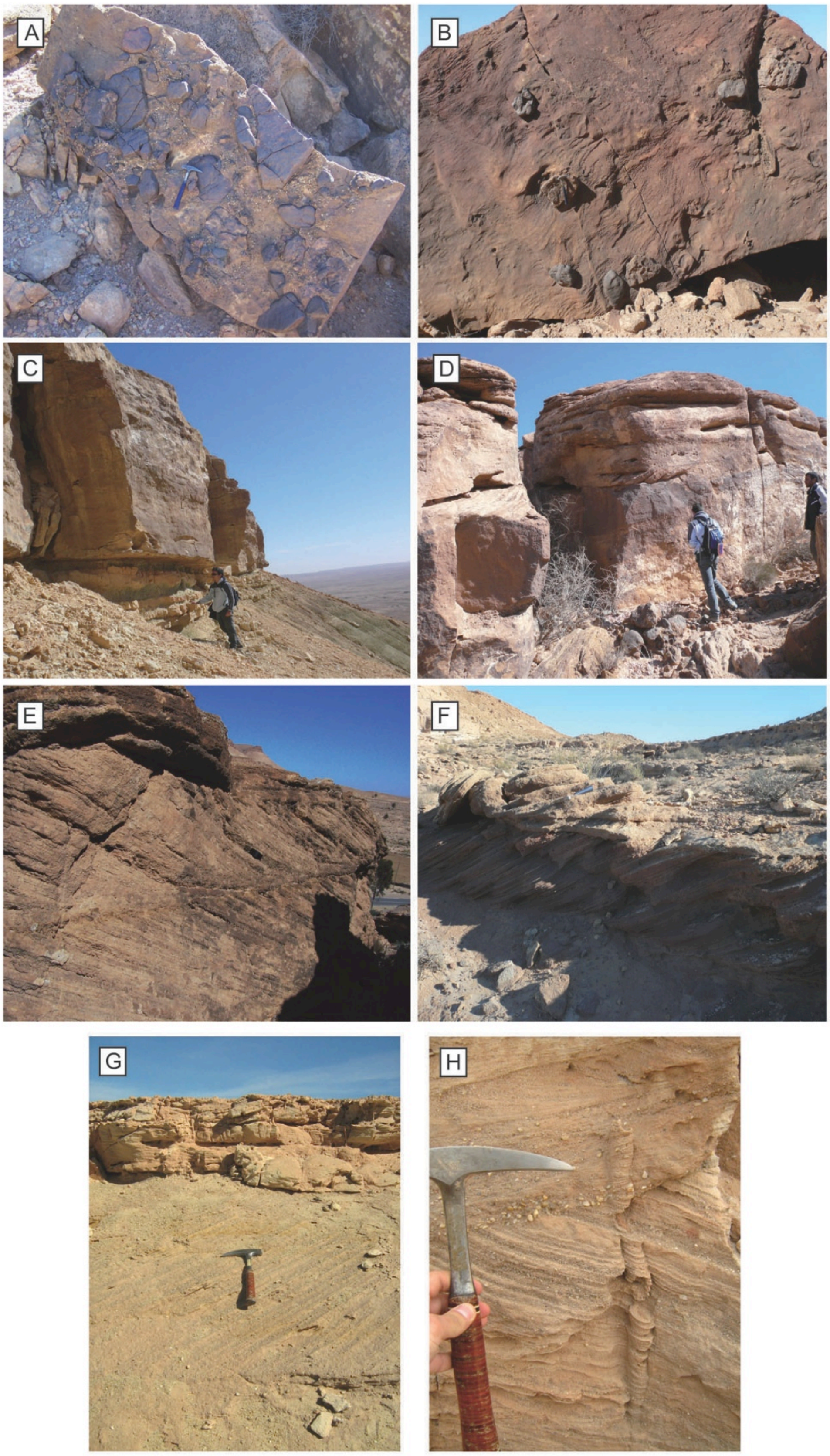

Figure 9 - Field photographs of the Chenini Member. (A) The basal conglomerate is characterized by distinctive angular, quartz-arenitic blocks up to 1.5 meter wide indicating high-energy hydraulic regime. (B) Example of the erosive surface marking the base of the Chenini Member. (C) The sharp contact between the clay of the Douiret Formation and the coarse sand of the Chenini Member at Jebel Boulouha. (D)

Massive sandstone deposits of the lower Chenini Member, El Kambout locality. (E) Fining-upward cycles of cross-stratified, coarse sandstone and minor siltsone characterize the lower deposits of the Chenini Member. (F) Fine-grained, cross-bedded sandstones of the upper Chenini Member preserve vertebrate remains (crocodylian and actinopterygians) and are locally interbedded with light-grey clay lenses. (G) Fine, high-angle, aeolian deposits interbedded with the channelized sandstones of the Chenini Member. (H) Rhizocretions, as well as root casts, moulds, and tubules are common in the uppermost Chenini deposits. A, B, D, El Asfer section; C, Boulouha section; E, Chenini section; F, El Mra section; G, H, Oum ed Diab section.

Farther north, the lower deposits of Chenini Member extend discontinuously to approximately the Jebel Haddada section. The base of the Chenini Member is a regional, angular, erosive unconformity that juxtaposes coarse conglomeratic beds on top of the underlying Douiret Formation clays (Fig. 9). Basal conglomeratic beds are characterized by large, angular, quartz-arenitic blocks up to 1.5 meter wide indicating high-energy hydraulic regime and relatively short transportation from the sediment source area (Fig. 9A-B). Paleocurrent measurements taken on trough cross-bedding structures (n=182) indicate a predominant north-west flows direction. These conglomeratic beds reach a maximum thickness of 5 meters in the south, and fine upward into fluvial cross-bedded sandstones. Where preserved, the latter deposits grade into tabular, fine grained sandstones locally interbedded with light-grey clay lenses (Fig. 9E-F). Root casts, moulds, tubules, and rhizocretions are common in these tabular deposits, as well as extensive hard grounds. The latter appear as strongly phosphatised, Fe-rich levels with rounded quartz-sandstone pebbles and organic remains and logs fragments. The presence of iron oxides and oxyhydroxides, rounded clasts and phosphatised organic remains is typical of arid environment paleosoil (Walker and Honea 1969; Harrison, 1973; Lehman, 1989). The upper contact of the Chenini Member with the overlying Oum ed Diab Member is marked by an erosive conglomerate bearing a remarkable amount of vertebrate and plant remains.

1.6.1. Fossil vertebrate of the Chenini Member

Intense prospecting activities along the entire Tataouine basin indicate that the deposits of the Chenini Member, including the basal conglomerate previously considered as the major source of vertebrate remains in the region, are barren of fossils. As a consequence, vertebrate remains previously referred to these beds (Bouaziz et al., 1988; Benton et al., 2000; Buffetaut and Ouaja, 2002) are here placed within the lower Oum ed Diab Member. We conclude that the erroneous attribution of vertebrate remains to the Chenini Member by previous studies in the Tataouine region (Bouaziz et al., 1988; Ben Ismaïl, 1991; Benton et al., 2000; Ouaja et al., 2002; Ouaja et al., 2004) reflects systematic sampling in a restricted section of the basin, north of the “Touil el Hira” high, where fossil-bearing strata of similar lithology but of different age juxtapose.

1.6.1.1. Fishes

Actinopterygians remains found in the Chenini Member are represented by rare *Lepidotes* isolated teeth and scales. Specimens are virtually identical to those preserved in the Douiret Sands member but significantly less frequent.

1.7. The Aïn El Guettar Formation: Oum ed Diab Member

The transition from the fluvial deposits of the Chenini Member to the overlying, shallow-marine, fine grained sandstones of the Oum ed Diab Member is marked by an heterogeneous conglomerate rich in highly re-worked vertebrate remains, plant fragments, and clay chips. This marker bed varies in thickness from nearly five meters in the south (i.e.: Oum ed Diab and El Kambout sections) to a few centimetres in the north (El Mra, El Hmaima, Bir Miteur localities). The transgressive lag deposits on transgressive erosive surface show alternating low angle, cross-bedded, and flaser structures (Fig. 10). South of the "Touil el Hira" high the Oum ed Diab sands reach a maximum thickness of 150 meters and consist of fining-upward sequences of fine-graded sandstones with alternating ripple marks, herringbone cross bedding, symmetrical wave-formed ripples, and discontinuous clay lenses rich in fish remains and bivalves (Fig. 10). Unidirectional, bipolar (dominant/subordinate) palaeocurrent pattern is commonly observed in the same beds. Discontinuous conglomeratic lenses preserving bivalve shells are frequent in the upper section of the Oum ed Diab sandstones.

Measured sections at the Jebel Haddada, El Kamel, Bir Miteur, and Oued El Khil localities indicate that north of the "Touil el Hira" high, observed sandy, channelized deposits laying on top of the Douiret Formation are attributable to the Oum ed Diab Member (Fig. 11). These deposits, as previously observed by Bodin et al. (2010) are characterized by fining-upward, coarse to fine grained sandstone with herring-bones and flaser structures. Isolated fish remains (teeth and centra) and poorly preserved theropod teeth have been collected from these deposits by the authors. In addition, sandy strata are interbedded with meter thick, tabular, and bioturbated marly to carbonatic beds rich in bivalves and gastropod remains. This interfingering interval is evident at the Jebel Haddada section, where it is possible to distinguish three intervals of alternating sandy and carbonatic deposits (Fig. 11). Overall, this succession of interfingered siliciclastic and carbonatic beds does not exceed 50 meters in thickness, and is capped by the uppermost deposits of the Rhadouane Member (i.e. the "Vraconnian Barre"; Ben Youssef et al., 1985; Abdallah and Memmi, 1994; Robaszynski et al., 1994). Finally, in the entire study area the Oum ed Diab Member and its lateral-equivalent Rhadouane Member pass conformably to the marl-dominated sequences of the Cenomanian Zebbag Formation (see also Lüning et al., 2004; Rigane and Gourmelen, 2011). As a consequence, we include the Rhadouane Member within the Aïn El Guettar Formation rather than the Cenomanian Zebbag Formation, and reject the proposal of Bodin et al. (2010) of a new lithostratigraphic unit named Charenn Member at the base of the Zebbag Formation.

1.7.1. Fossil vertebrate of the Oum ed Diab member, and their paleogeographic distributions

The basal conglomerate of the Oum ed Diab member, previously misinterpreted as the Chenini member in the northern section of the Tataouine basin, consists of more than 60% of vertebrate remains poorly washed and hardly reworked, mixed with centimetre size clay chips, quartz-arenite rounded clasts, and ironstone pebbles.

1.7.1.1. Fishes

The hybodontid *Priohybodus* typical of the Douiret Formation, is absent, whereas the lamniform *Leptostyrax macrorhiza* is the most abundant elasmobranch. Teeth referred to this taxon present cutting edges non continuous with the cusplets, root lobes forming a "V" shape, developed lingual protuberance, longitudinal ornamentation in the lingual side of the main cusp, and the absence of nutrient grooves in the root (Fig. 12). Despite the fact Cuny et al. (2004) referred similar teeth to *Protolamna* sp., specimen described in this study support an attribution to *Leptostyrax* instead. The second most common type presents a single, sigmoidal, elongated cusp with well-developed cutting edges. The lingual side is convex and ornamented, whereas the labial one is smooth. These teeth are referred to *Scapanorhynchus sp.* following the attribution by Cuny et al. (2004).

Actinopterygians remains are extremely common in the Oum ed Diab member, and are represented by well-preserved *Lepidotes* teeth, scales, and centra. Sarcopterygian include the giant coelacanthiform *Mawsonia* sp. (Fig. 12H-L) and the large dipnoans *Neoceratodus sp.* and *Ceratodus sp.* (Haug, 1905; Tabaste, 1963; Soto and Perea, 2010) (Fig. 12M-N). Upper and lower tooth plates of the latter genera range in size from 20 to 65 mm and present five or six ridges; lower plates commonly have bigger dimensions, smoother furrows and larger sulcis.

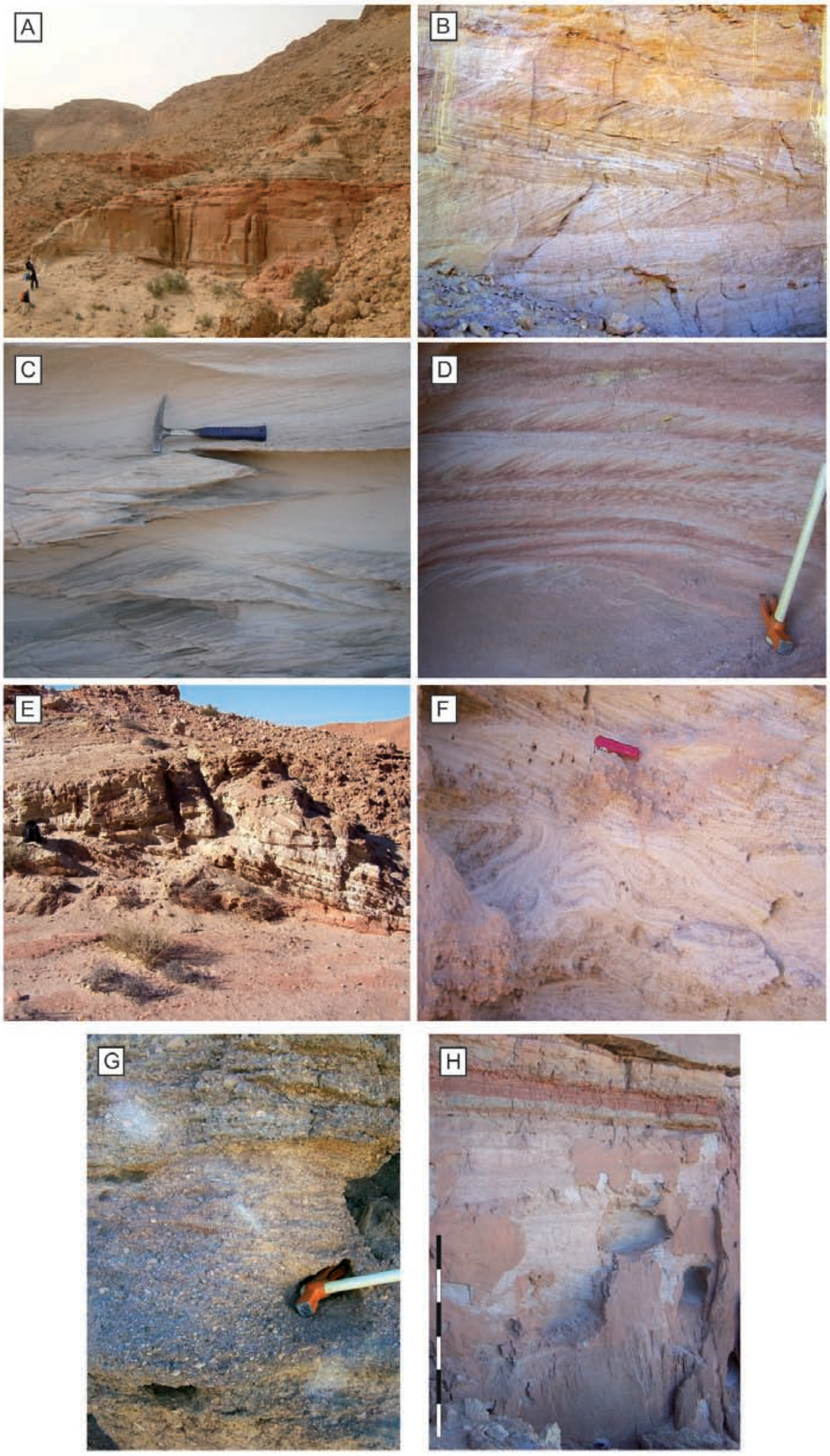

Figure 10 - Field photographs of the Oum ed Diab Member. (A) Exposures of the sandy Oum ed Diab Member at the homonymous type locality. (B-D) Types of herring-bone cross-stratification within the fine-grained sandstone of the Oum ed Diab Member. (E) Large scale cross-bedded sandstone, El Kambout locality. (F) Convoluted lamination are frequent in the finer deposits of this unit. (G) The fossil-rich, fine conglomerate marking the base of the Oum ed Diab Member, Jebel Haddada. (H) The upper boundary of the Oum ed Diab member is marked by marl and decimeter-thick dolostones. A, D, Oum ed Diab section; B, Oued El Khil section; C, El Mra section, E-H, El Asfer section.

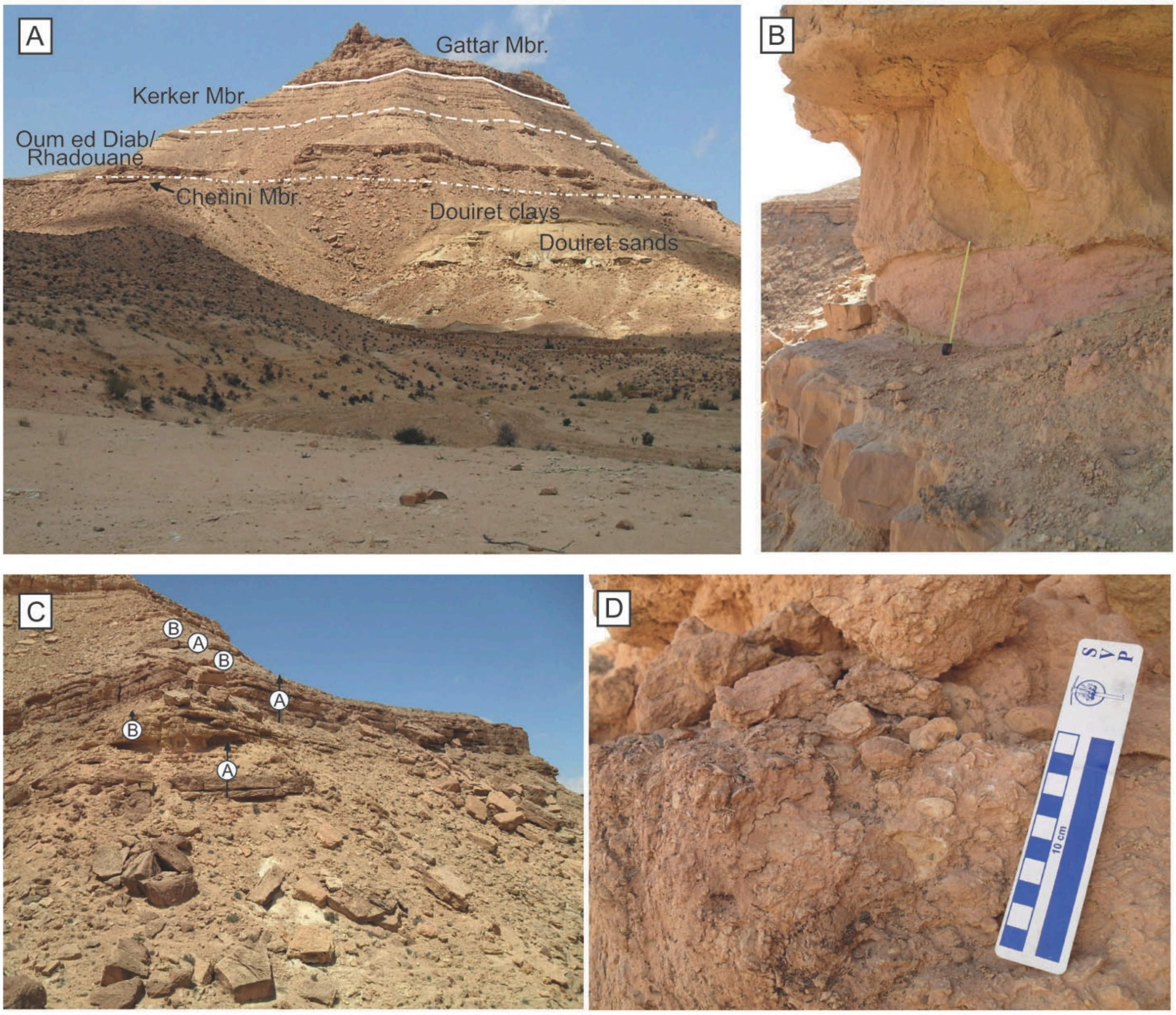

Figure 11 - (A) Field photographs of the Jebel Haddada section, showing the Oum ed Diab – Rhadouane interfingering interval. (B) Fine grained sandtones of the Oum ed Diab member overlying and overlaid by tabular carbonatic beds of the Rhadouane Member. (C) Alternation of fining upward, channelized, sandy deposits of the Oum ed Diab Member (1) with carbonates and marls referred to the Rhadouane member (2). (D) In situ bivalves in the silty deposits of the Oum ed Diab beds.

1.7.1.2. Crocodyliforms

Isolated teeth and osteoderms are common in the Oum ed Diab sands. The most abundant teeth show a regular curvature, fine parallel grooves and nearly circular basal section; a second morphotype includes teeth with an additional curvature on the tip and two distinctive ridges along the crown. Teeth pertaining to the third morphotype differ from the others in having an overall triangular shape, serrations on both carinae and a strongly labio-lingually compressed basal cross section. Based on the dentition of *Araripesuchus wegeneri* of Sereno and Larsson (2009, fig. 19), morphotype three is here referred to *Araripesuchus sp.*

Several large osteoderms still in anatomical connection and two teeth are referred to the genus *Sarcosuchus* based on comparison with specimens described by Sereno et al. (2001, fig. 2 and 3), as well as with specimens collected in the Gadofaoua beds of Niger and now on display at the MNSV. Teeth are stocky with no carinae, sub-circular basal cross-section (BW 39 mm), and with a crown height of 72 and 75 mm respectively (Fig. 13A-D). Recovered trunk scutes range between 15 and 28 mm in thickness (Fig. 13E-F), and reach a maximum length of 18 cm. Early Cretaceous crocodyliform from the circum-Sahara are represented by the genera *Sarcosuchus*, *Araripesuchus*, *Elosuchus*, and *Stolokrosuchus* (Lapparent and Taquet, 1966; Buffetaut and Taquet, 1977; Larsson and Gado, 2000; Sereno et al., 2001; Lapparent, 2002; Sereno and Larsson, 2009).

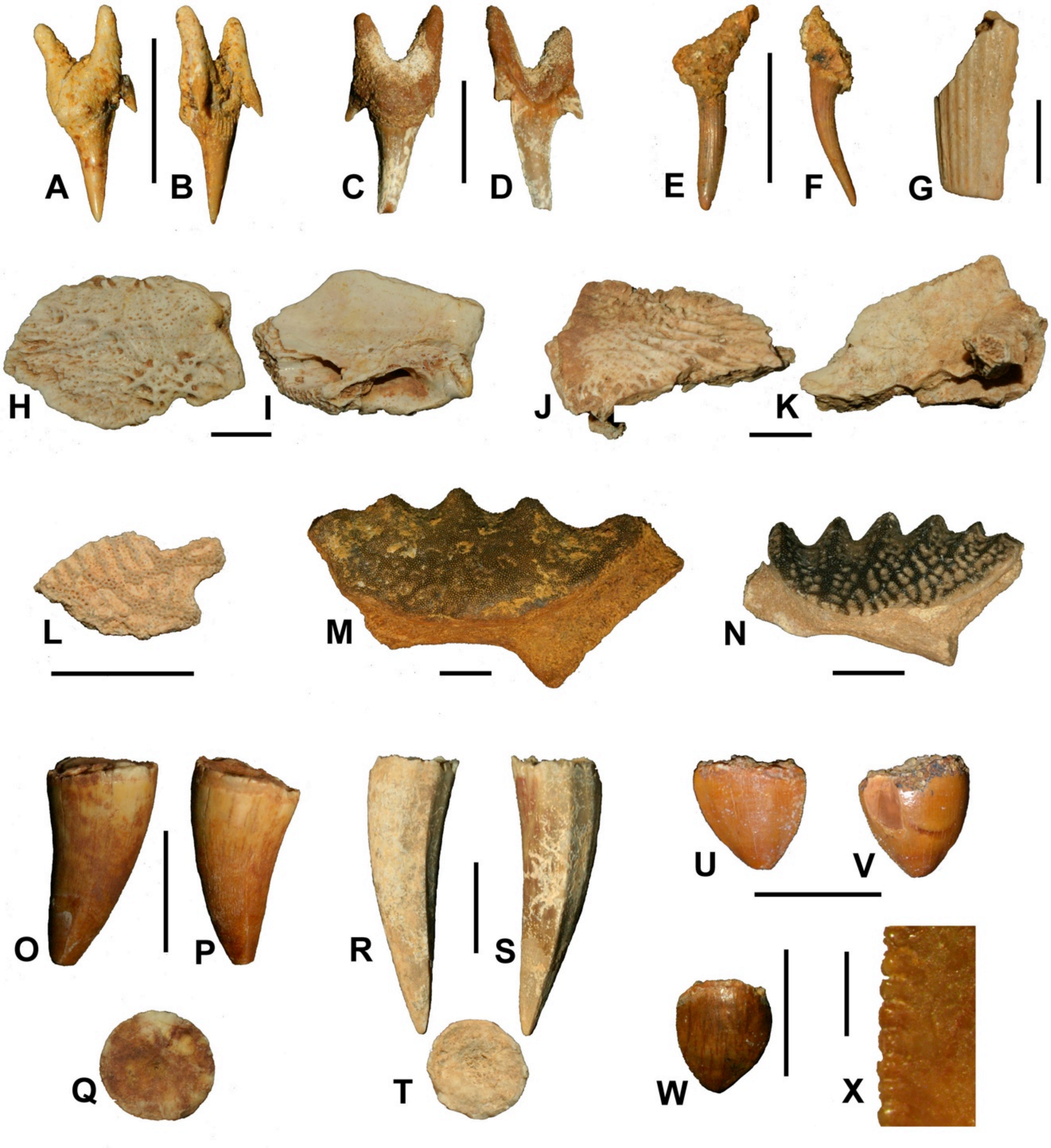

Figure 12 - Representative fossil from the Oum ed Diab Member, Aïn El Guettar Formation. (A-D) Teeth of *Leptostyrax macrorhiza*. (E-F) Tooth referred to *Scaphanorinchus sp.* (G) Dorsal fin spine referred to a lamniform shark. (H-K) Post-parietal fragments referred to *Mawsonia* sp. (L) *Mawsonia* sp., fragment of tooth plate. (M) *Ceratodus* sp. tooth plate. (N) *Neoceratodus* sp. tooth plate. (O-Q) crocodilian tooth, morphotype 1. (R-T) crocodilian tooth, morphotype 2. (U-W) *Araripesuchus* teeth. (X) Detail of the serrated carina of *Araripesuchus* (Scale bar 1 mm). Scale bar A-Y 1 cm.

A number of coprolites have been collected from the Oum ed Diab sandstones; overall the shape is elongated and cylindrical, slightly flattened in cross section. Similar shapes have been observed in crocodylian coprolites (Milàn and Hedegaard, 2010); thin sections performed on four coprolites showed bone remains, and their size (5 cm long in average) and shape support an attribution to crocodiles[1].

1.7.1.3. Dinosaurs

1.7.1.3.1. Theropoda

Many of the isolated teeth recovered from the Oum ed Diab member are incomplete and the root area almost never preserved. Nevertheless, it is still possible to study their overall morphology, the size and shape of denticles, as well as the characteristics of the carinae, including blood groves.

Seventeen teeth are referred to carcharodontosaurid theropods (Fig. 14A-G). They are blade-shaped, with the posterior margin of the crown slightly recurved toward the apex, and strongly labio-lingually compressed (CR 1.62-1.7; ER 0.43-0.53) (Fig. 14B). Both carinae have serrations (DPMa 2-2.5; DPMp 3) and the size of the distally hooked denticles decreases toward the apical ends of both carinae. Blood grooves (*sensu* Fanti and Therrien, 2007) are either absent or in the form of small sulcis restricted to the base of denticles. On both sides of the crown enamel wrinkles extend across the crown. This peculiar dental features has been considered as diagnostic for *Carcharodontosaurus saharicus* but are also similar to those of *Eocarcharia dinops* from Niger (Sereno and Brusatte, 2008, Fig. 17).

Teeth assigned to *Spinosaurus* (n=143) display characteristic conical, straight or at most slightly curved crown with vertical ridges extending the height of the crown on both the labial and lingual surfaces (Fig. 14K-M). Cross-section is sub-circular to elliptical, and both carinae extends the full height of the crown to its apex and devoid of serrations.

Furthermore, a total of 11 isolated teeth are referred to an undetermined abelisaurid theropod and represent the first report of this clade from Tunisia (Fig. 14H-J). The basal cross-section is laterally compressed, teardrop-shaped, and usually symmetrical (CR 1.72-2.2; ER 0.6-0.78). Denticles are slightly smaller on the anterior carina (DPMa 3.5-4; DPMp 3) and their size decreases toward the basal and apical ends of both carinae. Blood grooves, here considered as diagnostic for this clade (Fanti and Therrien, 2007; R. Candeiro, personal communication.), are clearly visible to the naked eye and strongly inclined toward the basal end of the tooth relative to the denticles. The posterior carina also displays an inflection point where the curvature becomes more pronounced lingually. Such features have been observed in other abelisaurid such as *Majungatholus atopus* and *Carnotaurus sastrei* (Smith and Dalla Vecchia, 2006; Fanti and Therrien, 2007). This referral broadens the distribution of abelisaurids on continental Africa to include Tunisia, Niger (Sereno et al., 2004; Sereno and Brusatte, 2008), Egypt (Smith et al., 2006), and Libya (Smith and Dalla Vecchia, 2006; Le Loeuff et al., 2010), and Morocco (Mahler, 2005; D'Orazi et al., 2011).

1.7.1.3.2. Sauropoda

Four isolated teeth collected at the Oued el Khil locality can be referred to a sauropod dinosaur (Fig. 14 N-S). The largest of these spatulate teeth has a preserved height of 39 mm with a convex labial face and a flat lingual surface with no ridges. The edges of the tooth are narrow, parallel and sub-vertical, and do not expand relative to width of the tooth. Near the base of the tooth the cross section is oval whereas it becomes more D-shaped toward the apex of the crown. Considering the basal width of 11 mm, the complete tooth would have been nearly four times as tall as it is wide, a characteristic of both Diplodocoidea and Titanosauria (Upchurch et al., 2004). The second tooth has a better preserved enamel and displays longitudinal wrinkles close to its base. In both teeth there are no evidences of constriction between the crown and the root as in the case of Camarasaurid sauropods, and lack marked lingual concavity as in Brachiosauridae. These teeth differ also from those of *Jobaria* and *Nigersaurus* (Sereno et al., 1999) from the Early Cretaceous of Niger. Thus we refer such specimens to a rebbachisaurid diplodocoid. Similarly, several poorly preserved dorsal and caudal vertebrae collected at Bir Miteur are tentatively referred to a rebbachisaurid sauropod. In addition, a partial, articulated skeleton of a rebbachisaurid sauropod has been recovered from the basal deposits of the Oum ed Diab Member (F.Fanti, unpublished data). Rebbachisaurids have been reported from the Early Cretaceous of northern Africa, South America, and recently from Europe (Calvo and Salgado, 1995; Salgado et al., 2004; Gallina and Apesteguía, 2005; Sereno et al., 2007; Canudo et al., 2009; Zarcone et al., 2010; Torcida Fernández-Baldor et al., 2011; Mannion, 2011; Mannion et al., 2011; Fanti, 2012) and therefore play a fundamental role in our comprehension of paleobiogeographic evolution of northern Africa in the Cretaceous.

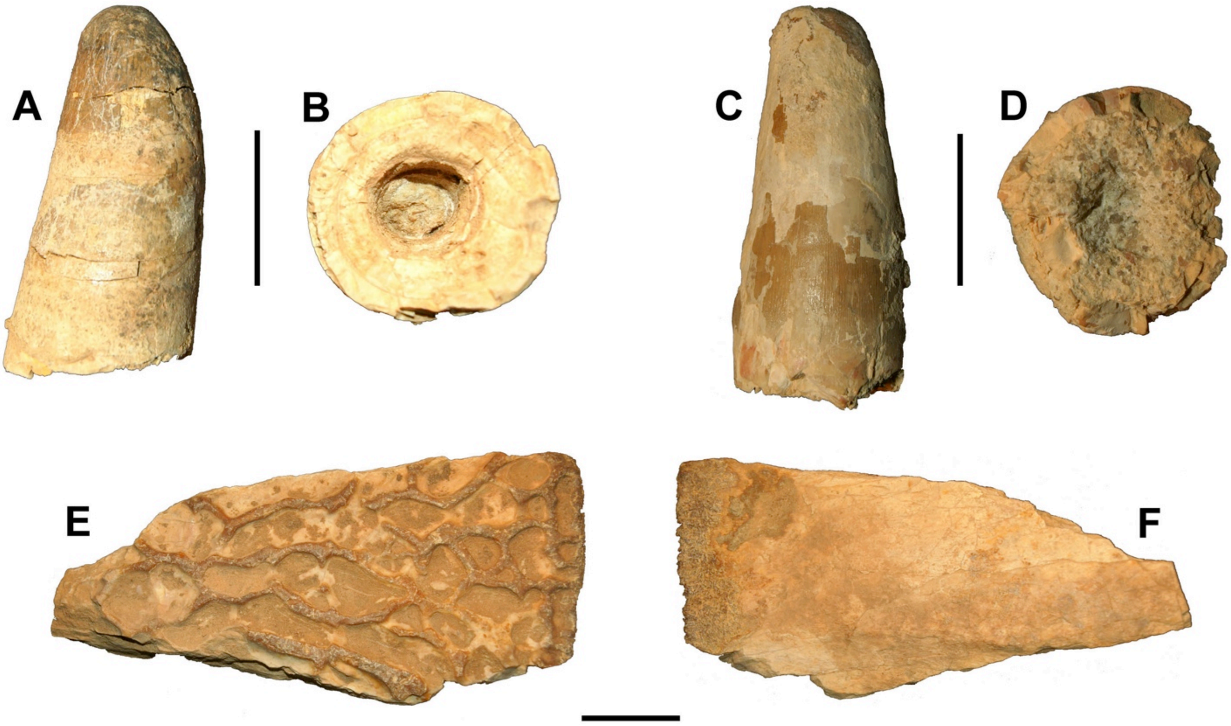

Figure 13 - Representative fossil from the Oum ed Diab member, Aïn El Guettar Formation. (A-D) *Sarcosuchus* teeth in lateral view and relative basal cross-sections. (E-F) Large trunk scutes referred to *Sarcosuchus* recovered at the El Kambout locality. Scale bar 3 cm.

1.7.1.3.3. Ornithopoda

Iguanodontians are represented by five, poorly preserved teeth which are virtually identical in overall shape and size to those collected from the Douiret Formation (Fig. 14T-X). Teeth display a pronounced ridge in lingual view and denticles similar to those observed in hadrosaurid iguanodontians (Lapparent, 1960; Norman, 2004): however, it is not possible to refer such specimens to the genus Iguanodon or to other iguanodontid (such as *Ouranosaurus* or *Lurdusaurus* from Niger, Taquet, 1976, Taquet and Russell, 1999). Srarfi (2006) reports ten isolated ornithopod teeth from the Oum ed Diab and Oued el Khil localities, here referred to the Oum ed Diab Member and no longer to the Chenini Member.

1.7.1.4. Microvertebrate assemblage

Sandstones sampled for micropaleontological analyses indicate a nearly exclusive marine assemblage in the Oum ed Diab Member. Teeth referable to elasmobranchs, bony fishes and crocodylians represent the bulk of identifiable microremains, with minor shell fragments and bones.

Shark teeth recovered are representative of three different taxa: *Caturus* sp., *Onchopristis dunklei*, and *Hybodus* sp. Teeth referred to the first species are characterized by a triangular shape with well-developed mesial and distal cutting edges running from the apex to the base of the crown. *Onchopristis* teeth have a main cusp directed lingually and two accessory cusps; the labial apron is very well developed and protruding labially (Cuny et al., 2010). Finally, two postero-lateral teeth are referred to the genus *Hybodus*. Teeth show an elongated and asymmetric shape with a low main cusp flanked by two very low accessory cusps by each side and ornamenting ridges from the base of the crow to the apex of each cusp.

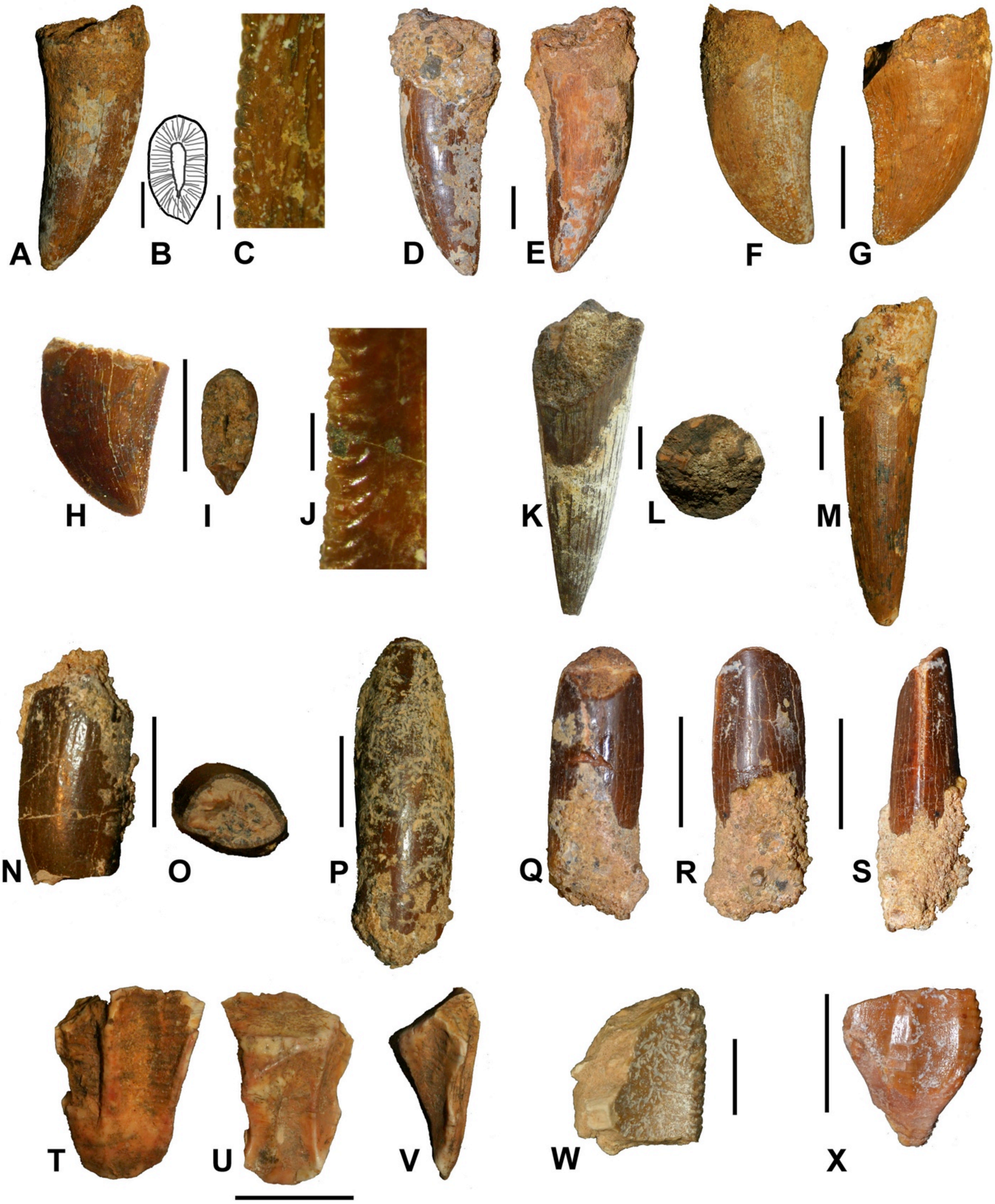

Figure 14 - Representative dinosaur remains from the Oum ed Diab Member, Aïn El Guettar Formation. (A-G) *Carcharodontosaurus* teeth. (H-J) Abelisaurid tooth. Note the well- developed blood grooves which are considered as diagnostic for this clade. (K-M) *Spinosaurus* teeth and basal cross section. (N-S) Isolated teeth referred to a rebbachisaurid sauropod. (T-X) Undetermined iguanodontian teeth. Scale bar 1 cm.

The genus *Lepidotes* is represented by well-preserved teeth, here classified in two different morphotypes. The first and most common type include elongate, slightly compressed teeth with a hook-like shape in the apical region; the second morphotype is represented by nearly hemispherical teeth similar in shape to those described at macroscopic scale. Well preserved vertebrae are referred to undetermined actinopterygians.

In addition, samples yielded a number of well-preserved crocodylian teeth: they are slightly labially curved toward the apex of the crown, have a sub-circular cross-section and longitudinal ridges. However, features observed in our specimen do not permit to refer our material teeth to any known genus.

Overall, according also to the taxa listed by Cuny et al. (2004, 2010, and references therein) the upper Chenini and lower Oum ed Diab deposits preserve a similar microfossil faunal assemblage which also include *Lepidotes* sp., semionotidae indet., *Caturus* sp., teleostei indet., actinistia indet. and *Cretodus*.

1.8. Discussion

Stratigraphic, sedimentological, and paleontological observations presented here combined with a revision of available data in the literature allow to define the stratigraphic architecture in the study area. The main basin-scale features documented in the "*Continental Intercalaire*" deposits in southern Tunisia are: 1. the "Môle de Touil el Hira" (Touil el Hira High) anticline structure and associated syn-depositional variation in accommodation in the Tataouine basin; 2. a regional, erosive unconformity at the base of the Douiret Formation; 3. a regional, subaerial unconformity at the base of the Chenini Member, 4. a regional erosive unconformity at the base of the Oum ed Diab Member (Fig. 15). Data presented in this study document the progressive truncation and pinching out of the Late Jurassic and Early Cretaceous rocks (and in particular of the Bir Miteur, Boulouha, and Douiret formations) toward the north (Tebaga de Medenine High; Raulin et al., 2011). This tilting trend of the Tataouine basin that started in the Triassic (Bouaziz, 1995, 2000; Bodin et al., 2010; Raulin et al., 2011) is interrupted by the compressive event that led to the formation of the Touil el Hira High.

The unconformity at the base of the Douiret Formation marks a major marine ingression that eroded the fine lagoonal deposits of the upper Boulouha Formation. The transgressive lag is represented by a metric thick, coarse quartz-arenite, showing a mixed (marine and non-marine taxa) and highly reworked vertebrate assemblage, as well as large logs. The Douiret sands member register a transgressive transition from shoreface to backshore deposits: the occurrence of dolomitized quartz-arenite (*lumachella* layers) at the top of fining up sequences indicate repeating, smaller scale, transgressive-regressive cycles. The abundance of fossil-rich conglomerate and sandstone combined with recurrent tree trunks also suggests deposition under rapid rates of sediment accumulation, and susceptible to ecological disturbance. Based on stratigraphic and paleontological data, the lower Douiret Formation is interpreted as tide-dominated coastal/deltaic plan characterized by relatively high marine ecosystems productivity. The overlying Douiret Clay member is interpreted to represent deposition within a vast, subsident, lagoonal system that was occasionally subject to evaporitic condition (*sabkha*-like system). Clays are locally interbedded with light-colored marls and occasionally cut by coarse, high-energy, gravel channel deposits interpreted as fluvial discharge into the lagoonal system. The tabular, dolomitic beds within this stratigraphic interval have a typical *lumachella* fabric indicating significant hydraulic turbulence during the sedimentation, and therefore are here interpreted as tempestitic events within the lagoonal system.

The second regional unconformity recorded in the Tataouine Basin (the Late Aptian "Austrian" unconformity of Bodin et al., 2010), corresponds to the base of the Chenini Member (Aïn El Guettar Formation) and represents a tectonically-driven, strongly erosive, subaerial unconformity (Fig. 15). Available data do not allow to estimate the time gap represented by this unconformity. Data presented in this study do not support a long-distance sediment source area for the Chenini beds as previously suggested by Benton et al. (2000) and Lefranc and Guiraud (1990). A source of sediment located near the anticline structure is also supported by the overall size and sharp edges of the large allogenic blocks characterizing the basal, high-energy, fluvial conglomerate of the Chenini Member. The coarse, basal Chenini Member beds accumulated under high energy hydraulic regime are interpreted as channel deposits similar to those of the present day *wadi*-like drainage systems. Such deposits represent dry or ephemeral riverbeds strongly influenced by seasonal precipitations and are characterized by poorly-sorted gravels and sands. As in present day analogues, often reworked by aeolian processes, the Chenini beds are locally interbedded with finer, high-angle, aeolian deposits, supporting dry climatic conditions at the time of deposition. This interpretation is also supported by the lack of plant remains in these beds and by the presence of iron-rich pebbles coming from the above hard grounds showing typical arid palaeo-soil characteristics.

Finally, the transition to the overlying deposits of the Oum ed Diab Member is marked by an erosive surface which extends throughout the entire Tataouine Basin. Sedimentological data, as well as a distinctive mixed, highly re-worked faunal assemblage recovered from this bed support that this deposits originated as a transgressive lag. Vertebrate remains associated with this marker bed have been incorrectly referred as the Chenini Member bonebeds. The Oum ed Diab Member preserves shoreface and tidal flat/foreshore deposits. Shoreface deposits are characterized by low angle, cross-bedded structures, whereas foreshore deposits present typical bidirectional tidal foreset and flaser stratification with predominant coarse siliciclastic sandstone. These shallow marine succession grades into more marine sediments characterized by low angle cross stratification and in some cases hummoky cross-stratification.

The conformable transition from the Oum ed Diab and Rhadouane members to the overlying Zebbag Formation documents the instauration of shallow marine conditions in the area from the Cenomanian ongoing due to a basin scale marine ingression.

1.9. Paleoecological interpretation

The lower Douiret Formation fossil record is primarily represented by elasmobranchs (*Hybodus*, *Ergenodus*, *Priohybodus arambourgi*, *Lissodus*, and *Rhinobatos*), actinopterigians (picnodontiformes, *Gyrodus*, and *Lepidotes*), and sarcopterygians (*Mawsonia*), all considered as representative of fresh water environments. Reptiles include plelurodiran turles, mainly referred to freshwater and brackish environments, and crocodylian remains that similarly support both fluvial or near coast environments. *Priohybodus* is the sole biostratigraphic marker for this unit and its occurrence in the Douiret Formation allows to separate the Douiret beds from the overlying Chenini and Oum ed Diab deposits in the northern section of the Tataouine basin (Fig. 15). The association of *Priohybodus* with taxa commonly recovered in freshwater and brackish deposits supports a broad channel system near the coast characterized by a high diversity of taxa with various dietary adaptations. Furthermore, as pointed out by Cuny et al. (2004) individuals of this species may have outreached two meter in body length and probably tolerate occasionally brackish and freshwater streams if deep enough to support their body mass. A present day analogue is represented by the bull shark (*Carcharhinus leucas*) which is common worldwide in warm, shallow waters along coasts but is also found in rivers and lakes. Furthermore, large logs are fairly common within the finer deposits of the Douiret sand member, thus indicating a highly vegetated environment. However, the co-occurrence of calcretes and desiccation cracks on top of dolomitic beds suggest alternating, possibly seasonal, dry and more humid conditions. Environmental and climatic conditions shifted toward more arid conditions during the deposition of the Douiret Clay member, with the instauration of *sabkha*-like condition along the coastal areas. The nearly absolute absence of fossils and organic matter within these beds indicate extreme environmental conditions and the disappearance of vegetation along the coast.

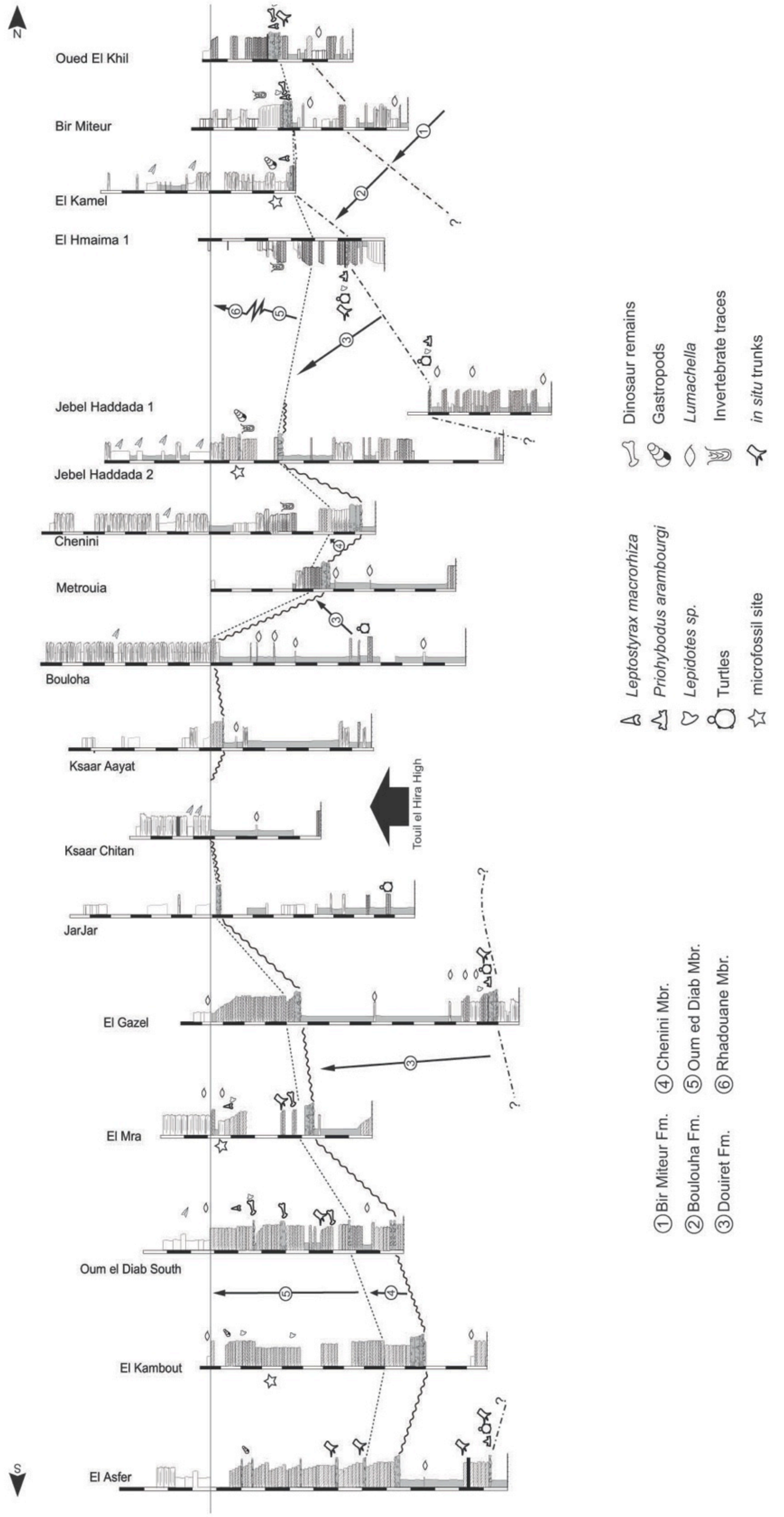

Figure 15 - Proposed stratigraphic correlation of discussed units and fossil-bearing strata based on sedimentological data and paleontological assemblages respectively north (A) and south (B) of the Touil

el Hira High. Note that the fossiliferous bed exposed at Bir Miteur and Oued El Khil pertains to the Oum ed Diab member and not to the Chenini beds.

The deposition of the Chenini member marks and abrupt shift in both depositional and environmental conditions in the Tataouine basin during the latest Early Cretaceous. The absence of plants and the abundance of iron oxides and phosphatised organic remains support arid to strongly seasonal environments.

Finally, the marker bed at the base of the Oum ed Diab Member preserves a rich and diverse faunal assemblage recovered includes marine elasmobranchs (*Tribodus tunisiensis, Lissodus sp., Diabodus tataouinensis, Cretodus semiplicatus, Leptostyrax macrorhiza, Scaphanorinchus sp.,* and *Onchopristis dunklei*), bony fishes (*Lepidotes sp., Mawsonia sp., Ceratodus sp. and Neoceratodus sp.*), crocodylians (*Sarcosuchus, Araripesuchus and Hamadasuchus sp.*), turtles, and dinosaurs (*Carcharodontosaurus*, spinosaurs, abelisaurs, rebbachisaurid, and ornithopods) (Fig. 15). This peculiar assemblage in the basal beds of the Oum ed Diab member, characterized by a sharp, erosive base is interpreted as the result of a transgressive lag, and therefore part of the taxa did probably belong to the underlying Chenini Member. Upper deposits of the Oum ed Diab member are interpreted as a vast embayment dominated by marine taxa (Fig. 16).

1.10. Timing of depositional events

The new stratigraphic framework presented in this study allows us to propose a new interpretation of the depositional history of the "*Continental Intercalaire*" deposits of the Tataouine basin in the Hauterivian – Cenomanian interval. However, chronostratigraphic constrains are in the urge of additional data, and in particular depositional gaps expressed by discussed tectonic unconformities. During the Upper Jurassic- Lower Cretaceous, the Tataouine basin was subject to differential subsidence driven by regional tectonic with consequent increase of accommodation to the south, as documented by the progressive truncation and pinching out of Mesozoic deposits toward the Permian Tebaga de Medenine structure. Tectonically-driven subsidence of the Tataouine Basin led to the deposition of the Douiret Formation during the Barremian-lower Aptian. Both the sandy and clay members of the Douiret Formation display pinching out termination toward the north, where they progressively cut the Hauterivian-Barremian Boulouha Formation. The Douiret Formation is bounded at the top by the late Aptian unconformity (also known as Austrian unconformity), which represents a major and undetermined gap in the deposition. The deposition of the Chenini Member and overlying Oum ed Diab Member started during the lower Albian, prior to the formation of the Touil el Hira anticline. Measured sections presented in this study document that the Chenini deposits pinch out toward the north: from the Jebel Haddada section, near the village of Guermessa, the overlying Oum ed Diab member truncate progressively the Merbah el Asfer Group and the Chenini deposits northward. The compressive event that led to the formation of the Touil el Hira anticline is here interpreted as coeval to the deposition of the upper Oum ed Diab and the lateral equivalent Rhadouane Member. The developing anticline progressively exhumed the Chenini and the lower Oum ed Diab deposits near the present day Jebel Boulouha area. Consequently. this folding of the Lower Cretaceous succession led to the formation of two, subsiding, syn-tectonic depocenters. South of the Touil el Hira high, the siliciclastic deposition of the Oum ed Diab member continued avoiding significant variation in depositional facies. In a different way, a regional transgressive event during the late Albian resulted in the deposition of the Rhadouane carbonates which interfinger with the shallow marine Oum ed Diab sandstones toward the south (Fig. 16). By the Albian-Cenomanian boundary, the compressive event that formed the present day Touil el Hira high terminated, leading to the conformable deposition of the lower Zebbag deposits over the entire Tataouine basin. The sole unconformable contact between the

Zebbag Formation and underlying "*Continental Intercalaire*" deposits is found at the top of the Touil el Hira folded layers at the Ksaar Chitan section.

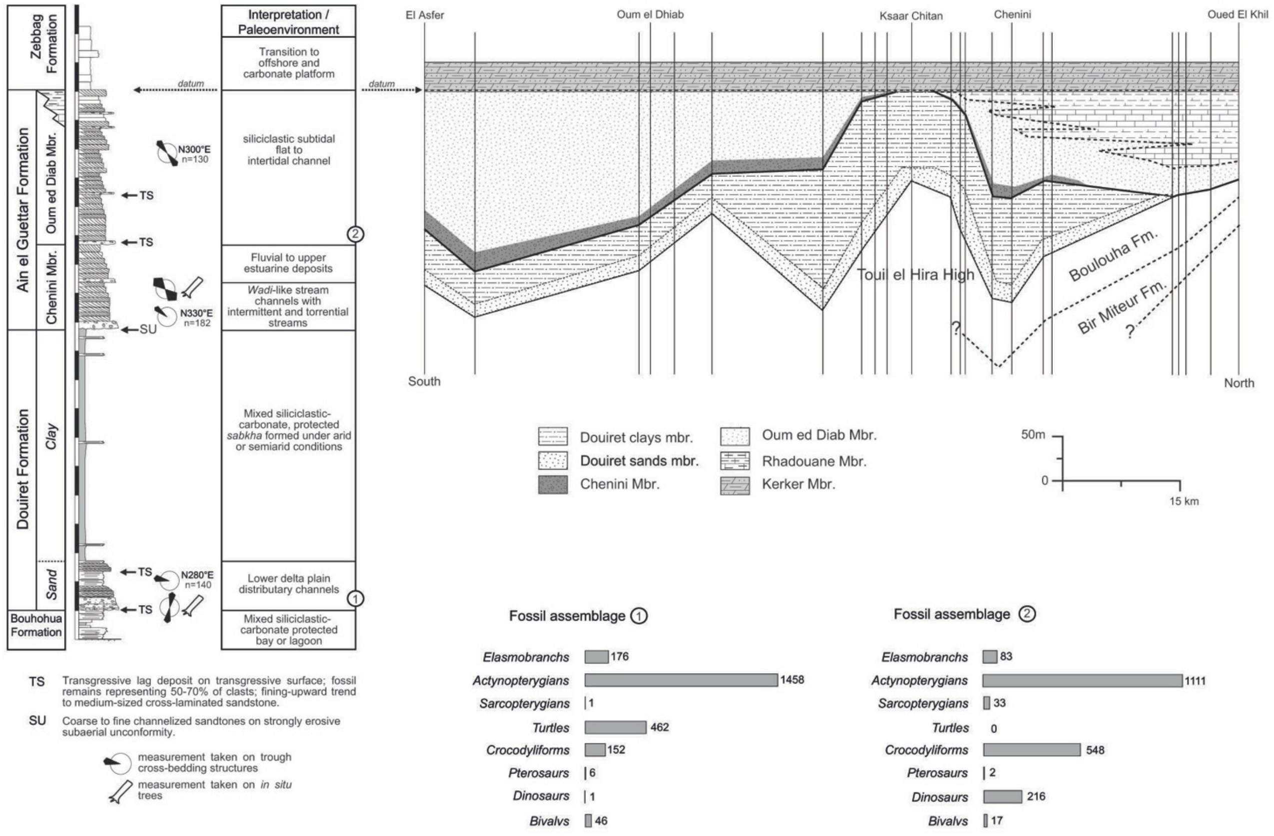

Figure 16 - Simplified and comprehensive stratigraphic log of the Early Cretaceous beds exposed in the study area and relative paleoenvironmental interpretation. The different fossil assemblages found in the Douiret Formation and Oum ed Diab member allowed to refer vertebrate remains to a specific chronostratigraphic framework.

1.11. Conclusions

One of the characteristics of the Mesozoic successions exposed in the northern edge of the Sahara is the presence of well documented transitions between the continental domain and the marine domain. Stratigraphic and paleontological data are extraordinary both because of the size of the area over which they extend, and also because of the repeating facies which are dominant in these regions. Southern Tunisia, and in particular the Tataouine basin, plays an important role in the definition and comprehension of the Early Cretaceous evolution of Northern Africa, even though the chronostratigraphic framework is in the urge for a revision. In the region, macro- and microvertebrate remains are recovered from three distinct stratigraphic intervals: the lower Douiret Formation (Barremian), and the Chenini (rare) and Oum ed Diab members of the Aïn El Guettar Formation (Albian). The Douiret Formation represents deposition of mainly siliciclastic deposits in coastal environments (foreshore to coastal *sabkha* facies): fossils recovered from this interval are essentially representative of freshwater taxa. The Chenini sandstones of the "*Continental Intercalaire*" are known in the literature as the richest fossil-bearing unit in southern Tunisia: this is historically due to a fossiliferous lag that crops out at the Oued el Khil, Bir Miteur, and El Hmaima localities that has been referred to this member since the works of Bouaziz et al (1988) (see also

Benton et al., 2000; Anderson et al., 2007, and references therein). However, a basin-scale detailed revision of 1. the stratigraphic occurrence and lateral variability of fossil-bearing strata, 2. accurate sampling through the entire Tataouine basin, and 3. an accurate description and comparison of different faunal assemblages, indicate that such deposits are not referable to the Chenini Member, but to the basal beds of the Oum ed Diab Member and consequently are middle Albian in age. In fact, data presented in this study document that the basal deposits of the Chenini Member, which consist of an indurate conglomerate representative of a depositional system similar to those of the present day *wadi*, are barren of fossils with the exception of rare and fragmentary actinopterygians remain.

The Early Cretaceous Tataouine succession is characterized by a strong lateral facies variability in a low gradient, coastal environment. Particularly clear is the transition between the shallow marine to coastal environment (embayment, lagoon and/or *sabkha*) within the Douiret and Oum ed Diab formations, both characterized by high accommodation rate, and the fluvial sediments of the Chenini formation which deposited under low accommodation setting.

Table 1: Vertebrate fauna of the "*Continental Intercalaire*" of southern Tunisia, gathered by stratigraphic age. Principal references for each record are provided in parentheses.

Douiret Formation (sandy member)
Chondrichthyes
    Elasmobranchii
        Hybodontiformes
            Hybodontidae
                Hybodus sp. (Cuny et al., 2004)
                Egertonodus sp. (Cuny et al., 2010)
                Priohybodus arambourgi (Cuny et al., 2004)
                Lissodus sp. (Cuny et al., 2010)
        Rajiformes
                Rhinobatos sp. (Cuny et al., 2004)
Osteichthyes
    Actinopterygii
        Neopterygii
            Pycnodontiformes indet.
                Gyrodontidae
                    Gyrodus sp. (Cuny et al., 2010)
            Semionotiformes
                Semionotidae
                    Lepidotes sp. (Cuny et al., 2010)
    Sarcopterygii
            Coelacanthiformes
                Mawsonia sp. (Grandstaff et al., 2002 ; Candeiro et al., 2011)
Testudines
    Pleurodira indet.
Crocodylomorpha
    Crocodyliformes
    Crocodyliformes indet.
Pterosauria
    Ornithocheiroidea
        Ornithocheiroidea indet.
Dinosauria
    Ornithischia

- Ornithischia indet.

Aïn El Guettar Formation, Chenini Member

- Osteichthyes
  - Actinopterygian indet.

Aïn El Guettar Formation: Oum ed Diab Member

- Chondrichthyes
  - Elasmobranchii
    - Hybodontiformes
      - Hybodontidae
        - *Tribodus tunisiensis* (Cuny et al., 2004)
      - Lonchidiidae
        - *Lissodus* sp. (Cuny et al., 2004)
        - *Diabodus tataouinensis* (Cuny et al., 2004)
    - Laminiformes
      - Cretoxyrhinidae
        - ?*Cretodus* (Cuny et al., 2010)
        - *Cretodus semiplicatus* (Cuny et al., 2004)
        - *Leptostyrax macrorhiza* (Cuny et al., 2004)
      - Mitsukurinidae
        - *Scapanorhynchus* sp. (Cuny et al., 2004)
    - Rajiformes
      - Sclerorhynchidae
        - *Onchopristis dunklei* (Cuny et al., 2010)
- Osteichthyes
  - Actinopterygii
    - Neopterygii
      - Pycnodontiformes
      - Pycnodontiformes indet. (Cuny et al., 2010)
      - Semionotiformes
        - Semionotidae
          - *Lepidotes* sp. (Benton et al., 2000; Cuny et al., 2010)
  - Sarcopterygii
    - Actinistia
    - Actinistia indet. (Cuny et al., 2010)
    - Coelacanthiformes
      - *Mawsonia* sp. (Grandstaff et al., 2002 ; Candeiro et al., 2011)
    - Dipnoi
      - *Ceratodus* sp. (Tabaste, 1963; Soto and Perea, 2010)
      - *Neoceratodus* sp. (Tabaste, 1963; Soto and Perea, 2010)
- Arcosauria
  - Arcosauria indet.
    - Crocodyliformes
    - Crocodyliformes indet.
      - Mesoeucrocodylia
        - *Araripesuchus* sp.
        - *Araripesuchus wegeneri* (Sereno and Larsson, 2009 ; Cuny et al., 2010)
      - Neosuchia
        - *Sarcosuchus imperator* (Sereno et al., 2001)

      - Sebecia
        - Peirosauridae

            Hamadasuchus sp. (Cuny et al., 2010)
        Neosuchia
            Bernissartidae (Cuny et al., 2010)
Pterosauria
    Ornithocheiroidea
        Ornithocheiroidea indet.
Dinosauria
    Saurischia
        Sauropoda
            Rebbachisauidae indet.
    Ornithischia
        Ornithopoda
            Ornithopoda indet.
    Theropoda
        Spinosauridae
            Spinosaurus sp. (Russell, 1998; Buffetaut and Oueja, 2002)
        Carcharodontosauridae
            Carcharodontosaurus saharicus (Sereno and Brusatte, 2008)
        Abelisauridea
            Abelisauridea indet.

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[1] I personally thank Dr. Cristiano Dal Sasso who revised my thesis, suggesting some minor corrections, as the paper was already published, I have decided to report his suggestions here:
"The coprolites mentioned on page 26 were referred to crocodiles on the basis of their bone contents. However bone fragments bigger than 5 cm could not pass through a crocodile pylorus, which is smaller. Veterinarians have demonstrated how crocodiles regurgitate bones, even after long retention times (e.g. Huchzermeyer, 2011). On the other hand, paleobiological studies have demonstrated how bones ingested by theropods could go though the whole intestine (Dal Sasso and Maganuco, 2011; Xing et al., 2012), thus coprolites containing bone remains, as Tunisian ones, should thus be referred to theopoda indet., as firstly hypnotized by Chin et al. (1998, 2003)."

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CHAPTER 2 - Vertebrate tracksites in the Middle Jurassic-Upper Cretaceous of South Tunisia

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ABSTRACT

Four vertebrate tracksites from the Middle Jurassic and Upper Cretaceous in the Tataouine basin of southern Tunisia are described. Approximately 130 tridactyl footprints distributed over an area of 200 square meters, preserved on Callovian beds exposed at the Beni Ghedir site, represent the oldest evidence of a dinosaur fauna in Tunisia. In addition, three tracksites – named Chenini, Ksar Ayaat, and Jebel Boulouha – have been discovered in the Cretaceous beds of the upper "*Continental Intercalaire*", previously considered as a strictly marine depositional sequence. In addition to dinosaur tracks, the Chenini tracksite (late Albian) includes poorly preserved crocodilian tracks and footprints assigned to a pleurodiran turtle have been recovered at the Ksar Ayaat locality (early Cenomanian). The Jebel Boulouha tracksite is dominated by well-preserved tridactyl tracks referred to small-sized theropods. Depositional settings of each tracksite have been defined on stratigraphic and sedimentologic data and tracks were ascribed to different ichnocoenoses in relation to their paleoenvironments. This new and differentiated track record gives important information on how the fossil vertebrate fauna changed in southern Tunisia during mid-Jurassic to mid-Cretaceous times. These data provide a unique and useful census of tetrapod associations along the southern margin of the peri-Mediterranean area.

2.1. Introduction

Recent field work conducted in the Tataouine region of southern Tunisia (Fig. 1) led to the discovery of previously unrecognized Middle Jurassic and Upper Cretaceous bedding planes with footprints attributable to dinosaurs and other small-sized vertebrates. African dinosaur tracks have been previously reported from the Jurassic of South Africa, Zimbabwe, Niger, and Morocco (Ellenberger, 1972a, b; Olsen and Galton, 1984; Ait-Kaci Ahmed et al., 2004; Boutakiout et al., 2008; Belvedere et al. 2011; Mudroch et al., 2011; Nouri et al., 2011), whereas the Cretaceous record is restricted to a few localities in Cameroon, Morocco, and Egypt (Ambroggi and De Lapparent, 1954; Demathieu and Wycisk, 1990; Jacobs et al., 1996). Despite evidence of rich and diversified terrestrial vertebrate faunas in the Jurassic-Cretaceous deposits of southern Tunisia (De Lapparent, 1951, 1960; Taquet, 1980; Bouaziz et al., 1988; Benton et al., 2000; Russell and Paesler, 2003) this is the first report of dinosaur tracks from this region. In this paper we summarize the stratigraphy and sedimentology from four new ichnosites, Late Jurassic to Cretaceous in age, and we provide a description of tracks. Finally we discuss the tracks within the context of their respective depositional environments.

2.2. Geological setting

In southern Tunisia, the Jeffara plain and the Dahar escarpment provide excellent exposures of Permian to Upper Cretaceous successions that form the bulk of a subsiding region known as the Tataouine Basin. Permian and Triassic successions consist of tectonically deformed marine beds that crop out primarily in the northern part of the basin (Burollet, 1956; Busson, 1967; Bouaziz et al., 1987; Bodin et al., 2010). Evaporitic deposits accumulated during the Liassic, whereas mainly shallow-marine and lagoonal carbonates characterize the Middle Jurassic (Busson, 1967; Peybernes et al., 1985; Bouaziz et al., 1987; Chandoul et al., 1993). Limestones of the Foum Tataouine Formation have been assigned a Callovian age based on distinctive ammonites (*Pachyerymnoceras*), brachiopods (*Daghanirhynchia daghaniensis* and *Bihenithyris barringtoni*), and echinoids (*Monodiadema cotteaui*) (Ben Ismaïl, 1991).

A major hiatus marked by a regional erosive unconformity separates the carbonate-dominated mid-Jurassic successions from the siliciclastic deposits of the "*Continental Intercalaire*" (Kilian, 1931). This siliclastic sequence has been formally divided into four formations: in ascending order, Bir Miteur, Boulouha, Douiret and Aïn el Guettar (Chenini and Om Diab members), which consist of alternating continental to shallow marine deposits (Busson, 1967; M'Rabet, 1987; Bouaziz et al., 1989; Peybernes 1996; Zarbout et al., 1994; Benton et al., 2000; Bodin et al., 2010). The lack of unequivocal biostratigraphic markers has made it difficult to refine the age of this succession, which has tentatively been assigned a Kimmeridgian to Albian age (Busson, 1967; Peybernes et al., 1996; Ben Ismaïl, 1991; Ben Youssef, 1999; Bodin et al., 2010).

For more than 50 years, vertebrate remains have been collected from the ?Aptian-Albian Aïn el Guettar Formation: conglomeratic deposits of this interval preserve one of the most diverse Early Cretaceous vertebrate faunas from Africa, consisting of elasmobranchs, actinopterygians, sarcopterygians, turtles, crocodyliforms, pterosaurs, and non-avian dinosaurs (De Lapparent, 1951, 1960; Tabaste, 1963; Taquet, 1980; Bouaziz et al., 1988; Ben Ismaïl, 1991; Benton et al., 2000; Barale and Ouaja, 2001; Buffetaut and Ouaja, 2002; Ouaja, 2003; Russell and Paesler, 2003; Cuny et al., 2004; Ouaja et al., 2004; Anderson et al., 2007; Amiot et al., 2010; Cuny et al., 2010; Fanti et al., 2012).

Lastly, the Upper Cretaceous (Cenomanian and Turonian) is represented by evaporitic and carbonate sedimentation. This stratigraphic interval is represented by the Zebbag Formation, which includes the Rhadouane, Kerker and Gattar members (M'Rabet et al., 1995; Barale and Ouaja, 2001; Ouaja et al., 2004). Such formal members have been dated as late Albian, Cenomanian and Turonian, respectively, based on the occurrence of *Knemiceras*, *Neolobites* and *Choffaticeras* ammonite associations (Busson, 1967; Ben Youssef et al., 1985; Razgallah et al., 1994). The basal Rhadouane Member is restricted to the northern section of the Tataouine basin and is characterized by biolaminated mudstone and fossil-rich (gastropods and bivalves) rudstone. The transition to the overlying Kerker Member is marked by a shift from limestone-dominated to marl-dominated beds: basal deposits are characterized by extensive, up to 5 meter thick evaporitic deposits. Finally, the Gattar Member consists of a thick succession of dolomitic limestone with minor chert nodules deposited during a regional transgressive event during the Turonian (M'Rabet, 1987; Razgallah et al., 1994; Bodin et al., 2010).

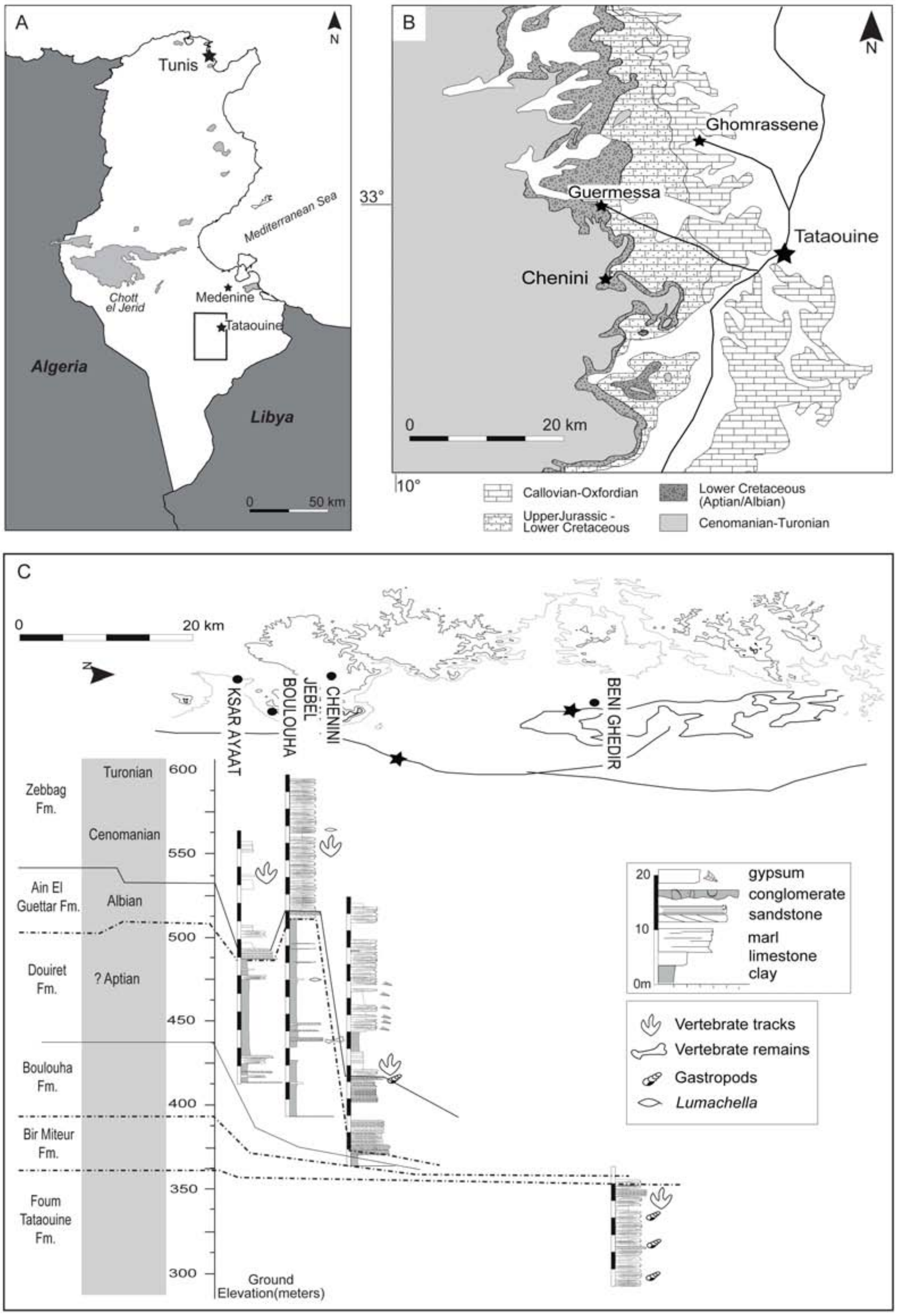


Figure 1 - A) Map of Tunisia showing the study area in the Tataouine region. B) Geological map of the Tataouine region showing the distribution of Upper Jurassic – Upper Cretaceous deposits of the *Continental Intercalaire*. C) Detailed reference map of the Tataouine region showing tracksites discussed in the text and geological sections of the tracksites and stratigraphic occurrence of track bearing surfaces and fossiliferous beds.

2.3 Material and Methods

This study is the result of four field seasons undertaken in the Tataouine region between 2009 and 2011, led by the authors with the support of the University of Bologna (Italy) with the support of the Office National des Mines (Tunis). GPS data on the tracksite locations are deposited at both the University of Bologna (Italy) and Office National des Mines (Tunis). Tracksites were first of all documented by standard stratigraphic and sedimentological methods, resulting in a detailed stratigraphic log of the track-bearing locality. Isolated tracks were photographed on site, whereas for large (>2 square meters) track-bearing surfaces a square meter grid was used to map the tracks. Representative tracks were traced using transparent acetate film, and molds of best-preserved footprints were made using Silical 110 silicon putty. Three molds were used to generate 3D digital models, from the Ksar Ayaat, Jebel Boulouha and Chenini localities. Fiberglass replicas were also made from the molds and deposited at the Museo Geologico Giovanni Capellini in Bologna (Italy) under inventory numbers MGGC 21845, 21851 and 21856, respectively. Three dimensional models were acquired using Next Engine HD Desktop 3D scanner with a resolution of 0.4 mm. Image data rendering was carried out using Next Engine Scann Studio HD Pro® (alignment of the scans). 3D modeling was preferred to the classical drawing representation because the former technique provides a more objective representation of tracks. Standard track parameters used here include: footprint length (FL), footprint width (FW), digit length (L) for digit II, III and IV (*sensu* Leonardi, 1987) and interdigital angles (angle of divarication, α) between digits II-III, III-IV and II-IV (Tables 1, 2). Measurements on trackways include pace, stride and pace angulation between two steps (*sensu* Leonardi, 1987).

2.4. Description of the tracksites

Tracksites described herein occur in the Mesozoic escarpment of the Tataouine region (Figs. 1, 2) and are representative of three different time intervals: Middle Jurassic (Callovian), Early Cretaceous (Aptian-Albian), and Late Cretaceous (Cenomanian).

2.4.1 Beni Ghedir site

The Beni Ghedir valley is located just north of the village of Ghoumrassene, approximately 20 km northwest of Tataouine (Fig. 1). Middle to Upper Jurassic strata of the Foum Tataouine Formation are exposed in the valley and have been the subject of several litho- and bio-stratigraphic studies (Busson, 1967; Ouaja, 2003, and references therein). The trampled surface occurs on the west flank of the valley on top of a limestone layer of the Khechem el Miit Member of the Foum Tataouine Formation (Fig. 2). Overall, the 200 meter thick deposit of the Khechem el Miit Member is represented by shallow marine sequences that accumulated during the Callovian (Busson, 1967, Ouaja, 2003; Ben Ismaïl, 1991). These tabular deposits include alternating nodular limestone beds and yellowish marls rich in brachiopods, echinoderms and scattered plant remains. The track-bearing surface also preserves mud cracks and a distinctive texture interpreted to represent ancient microbial mats (Fig. 3A), virtually identical to those observed in modern tidal-flat environments (Fig.

3B). The co-occurrence of dinosaur footprints and microbial mats whithin shallow marine and lagoonal environments, has been observed in other track-bearing localities (Kvale et al., 2001; Marty et al., 2009; Petti et al., 2011) and hypothesized to facilitate the preservation of the tracks avoiding weathering and erosion. The trampled surface is overlain by fine, horizontally-laminated marls that have been largely eroded.

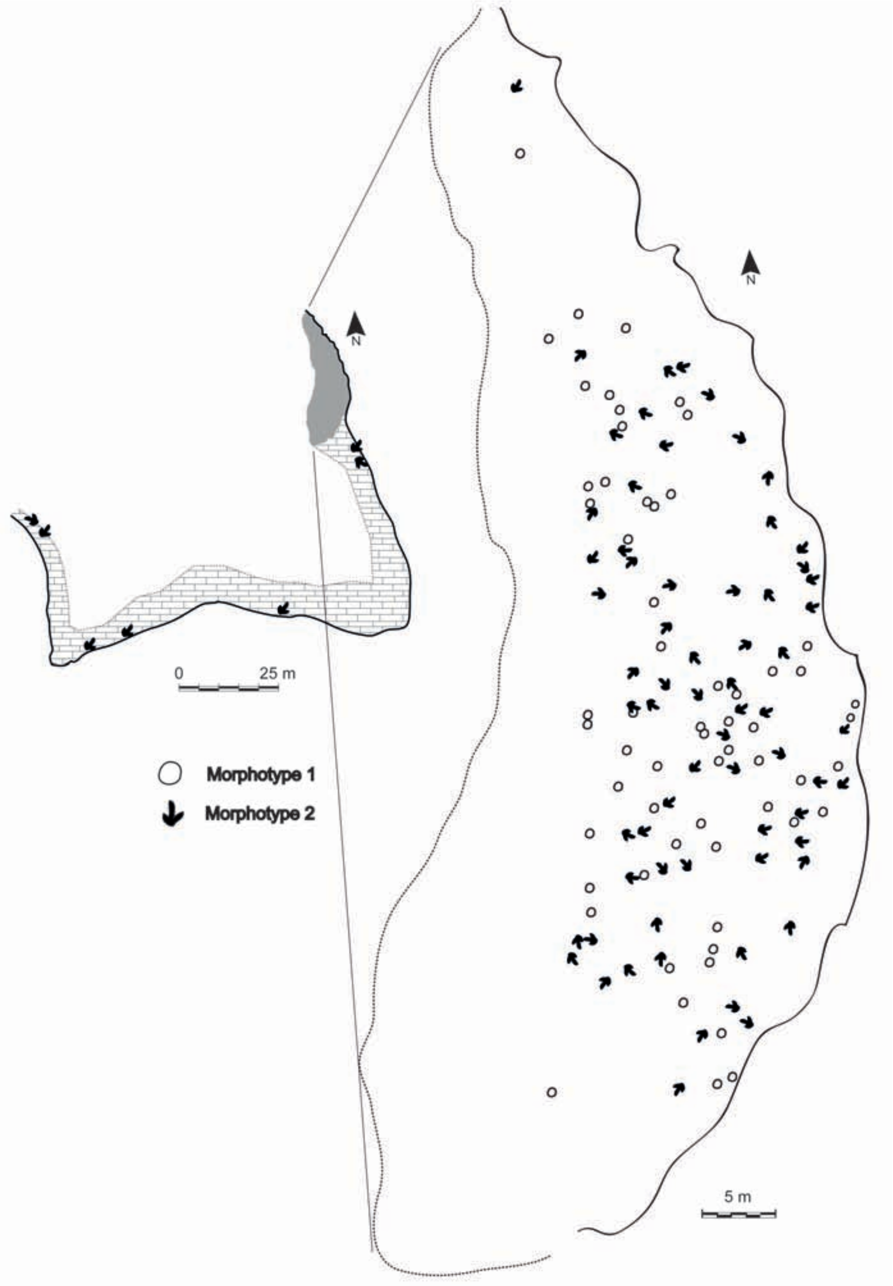


Figure 2 – Field map of the track-bearing surface at the Beni Ghedir locality (Callovian). Two basic footprint types were recognized at the site: medium sized subcircular tracks and large tridactyl tracks.

Track description. As both mud cracks and microbial mats occur on the track-bearing surface, we interpret the footprints as true tracks (*sensu* Lockley, 1991). The preservation of the footprints is very poor due to weathering, thus distinctive morphological features in the tracks are often not preserved. A total of 136 footprints were identified on about 200 m^2 of exposed surface (Fig. 2). Only a few trackways, consisting of no more than four successive tracks, were identified.

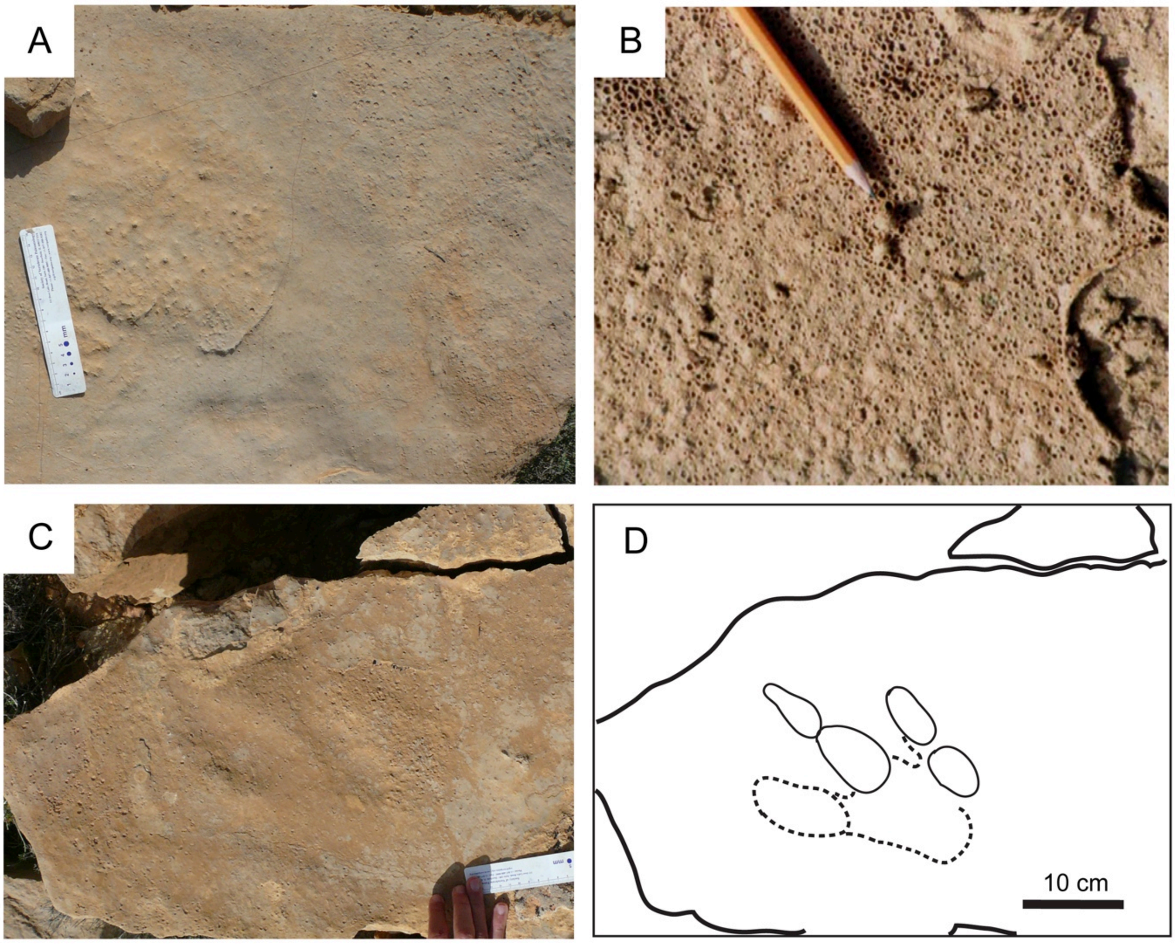


Figure 3 – Field photographs of the trampled surface at the Beni Ghedir tracksite. A. The distinctive texture observed on the track-bearing surface is interpreted here as ancient microbial mats. B Virtually identical surface observed in modern environments (picture courtesy of A.R. Fiorillo). C. Medium-sized tridactyl footprint pertaining to morphotype 2 at Beni Ghedir. D. Outline drawing of footprint in picture C. Change to this block.

Two basic footprint types were recognized: medium-sized (15-20 cm) subcircular tracks and larger (> 25 cm in length) tridactyl track. The first type of track is represented by poorly preserved sub-circular impressions; they are here interpreted as footprints as they exhibit mud rims, which are a characteristic of tracks (Thulborn, 1990). Tridactyl tracks are better preserved (Fig. 4 C, D): footprints are medium to large, broad, and digit III, where observed, is longer than other digits. Tracks measure on average 27.8 cm in length and 20.5 cm in width, the length to width ratio is >1, whereas divarication of the outer digits is 50° on average (Table 1). Tracks are characterized by a greater divarication of digits III-IV compared with digits II-III (Table 1). Pad impressions are rarely recognizable due to poor preservation.

Although Jurassic theropod tracks have been reported from a number of locality worldwide only four ichnogenera (Lucas et al., 2006) are currently used for ichnotaxonomical purposes: *Grallator* (Hitchcock, 1858), *Anchisauripus* (Lull, 1904), *Eubrontes* (Hitchcock, 1845) and *Kayentapus* (Welles, 1971). The first three ichnogenera are distinguished primarily on their size (Olsen, 1980; Olsen et al., 1998), whereas the latter is a track intermediate in size and shape between small and slender *Grallator* and larger and robust *Eubrontes* (Lockley et al., 1998). *Kayentapus* is characterized by length between 11.5 and 40 cm, wider interdigital angles, well preserved metatarsophalangeal pads and divarication angle between digits III and IV greater than between II and III (Lockley et al., 1998; Milner et al., 2009). Tridactyl tracks at Beni Ghedir site average 28.8 cm in length, with digit III longer than other digits and interdigital angle between digits III-IV greater than II-III (Table 1), but due to the poor preservation no clear morphological diagnosis is possible. Considering these characteristic, although Tunisian tracks share some common features with the *Kayentapus* ichnogenus, we refrain from assigning them to a specific ichnogenus, limiting the attribution to a generic theropod dinosaur. The scarce preservation of the second, rounded morphotype does not allow any morphological diagnosis.

2.4.2 Chenini site

Vertebrate tracks have been discovered by the authors in 2010 near the village of Chenini (Figs. 2, 5). Tracks are preserved on two blocks that have been referred to the basal deposits of the Rhadouane Member of the Zebbag Formation (late Albian-early Cenomanian). This unit consists of alternating beds of bioclastic limestone rich in bivalves and gastropods and biolaminated mudstone (Bodin et al., 2010). The lowermost limit of the Rhadouane Member is not well defined, representing a north-south diachronous transition from the fluvial and sub-tidal deposits of the Aïn el Guettar Formation to the nearshore and marine carbonate deposits of the Zebbag Formation. Invertebrate vertical burrows assigned to *Diplocraterion* (Fig. 4B) occur in fine-grained sandstones cropping out a few meters below the tracks, indicating a shallow-marine high-energy nearshore environment (Seilacher, 2007). The overlying low angle cross-bedded sandstones are barren of bioturbation and are interpreted as shallow marine deposits, whereas the track surface is located on the top of the first of four sandstone layers with a fining-up trend that passes from sand-dominated to marl-dominated deposits. Tracks occur on a 50 cm thick, massive sandstone dominated by quartz pebbles and rare shell fragments. Neither bioturbation nor mudcracks were observed on the track-bearing surface.

Track description. Each of the track-bearing blocks measures approximately 4 square meters with a maximum of 8 tracks preserved. The original orientation of the loose blocks and the preferential direction of the tracks could not be determined. Well-preserved displacement mud rims exclude the interpretation of footprints as undertracks (Thulborn, 1990). Footprints are poorly preserved and numerous cracks crossing the tracks make it difficult to define them accurately. Nevertheless, two track morphotypes can be identified (Fig. 4C): relatively small rounded tracks (averaging 9 cm in diameter) and larger, elongate impressions (20 cm in length). One well-preserved track of the first morphotype preserves five short and slender digit impressions, each terminating with a clear claw mark. The second morphotype includes tracks with four relatively elongate and slender digits with claw impressions.

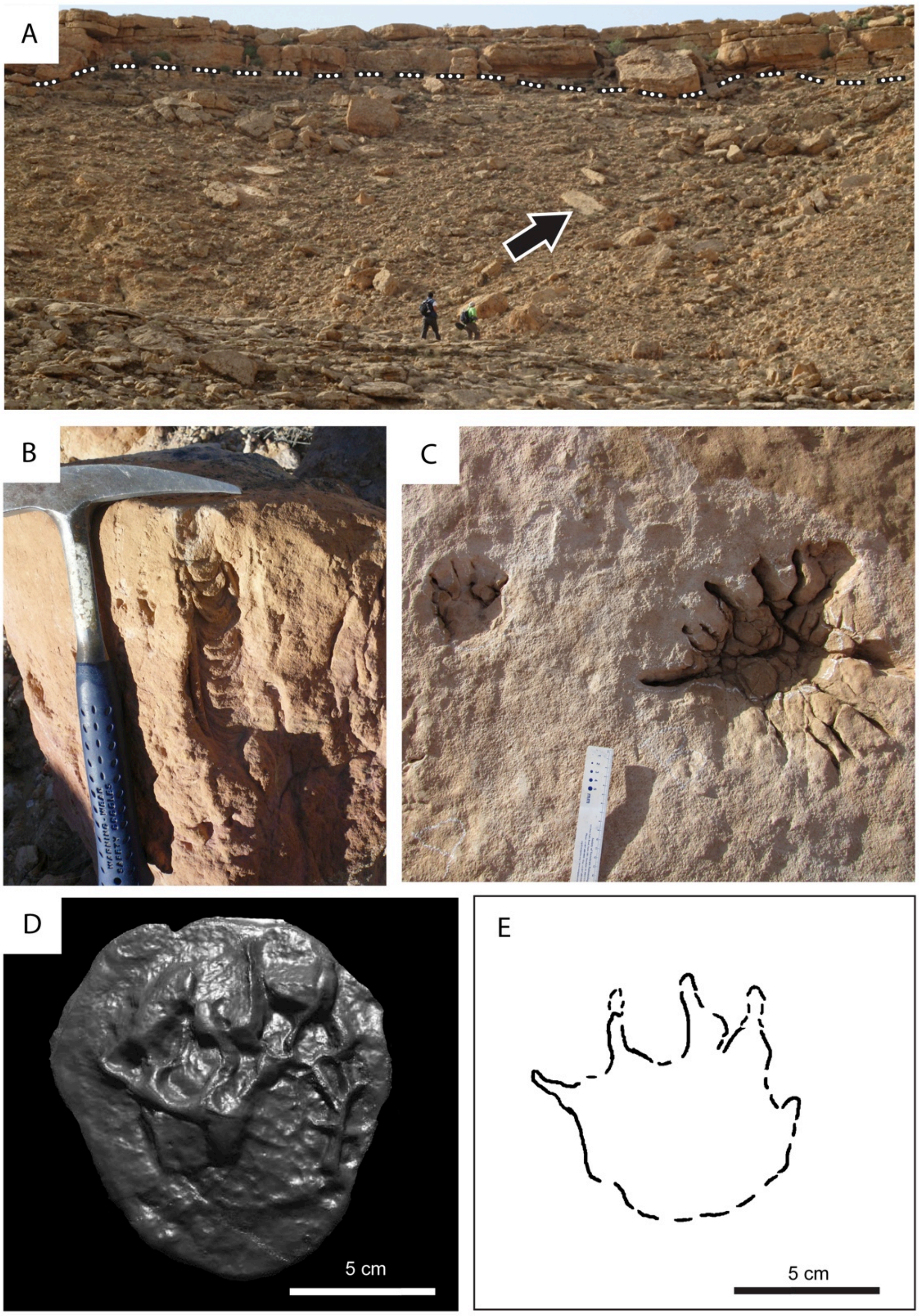


Figure 4 – The Chenini site. A) Arrow indicates the isolated track-bearing block. Dashed line marks the basal deposits of the Rhadouane Member (Zebbag Formation, Albian-Cenomanian). B) Invertebrate vertical burrows assigned to *Diplocraterion*. C) Field picture of the two track morphotypes identified at Chenini, small rounded track at left, large elongate impression at right. D) 3D model of better-preserved track mold (MGGC 21856). E) Outline drawing of MGGC 21856.

Crocodilian pes impressions are usually tetradactyl and manus impressions pentadactyl (Avanzini et al., 2007). One of the most diagnostic characteristics of crocodilian footprints is a pronounced heteropody, with manus impression much smaller than the pes. Normally pes tracks are more deeply impressed, elongate and larger, whereas manus impressions are smaller and more rounded (Kubo, 2008; Milàn and Hedegaard, 2010). No dinosaur or chelonian tracks described in the literature are similar to the ones described here. Thus, based on overall morphology, number and shape of digits, and relative size proportions, we tentatively identify the tracks as manus-pes couple of a generic crocodilian.

2.4.3. Ksar Ayaat site

The Ksaar Ayaat locality (Fig. 1) is in the basal deposits of the Kerker Member (Zebbag Formation, Cenomanian). The Kerker Member is characterized by a basal 4 meter thick evaporitic interval (primarily gypsum and halite) overlain by an alternation of horizontally laminated marls and biolaminated mudstones. Kerker deposits include alternating lagoonal and calcareous, shallow marine sediments with no previously reported evidence of subaerial exposure. The trampled surface is preserved on top of a 40 cm thick dolomitized mudstone located stratigraphically a few meters above the evaporitic beds, and supports episodes of subaerial exposure, possibly in a peritidal or tidal environment. The track-bearing surface contains neither distinctive sedimentological features nor bioturbation features, whereas 5 centimeters below the track surface intense bioturbation can be observed. This extensive bioturbation (Fig. 5B) can be referred to feeding traces of crustaceans, such as those found in soft sediments of shallow marine environments (Seilacher, 2007). The lack of microfossils in the sequence, together with the pervasive dolomitization and evaporitic gypsum, is here interpreted as indicative of an arid to semi-arid environment (see also Bodin et al., 2010). Thus, the track-bearing surface was likely to have been deposited in a shallow and confined marine embayment, where hyper salinity events occasionally led to the deposition of evaporites.

Track description. A set of 52 circular to elliptical depressions (Fig. 5C, D) occurs on a large micritic mudstone slab (250 x 180 cm); in addition, several similar, but poorly preserved tracks were found on smaller unassociated slabs. Overall, tracks have an elliptical or circular edge and only few tracks preserve digit impressions. Digit and/or claw impressions, when observed, are slightly impressed into the substrate, resulting in a track morphology consisting of a round impression with three or four rounded anterior depressions (digit and/or claw impressions, Fig. 5E, F). Tracks can be clustered in two size classes, the first 8 cm and the second 5 cm in diameter, possibly indicating manus and pes impressions. Most tracks are relatively deep (about 3 cm) compared with their size, suggesting high water content of the substrate. Even if a pattern can be recognized in the footprint association, there are no dinstinct trackways (Fig. 5D), and consequently the movement direction is unclear.

Tracks left by modern turtles in wet substrate show circular to elliptical depressions and not always evident claw marks: such tracks have been previously compared with fossil tracks from the Upper Jurassic of Spain (Avanzini et al., 2005), and from the Upper Cretaceous of Montana (Fiorillo, 2005). Ichnotaxonomy of turtle tracks is still controversial and several ichnotaxa are considered as *nomen dubium* (Moratalla et al., 1995; Avanzini et al., 2005) with the sole exception of *Chelonipus* (Rühle von Liliestern, 1939) and *Emydhipus* (Fuentes Vidarte et al., 2003).

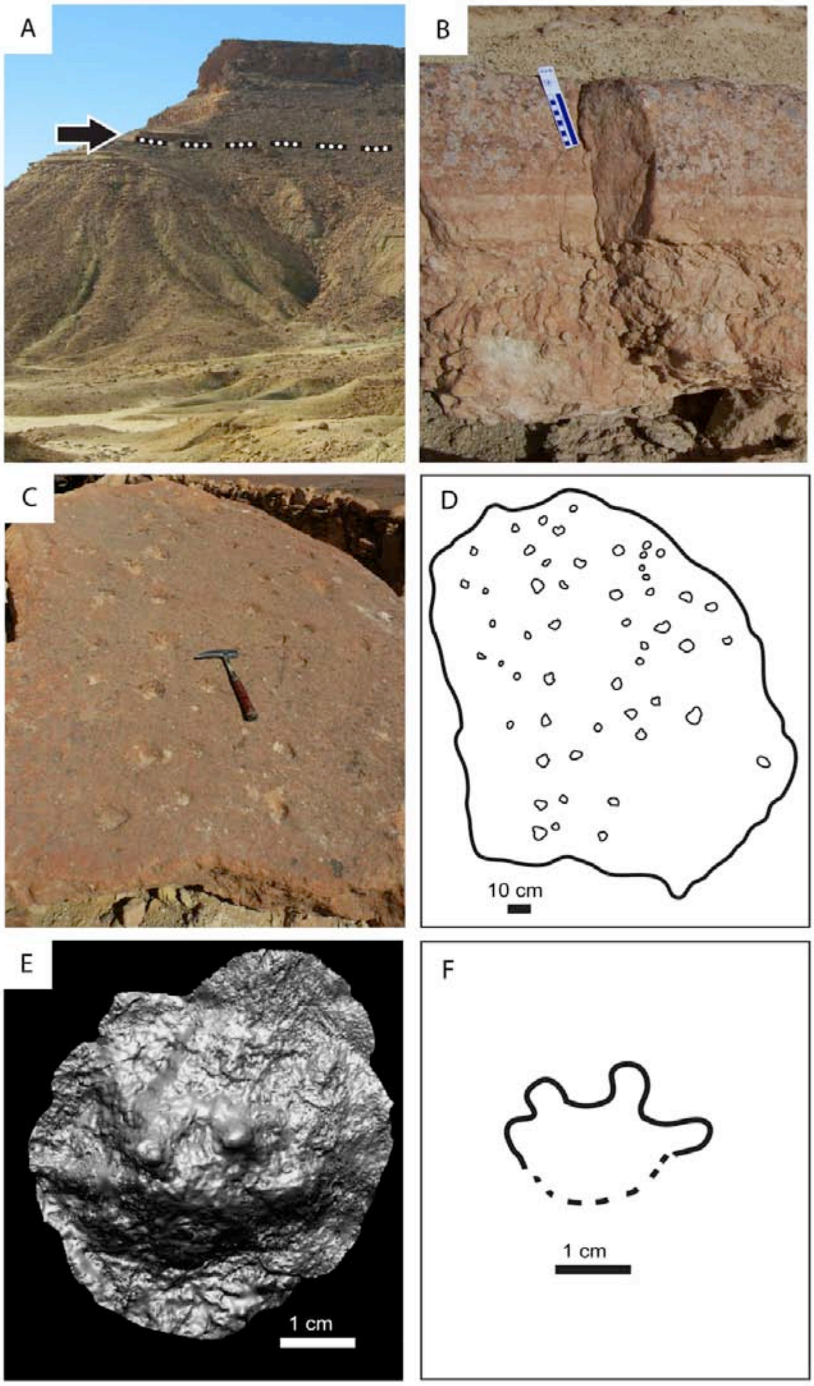


Figure 5 – The Ksar Ayaat site. A) Field picture; arrow and dashed line indicate the track-bearing layer. B) Tracks occur at the top of a finely laminated carbonatic layer which overlies intensively bioturbated deposits. C) Elliptical impressions with rare preserved digit impressions occur on a large micritic mudstone slab. D) Outline drawing of the track-bearing slab. E) 3D model of the silicone mold of the better-preserved track (MGGC 21845). F) Outline drawing of the MGGC 21845.

The latter is characterized by small (L= 1.7 cm) manus impression with four elongated claw marks parallel to the trackway midline, and plantigrade pes impression (L=1 cm) consisting of four digits with parallel claw marks and short, rounded sole (Fuentes et al., 2003). *Emydhipus* differs from *Chelonipus* in having manus impression with evident parallel ungual traces and different position of manus prints in the trackway (Avanzini et al., 2005). Unfortunately, the poor preservation of the Tunisian tracks does not allow any differentiation between these two ichnogenera.

Nevertheless, the combination of a distinctive subcircular shape, claw mark impressions, and possible manus-pes trackway, supports the attribution of the Tunisian tracks to an undetermined pleurodiran turtle.

2.4.4. Jebel Boulouha site

The Jebel Boulouha site is located approximately 12 kilometers to the southwest of Tataouine (Figs. 2, 3). It was originally discovered by a Tunisian student in 2006; later work by the authors revealed nearly 100 isolated dinosaur footprints and two trackways preserved at this site. The *in situ* track-bearing surface is located near the summit of the escarpment, a few meters below the basal deposits of the Gattar Member: therefore, all tracks are preserved in the upper Kerker Member deposits. In addition, a number of tracks have been recovered on isolated blocks located below the *in situ* layer, and referred to the same layer (Fig. 6A). The stratigraphic section of the Jebel Boulouha locality indicates an alternation of light-yellow, finely-laminated marls, biolaminated mudstone, and wackestone. With the exception of layers showing a *lumachella*-fabric (accumulation of shells) and isolated gastropods and bivalves, this stratigraphic unit is barren of fossils.

The track-bearing surface occurs at the top of a 60-cm-thick, fining-upward sequence of wackestone and finely-laminated grainstone capped by a 3-cm-thick stromatolitic lamination. Thin sections of the track surface show shell fragments, extensive dolomitization, birdseye structures and a fenestral fabric, indicative of arid climatic conditions (Petti et al., 2011). As at the Beni Ghedir locality, the track-bearing surface shows a distinctive texture indicative of the presence of ancient microbial mats. Furthermore, invertebrate feeding traces (*Planolites* sp.) are found on the track-bearing surface as well as in the filling sediment of some dinosaur tracks (Fig. 6B). Vertebrate tracks are relatively shallow (<1 cm) given their size, suggesting firm or partially consolidated substrate. Sedimentological data, the occurrence of microbial mats and vertebrate and invertebrate traces are here considered indicative of tidal flat environments.

Track description. The impressions at the Jebel Boulouha locality comprise medium-sized tridactyl and bird-like tracks. The site is dominated (95 %) by well-preserved tridactyl footprints (Fig. 6C, D), few tracks assigned to the *Koreanaornis* ichnogenus (Kim, 1969) are being described separately by the authors (Contessi and Fanti, 2012). The presence of bioturbation on the track-bearing surface and displacement mud rims support the interpretation of the footprints as true tracks (Lockley, 1991). Tracks measure 21.6 cm in length and 14.4 in width (on average), whereas FL/FW ratio is 1.5. Measurements of footprints (Table 2) show little variation, suggesting that tracks are likely to have been made by individuals of similar size. Digit impressions are slender, and pad impressions are commonly preserved; digit III is considerably longer compared to II and IV, that are subequal in length. Occasionally claw marks are preserved. Track density can be up to 7/m^2 and no preferential orientation of the tracks was observed.

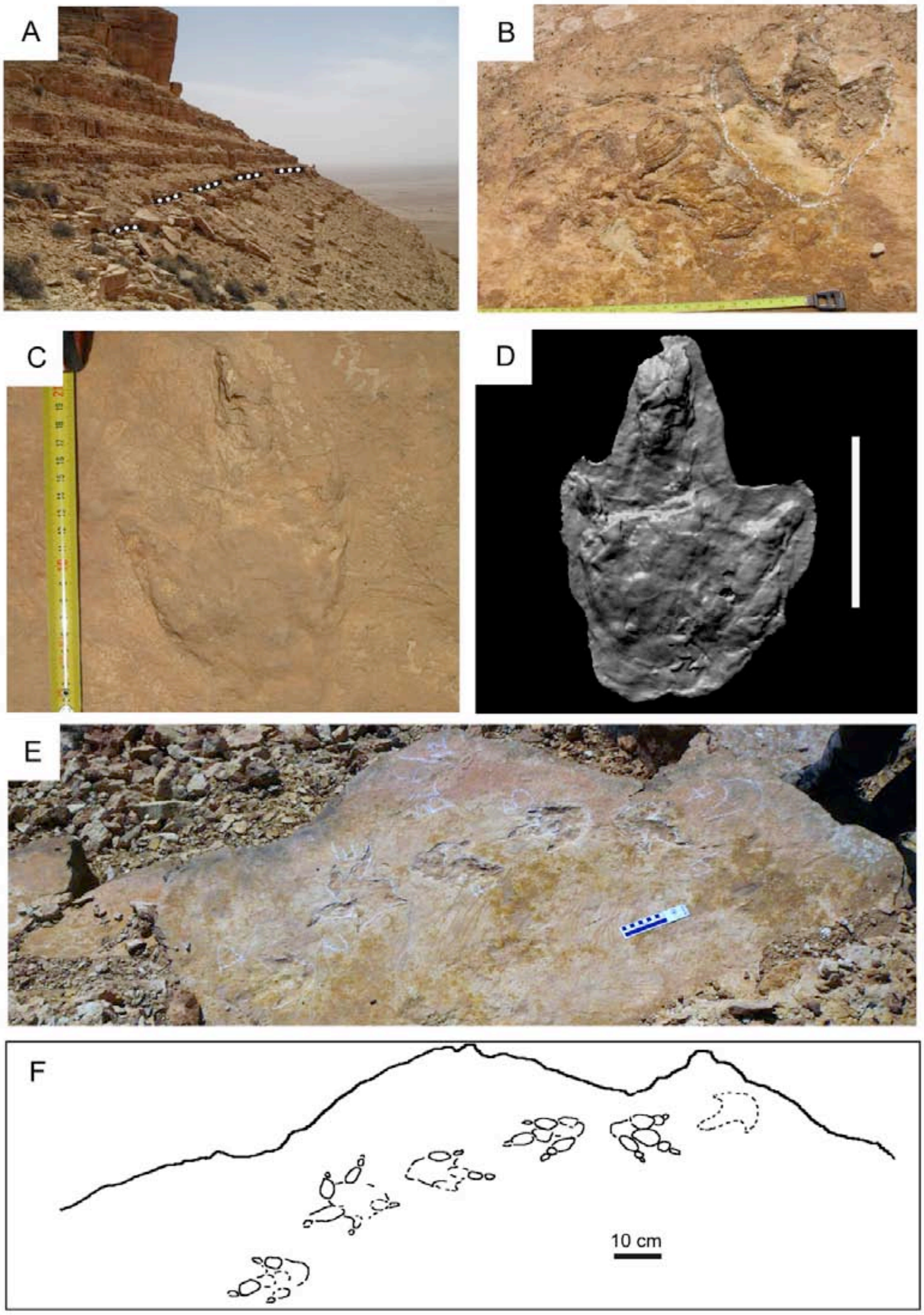


Figure 6 – A) Field picture of the Jebel Boulouha outcrop, dashed line indicates the track bearing-layer. B) Invertebrate feeding traces (*Planolites* sp.) are found on the track-bearing surface. C) Field picture and D) 3D model of the silicone mold of a well-preserved tridactyl footprint referred to a medium-sized theropod (MGGC 21851). E) Field picture and F) Simplified drawing of *in situ* trackways.

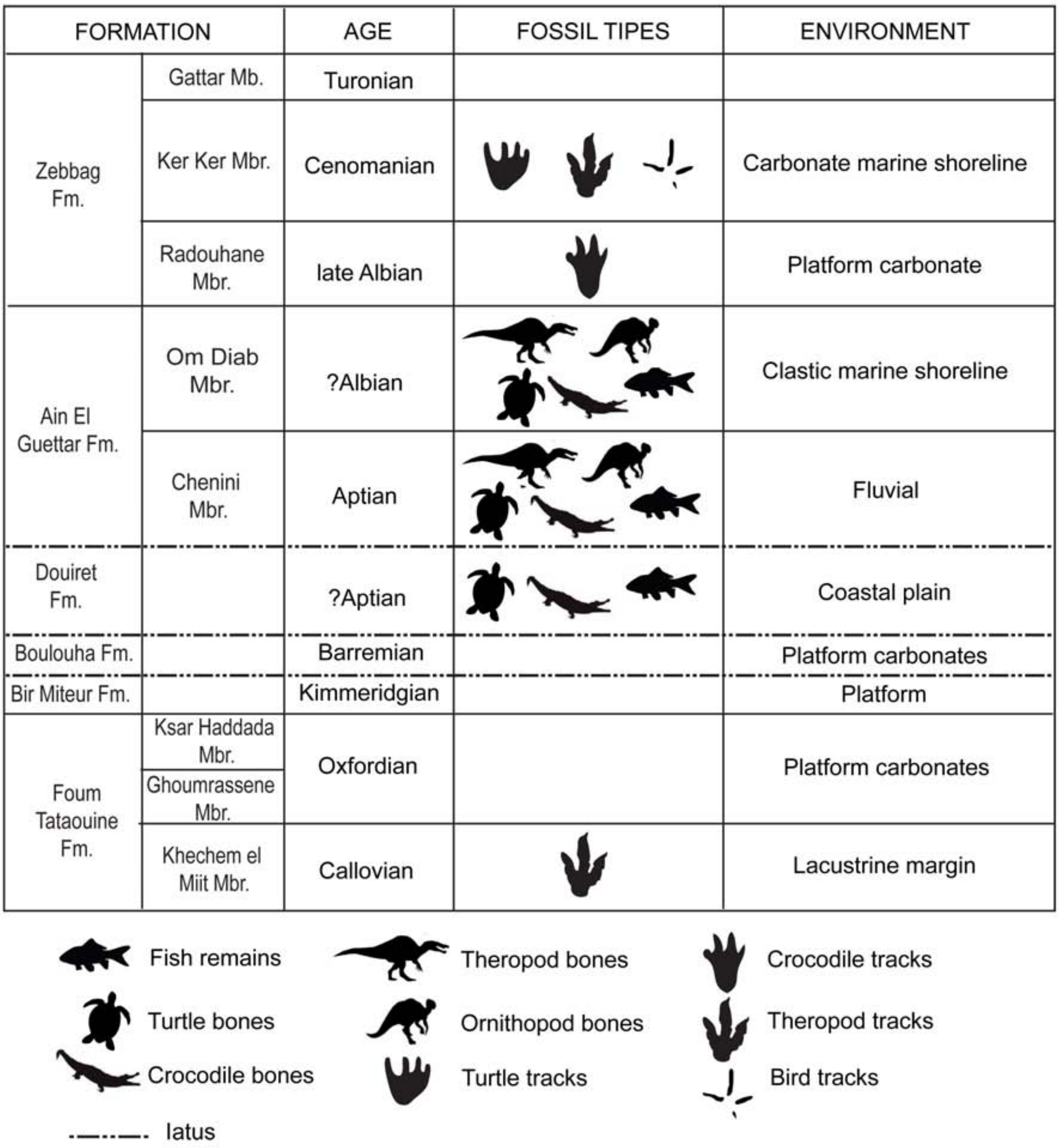
Two trackways, consisting of four and three impressions respectively, were found (Figs. 7E, F): the mean pace length is 40 cm, the stride 81 cm and the pace angulation is 12°. Theropod footprints are commonly differentiated from hadrosaur tracks by their long, narrow toes, that terminate with claw impressions, lower F/W ratio (<1.25) and lower divarication angle between digits II and IV. Cretaceous theropod tracks are well known worldwide, and a number o different ichnotaxa have been named in relation to the regional skeletal record (Sternberg, 1926; Matsukawa et al., 2006). Unfortunately, no theropod remains, which could be compared with the ichnological record, are known from the Upper Cretaceous of Tunisia. Tunisian tracks resemble those of *Grallator* (Hitchcock, 1858) and *Eubrontes* (Olsen, 1980). Originally described from Jurassic deposits, these ichnogenera have been later recognized in the Cretaceous (Li et al., 2011). *Grallator* is smaller (foot length 5-10 cm) more elongate and less mesaxonic, than large *Eubrontes* (foot length 25-40 cm) (Hitchcock, 1845). Several authors have attempted to distinguish these two ichnogenera (Weems, 1992; Olsen et al., 1998; Smith and Farlow, 2003). The most significant aspect differentiating these two *Grallator* and *Eubrontes* are the relative length of digit III in relation to digits II and IV, and the track length as a whole. We refrain from assigning Tunisian tracks to a specific ichnogenus as, although footprints are well-preserved, they all are isolated and just a single and short trackway is preserved. Thus, considering size and morphology, the assignation of tracks here described is limited to a generic mid-sized theropod.

2.5 Discussion

In the last 20 years, an increasing number of publications has dealt with the rich and diverse Lower Cretaceous micro- and macro-vertebrate remains from the Tataouine basin (De Lapparent, 1960; Benton et al., 2000; Ouaja et al., 2004 and references therein). To date, fragmentary elements of bony fish, sharks, turtles, crocodiles, pterosaurs, dinosaurs (sauropods and theropods) as well as gymnosperms and angiosperms have been recovered from tens of localities along the Jeffara escarpment, but no track localities have been reported until now (Fig. 7). In particular, fossil remains are known from the lower Douiret Formation (?Barremian), and the Chenini and Oum Diab members of the Aïn El Guettar Formation (Aptian-Albian) (Taquet, 1980; Ben Ismaïl 1991; Ouaja, 2003; Amiot et al., 2010). Therefore, sites described in this study significantly extend our knowledge of local fossil vertebrate distribution to the Middle Jurassic as well as to the Cenomanian, both considered as times of nearly exclusive marine deposition.

In addition, dinosaur remains have been recovered exclusively from high-energy, fluvial conglomeratic deposits referred to large deltaic river complexes hypothesized to extend over all of southern Tunisia and westernmost Libya (Benton et al., 2000; Bodin et al., 2010; Le Loeuff et al., 2010). Therefore, a number of authors suggested that dinosaur remains primarily originated tens or hundreds of kilometers to the south (Benton et al., 2000; Russell and Paesler, 2003; Ouaja, 2003). Tracks described herein document that theropod dinosaurs and other semi-aquatic vertebrates also inhabited coastal environments such as embayment and lagoon characterized by stromatolitic and carbonate deposition in an arid climate.

If we consider the fossil record of southern Tunisia, a decreasing morphometric trend can be recognized in theropod footprint size from the Middle Jurassic onward. For instance, tridactyl Middle Jurassic tracks at the Beni Ghedir locality range from 23 to 33 cm in length, and are thus referable to mid- to large-sized theropod dinosaurs. Although this is not indicative of a distinct trend, due to the scarcity of information available, these data are consistent with the Middle Jurassic-Lower Cretaceous fossil record, characterized by the remains of *Spinosaurus*, *Carcharodontosaurus*, and abelisaurid theropods collected in Morocco, Libya, Egypt and Niger (Stromer, 1936; De Lapparent, 1960; Taquet, 1960; Russell, 1996; Bodin et al., 2010; Le Loeuff et al., 2010) as well as in the Aïn El Guettar Formation of Tunisia (Lapparent, 1960; Benton et al., 2000; Srarfi et al., 2004). Differently, Upper Cretaceous tracks are significantly smaller in size, ranging from 16.3 to 24.6 cm in length suggesting smaller individuals: however, no vertebrate remains have been reported to date from the Cenomanian of Tunisia.



FORMATION		AGE	FOSSIL TIPES	ENVIRONMENT
Zebbag Fm.	Gattar Mb.	Turonian		
	Ker Ker Mbr.	Cenomanian		Carbonate marine shoreline
	Radouhane Mbr.	late Albian		Platform carbonate
Ain El Guettar Fm.	Om Diab Mbr.	?Albian		Clastic marine shoreline
	Chenini Mbr.	Aptian		Fluvial
Douiret Fm.		?Aptian		Coastal plain
Boulouha Fm.		Barremian		Platform carbonates
Bir Miteur Fm.		Kimmeridgian		Platform
Foum Tataouine Fm.	Ksar Haddada Mbr.	Oxfordian		Platform carbonates
	Ghoumrassene Mbr.			
	Khechem el Miit Mbr.	Callovian		Lacustrine margin

Figure 7 – Synthetic chart showing the succession of the Middle Jurassic – Upper Cretaceous vertebrate assemblages in southern Tunisia within a stratigraphic and environmental framework.

Vertebrate tracks presented here have been identified by distinctive morphological features and paleoenvironmental setting reconstructed by combining sedimentological and ichnological data. Correlating vertebrate ichnological association with specific depositional and environmental setting to establish tetrapod ichnofacies is still largely debated (Lockley et al, 1994; Hunt and Lucas, 2006, 2007; Lockley, 2007; Santi and Nicosia, 2008). Problems in applying ichnofacies to tetrapod ichnology are mainly related to the fact that ichnofacies are independent from temporal frameworks, whereas tetrapod tracks are strictly correlated to faunal evolutions and extinctions. To compensate this issue, Hunt and Lucas (2007) suggest to limit tetrapod associations by temporal, sedimentological and environmental framework, establishing the concept of *tetrapod ichnocoenoses* as ichnoassociations with reduced geographic and temporal extent, related with specific paleoenvironments. Applying the tetrapod ichnocoenosis concept to the Tunisian track record the Beni Ghedir site can be referred to the *Eubrontes* ichnocoenosis, dominated by medium to large theropod tracks, typical of lacustrine Jurassic deposits (Lockley et al., 1994). In contrast, the Ksar Ayaat tracks, characterized by turtle tracks in carbonate-dominated shorelines deposits, are representative of the *Chelonichium* ichnocoenosis (Lockley et al., 1998). Lastly, the Jebel Boulouha site is ascribed to the *Jindornipes-Koreanaornis* ichnocoenosis (Lockley et al., 1994) as it is dominated by theropods with the co-occurrence of shorebird tracks in an arid environment.

2.6 Conclusions

Pending further discoveries in the Jurassic and Cretaceous deposits of the Tataouine Basin, data presented in this study extend significantly the presence of dinosaurs and other vertebrates in southern Tunisia. In particular, theropod tracks from Middle Jurassic (Callovian) beds represent the oldest occurrence of dinosaurs in Tunisia. On the other hand, Cretaceous (upper Albian and Cenomanian) tracksites provide evidence of a diverse vertebrate fauna, which included turtles, crocodiles, theropod dinosaurs and birds.

Data presented in this study support a strict relationship between tracks and depositional environments; as such, the concept of tetrapod ichnocoenoses (Hunt and Lucas, 2007) was applied to the Tunisian track record, resulting in diversified track assemblages that be ascribed to the *Eubrontes*, *Chelonichium* and *Jindornipes-Koreanaornis* ichnocoenosis.

These discoveries shed new light on the still controversial analysis of vertebrate distribution in Tunisia during a time that is crucial for dinosaur diversification across northern Africa.

Table 1 – Parameters of footprints from Beni Ghedir site: FL, FW, FL/FW, L II, L III, L IV, α II-III, α III-IV and α II-IV, in centimeters and degrees.

Specimen	FL	FW	FL/FW	L II	L III	L IV	α II-III	α III-IV	α II-IV
BG 1A	25	20.5	1.22	19.7	25	17.7	27	32	58
BG 1B	26	18.5	1.41	19.5	26	18	20	38	58
BG 2	31	25	1.24	20	31	-	20	24	45
BG 3	30	17.5	1.71	21.2	30	21	22	25	49
BG 4	34.5	12.3	2.8	26	32	23	21	27	59
BG 5	33	21	1.57	23	33	25.5	25	30	55
BG 7	31	26	1.19						
BG 8A	30	16	1.88						
BG 9B	28	18	1.56						
BG13A	28	20	1.4	19	28	20	23	31	54
BG 15C	-	24		17.2	24	-			
BG 20A	26	18	1.44	21	26	23.5	20	22	42
BG 22A	30	22	1.36						
BG 22B	28.5	18.5	1.54						
BG 28A	28	18	1.56						
BG 37A	23	19	1.21	21	23	19	18	28	46
BG 60B	31	25	1.24	22	31	24			
BG 61A	32	18	1.78						
BG 63A	25	21	1.19						
BG 78A	23	18	1.28	14.5	23	18.5	23	28	51
BG 78B	25.5	17.5	1.46	19	25.5	16			
BG 81A	28.5	18	1.58	18.5	28.5	18	25	33	58
BG 83B	28	19	1.47						
BG 90A	30	24	1.25	21	30	24.5	19	31	50
BG 94A	30	23	1.3	22	30	23	21	24	45
BG 97B	25.5	16	1.59	15.5	25.5	14.5	24	28	52
BG 104A	31	18.5	1.68	19.5	31	17	19	24	43
BG 108A	28	16.6	1.69	27	28	21.5	16	22	38
BG 110B	33	22.5	1.47	30	33	26	18	20	38
BG 112A	31	25	1.24						
BG 113A	31	24	1.29						
BG 114B	28	20	1.4	21	28	17.5	24	27	51
BG 115A	25	21	1.19						
BG 117A	29	21.5	1.35	24	29	20	22	28	50
BG 118B	32	20	1.6	24	32	18.5	22	26	48
BG 122B	32	22	1.45	23	32	21	25	28	53
BG 123B	31	20	1.55	23	31	20.5	23	29	52
BG 124A	32	30	1.07						
BG 126	29.5	19	1.55						
Mean	29	20.4	1.5	21.3	28.6	20.4	22	28	50

Table 2 – Parameters of footprints from Jebel Boulouha site: FL, FW, FL/FW, L II, L III, L IV, α II-III, α III-IV and α II-IV, in centimeters and degrees.

Specimen	FL	FW	FL/FW	L II	L III	L IV	α II-III	α III-IV	α II-IV
BL 1A	23.3	13.5	1.73	15.6	23.5	15.5	20	25	45
BL 1B	23	15.5	1.48	16.5	26	26.6	19	23	42
BL 1C	19	14.5	1.31		19	14.3			
BL 2	15	16	0.94	14.2	22.8	16	26	33	59
BL 3A	23	14.2	1.62	15.3	23	16	24	31	55
BL 3B	22								
BL 5A	22	13.5	1.63	16.2	22	17.2	28	32	60
BL 5B	18.3								
BL7A					11				
BL 7B	17.6			15.2	17.6		33		
BL 8A	22.5	15	1.5	19	22.5	19.3		24	
BL 8B	22.3	15.2	1.47	20.4	22.3				
BL 9A	16.6	14.4	1.15	11	16.6	12.3	26	36	62
BL 11A						17.1			
BL 12A	18.3	13.2	1.39	9	18.3	9.2	28	32	59
BL 12B	19.7	13.5	1.46	14.1	17.7	15	26	31	57
BL 12C	22				22	15.3		35	
BL 12D	19.2	13.4	1.43	13.2	19.2	13	30	35	65
BL 12E	12.2				16.2	11		33	
BL 12F	21.6	13	1.66	11	21.6	14.8		32	
BL 12G	20.2	16.6	1.22	13.8	20.2	15.2	30	38	68
BL 13A	16.3	14	1.16	19	16.3	18.7	22	23	45
BL 13B	19.8	17	1.16	11.8	18.8				
BL 13D	22.2	13	1.71	11	22.2	12		20	
BL 14A				11.8			33		
BL 15		12.5					30	34	64
BL 16A	23	13.4	1.72	13.5	23	14	23	27	50
BL 16B	23.6	15.4	1.53	19.7	24	30	24	30	54
BL 16C	24.2	17	1.42	22	24.2	19	23	28	51
BL 17	24				24	19			
BL 18A	23.5	14.4	1.63	19	23.5	18	23	27	50
BL 18B		14		18		18	22	29	51
BL 18C	24	15	1.59	15	24	16	28	28	56
BL 18D		14		16.2	16.3				50
BL 18E	24.5			16.8	24.5				
BL 18F	22.5	16	1.41	15.5	19.2	13.4	28	37	65
BL 18H	21			13.2					
BL 18I	23.4	13	1.8		16	16.7	19	25	44
BL 19A	24	13.8	1.74	16.8	24	17.2		26	
BL 19B	21.5				21.5	16.5		26	
BL 19C	23.5	15	1.57	19.8	32.5	18.6	17	21	38
BL 20A	23.2	13.5	1.72	15.1	23.2	16.7	21	28	49
BL 20B	17.2					12			
BL 21A	29	15.5	1.87	20	29	20.2	18	24	42
BL 21B	21.3	12.5	1.7	13.5	21.3	13.2	23	26	49
BL 22A	21.8	13.7	1.59	12.2	21.8	15	25	33	58
BL 22B	16.3			11.8	16.3		23		
BL 23A	22.7	17.6	1.29	13.7	22.7	19.4	25	34	59

BL 24A	23.7	16.2	1.46	20.2	23.7	21.2	25	27	52
BL 24D	21				21	18		28	
BL 24E	23				23	15.5		27	
BL 25A	21.4	17.2	1.24	16.5	21.4	18.5	26	29	55
BL 25B	22.5	13.5	1.67	17.5	22.5	16.7	22	24	46
BL 25C	21.7	13.2	1.64	12.8	21.7	16.6	18	29	47
BL 26A	24.5			19.2	24.5	15			
BL 26B	22	12.9	1.71	18	22	15.1	25	25	50
BL 27	23.8	15	1.59	16.7	23.8	20.2	20	23	43
BL 28A	24.6	15.6	1.58	18	24.6	18.4	23	28	51
BL 28B	23	14.6	1.58	18.2	23	16.2			
BL29									
BL 30A	22.1	14.5	1.52	15.2	22.1	16.8	22	28	50
BL 30B	22.7	14	1.62	16.8	22.7	17.7	22	24	46
BL 31A	22.2	13	1.71	14.9	22.2	13.2	26	27	53
BL 31B	25					20			
BL 33A	20.5	11.2	1.83	13	20.5	13.2	22	28	50
BL 33B	21.5	12	1.79	11.5	21.5	13.2		35	55
Mean	21.6	14.4	1.5	15.6	21.6	16.5	24	29	52

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CHAPTER 3 – First record of bird tracks in the late Cretaceous (Cenomanian) of Tunisia

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ABSTRACT

The discovery of fossil bird tracks from the Cenomanian Kerker Member (Zebbag Formation) in southern Tunisia represents the oldest report of fossil birds from the Cretaceous of continental Africa. Three small bird tracks were discovered in a track-bearing surface dominated by tridactyl dinosaur footprints and are attributed to the ichnogenus *Koreanaornis*. This represents the first occurrence of this ichnogenus in Africa and indicates a worldwide distribution of these shorebirds-like tracks that were previously known only from Asia and North America. Tracks described in this study are also smaller than any other fossil bird track known to date, thus they can be included in the minute class size following modern bird tracks groups. A comparison with present day shorebirds tracks indicate strong similarities in size, morphology, and environment with extant members of the *Actitis* genus, commonly known as sandpipers, which inhabit arid central African tidal flats. The occurrence of bird tracks in the early-Late Cretaceous of Tunisia also brings new important insight in the paleoecology of an area previously thought to be a site of exclusively marine deposition.

3.1 Introduction

Lower and Upper Cretaceous beds crop out extensively over a vast section of northern Africa, from Morocco to Egypt and southward to Niger and Sudan. These exposures have been the subject of a number of studies since the beginning of the 20th century (Pervinquière, 1912) and were named *Continental Intercalaire* by Kilian (1931) due to repeating alternation of continental and coastal or shallow marine deposits. In southern Tunisia several international expeditions (De Lapparent, 1951, 1960; Tabaste, 1963; Taquet, 1980; Bouaziz et al., 1988; Ben Ismaïl, 1991; Benton et al., 2000; Barale and Ouaja, 2001; Buffetaut and Ouaja, 2002; Ouaja, 2003; Russell and Paesler, 2003; Cuny et al., 2004; Ouaja et al., 2004; Anderson et al., 2007; Amiot et al., 2010; Cuny et al., 2010) have focused primarily on dinosaur and other macro- and microvertebrate remains from a fossil-rich conglomerate known as the Chenini sandstone (Bouaziz et al., 1988; Ben Ismaïl, 1991; Benton et al., 2000). In the last few decades, however, more comprehensive studies of the Tunisian outcrops have yielded evidences of a diverse late Lower Cretaceous ecosystem composed of bony fish, sharks, turtles, crocodiles, pterosaurs, sauropods and theropods, gymnosperms and angiosperms (de Lapparent, 1960; Benton et al., 2000; Ouaja et al., 2004). Such discoveries consist exclusively of fragmentary elements and no vertebrate tracks have been reported until now.

In this study we describe the first bird tracks recovered in the Cenomanian beds of the *Continental Intercalaire* of the Tataouine region in southern Tunisia (Fig. 1). Despite the increasing number of discoveries of Cretaceous bird tracks, especially in East Asia (Lockley, et al., 1992, 2006a, 2006b, 2007; Yang et al., 1995; Li et al., 2005; Kim et al., 2006; Zhang et al., 2006; Anfinson et al., 2009) and North America (Mehl, 1931; Currie, 1981; Robinson, 1991; McCrea and Sarjeant, 2001; Lockley et al., 2001, 2004; Fiorillo et al., 2011), they remain extremely rare in Africa. The oldest bird tracks from the continent were reported in the Lower Jurassic of South

Africa by Ellenberger (1972) and given the name *Trisauropodiscus*, though there is still some question over their avian affinity because of the age of the units in which the tracks are found. For instance, their North American counterpart, *T. moabensis*, as it displays morphological features closer to theropod tracks, was referred to the theropod ichnogenus *Anomoepus* (Lockley and Gierlinski, 2006). More recently, Belvedere et al. (2011) reinterpreted some Jurassic tridactyl tracks from Morocco thought to have avian affinity as likely dinosaurian (*Anomoepus*-like). To date the sole bird tracks from the Cretaceous of Africa were reported by Ambroggi and De Lapparent (1954) in the Maastrichtian of Morocco, however, no exhaustive description of such traces is provided and the photographic material in the paper (Ambroggi and De Lapparent, 1954, Plate III, figs. 1, 2) is poor. Tracks described in this paper represent the first evidence of fossil bird tracks from Tunisia and increase our knowledge of vertebrate biodiversity of the *Continental Intercalaire*.

3.2 Study area and geological setting

The *Continetal Intercalaire* strata that crop out in the Tataouine basin are Berriasian to Cenomanian in age and consist of interbedded shallow-marine and continental deposits, with thin evaporitic beds (Fig. 1). This thick sedimentary succession has been divided into five formations (Burollet, 1956; Ben Youssef et al., 1985; Peybernès et al., 1985, 1996; M'Rabet, 1987; Bouaziz et al., 1988, 1989; Ben Ismaïl, 1991; Chandoul et al., 1993; Zarbout et al., 1994; Barale and Ouaja, 2002; Bodin et al., 2010), listed here in ascending stratigraphic order: the Bir Miteur, Boulouha, and Douiret formations of the Merbah el Asfer Group (Berriasian-Aptian), the Aïn El Guettar Formation (Aptian-Albian; Chenini and Oum ed Diab members) and the Zebbag Formation (Cenomanian-Turonian) containing the Rhadouane, Kerker, and Gattar members (Fig. 1C). In 2004 a Tunisian college student discovered a number of tridactyl footprints in a remote outcrop of the Kerker Member of the Zebbag Formation. The locality, known as Jebel Boulouha, is near the village of Chenini in the Tataouine region of southern Tunisia (Fig. 2).

At the track locality only the upper formations on the *Continental Intercalaire* crop out (Fig. 2). Relevant to this study, the carbonate-dominated Zebbag Formation represents consecutive stages of a basin-scale transgressive event that affected the Tataouine Basin during the Cenomanian and all of north Africa up to present day Niger in the Turonian (Lefranc and Guiraud, 1990; Moody and Sutcliffe, 1991; Russell and Paesler, 2003). The basal Radaouhane Member consists of interbedded siliciclastic and carbonate deposit; the contact with the overlying Kerker Member is not well defined (Bodin et al., 2010) and is placed within a transitional interval from limestone- to marl-dominated sequences. Sediments in the Kerker Member form an 80 meters thick sequence of alternating marls, carbonates and primary gypsum deposited in shallow-marine to coastal-evaporitic environments, similar to present day sabkhas (Bodin et al., 2010). Finally, the Gattar Member consists of a 50 to 70 m-thick carbonate sequence that also marks the top of the Dahar plateau. The Kerker Member has been dated as Cenomanian in the northern part of the Tataouine basin based on the occurrence of the ammonite *Neolobites medeninensis* (Busson, 1967), however, the J. Boulouha locality lacks this biostratigraphic marker. Fossils recovered at Jebel Boulouha include poorly preserved bivalves and gastropods (i.e. *Lumachella*), which likely accumulated in a proximal, shallow lagoon environment (Bodin et al., 2010). No vertebrate skeletal remains have been recovered from the Kerker Member to date. Fish scales and teeth, disarticulated turtle carapaces, and crocodile teeth, however, have been reported from the underlying Douiret Formation (Fig. 2D; Ouaja, 2003).

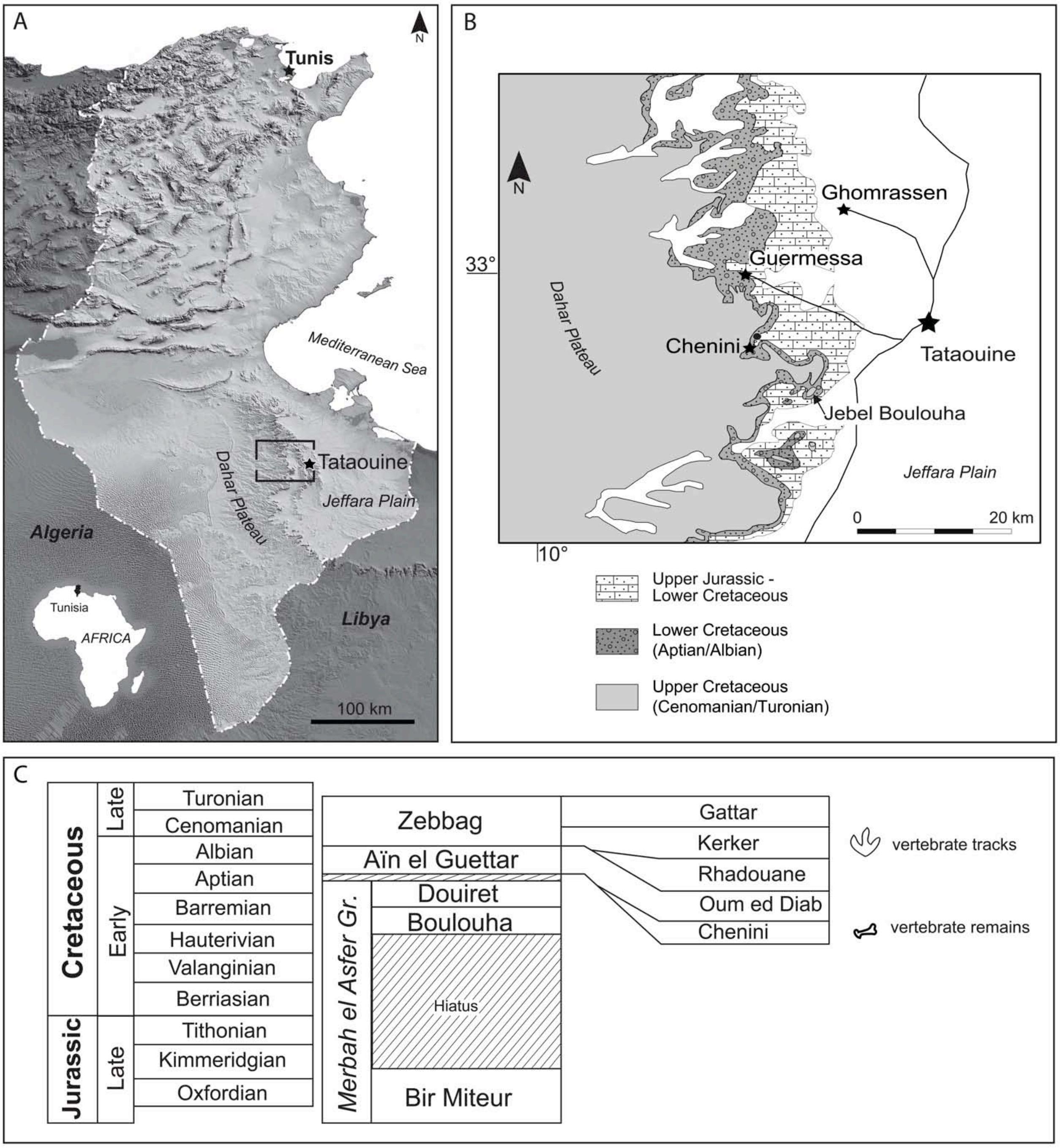

Figure 1 — Locality map. A) Map of Tunisia showing the study area in the Tataouine region. B) Location of the Jebel Boulouha site and distribution of the *Continental Intercalaire* outcrops. C) Stratigraphic subdivision of the middle Cretaceous deposits in the study area (modified after Bodin et al., 2010).

In 2010 and 2011 our field party from the University of Bologna, with the support of the Office Nationales des Mines (Tunis), engaged an intense survey at the locality and discovered more than 90 footprints on a laterally persistent layer of finely laminated limestone, 10 m below the Kerker-Gattar contact (Figs. 2, 3A). The track-bearing horizon is dominated by medium-sized (<30 cm long) tridactyl footprints (Fig. 3B), currently under study by us, that most likely can be ascribed to theropod dinosaurs. Small bird tracks described here were noticed on an exposed section of the same layer.

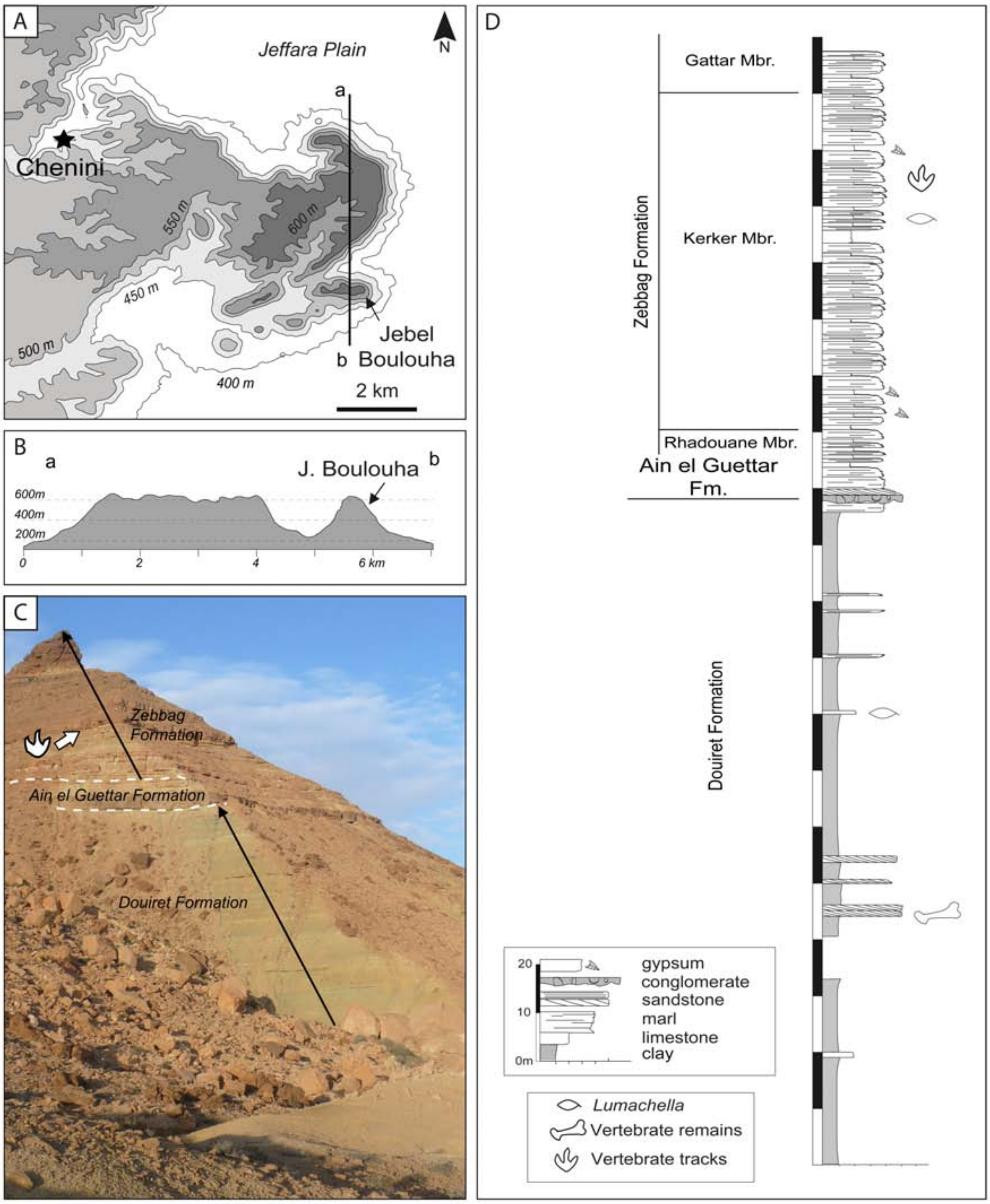

Figure 2 — Geologic and stratigraphic settings. A) Detailed topographic map showing the Jebel Boulouha locality. B) Topographic profile at the track locality. C) Jebel Boulouha outcrop; arrow indicates the track-bearing layer. D) Stratigraphic log of the Jebel Boulouha locality.

3.2.1 Sedimentology and facies analysis of the track-bearing layer

The track-bearing surface is located at the top of a 60 cm thick, fining-upward sequence consisting of moderately bioturbated wackestone (10 cm thick), which grades into a 50-cm thick, finely laminated grainstone (Fig. 3). The footprint surface consists of 3 cm of stromatolitic laminations (Fig. 3A). Thin sections of the finely laminated track surface show late dolomitization and a typical laminoid fenestral fabric (Fig. 3D). Early dolomitization has been observed in arid tidal-flat environments and claimed as one of the major processes of footprint preservation for such environment (Marty et al., 2009). The laminoid fenestral fabric texture is usually associated with drying out of intertidal cyanobacterial mats (Flügel, 2010; Petti et al., 2011) that, at the time of deposition, may have facilitated the preservation of the tracks by initiating the precipitation of calcium carbonate and stabilizing the tracks, preventing their reworking by wind or water-driven currents (Kvale et al., 2001; Marty et al., 2009; Petti et al., 2011). Finally, the trampled surface also exhibits wrinkle structures supporting the presence of an ancient microbial mat (Noffke, 2010), as well as invertebrate trace fossils. Similar shallowing-upward cycles have been documented in other intervals of the Kerker Member and are here interpreted as multiple transitions from subtidal to inter- and supratidal deposits that occasionally experienced periods of subaerial exposure.

3.3 Methods

Field data presented in this study were collected between February 2010 and March 2011. Rock samples from the track-bearing layer were collected and thin-sectioned in order to observe fine-scale sedimentological features. Thin sections were made normally to the bedding plane. The *in situ* trampled surface was photographed and molds of selected footprints were made using a silicon-molding compound (SILICAL 110). Relevant to this study, two molds were made: one of the best-preserved footprint and one of the best-preserved surface (37x18 cm) of the track-bearing bed. Molds were later used to measure track parameters and produce a 3D digital model of the surface for a more objective interpretation. Fiberglass replicas of the molds were also made and deposited at the Museo Geologico Giovanni Capellini in Bologna, Italy, and catalogued under the accession numbers MGGC 21849A-C. Measurements on molds were taken using calipers with a resolution of 0.01 mm.

Standard digit track parameters measured from the molds include: footprint length, footprint width, digit length for digit I, II, III and IV (*sensu* Leonardi, 1987), and interdigital angles (angle of divarication) between the imprints of the digit II–III, III–IV and II–IV (*sensu* Falk et al. 2011; Table 1). In order to determine ichnotaxonomic affinities, the Tunisian tracks were compared with Cretaceous bird tracks reported from Asia (Kim, 1969; Lockley et al., 1992; Azuma et al., 2002; Lockley et al., 2006a, 2006b; Zhang et al., 2006; Falk et al., 2010; Lockley et al., 2012), North America (Mehl, 1931; Currie, 1981; Lockley et al., 1992; Anfinson et al., 2009; Lockley et al. 2009; Lockley and Harris, 2010) and South America (Coria et al., 2002).

Data used to generate 3D (three dimensional) models were acquired with a laser scanner (Zsnapper *portable*, ViALUX®) with a 0.2 mm resolution and accuracy of 40 µm. The scanning, image data processing and manipulation were done at the Visualization Laboratory at the Huffington Earth Sciences Department of Southern Methodist University in Dallas (Texas, USA) using Rapidform® (alignment of the scans) and Surfer® (for contour-line and depth-color image analysis).

Abbreviations: FL (footprint length), FW (footprint width), FL/FW (width ratio).
Institutional abbreviations: MGGC, Museo Geologico Giovanni Capellini, Bologna, Italy.

3.4 Ichnological description

Class: Aves
Ichnofamily: Koreanornipodidae (Lockley et al., 2006a)
Ichnogenus: *Koreanaornis* (Kim, 1969)

Material: two superimposed footprints (epirelief) and one isolated footprint preserved on a stromatolitic surface. Specimen MGGC 21849A is the best preserved showing clear detail and pad impression, and is therefore used here for the formal description (Figs. 4–5).

Horizon and locality: Upper Cretaceous (Cenomanian) Kerker Member, Zebbag Formation; Tataouine region, Tunisia, Jebel Boulouha locality (Figs. 1–2).

Description: small asymmetrical anisodactyl footprints with reduced hallux impression and digit impressions continuous with the impression of the most distal part of the metatarsus. The footprint is 13.5 mm wide (measure between distal ends of digits II and IV), total footprint length is 14.3 mm (16 mm including hallux). Digit impressions are slender, with no claw marks. Digit lengths are: 6.2, 12.5 and 7.5 mm for digit II, III and IV respectively. The hallux impression is short, directed medial-posteriorly and measures only 3.3 mm long. Digits II, III and IV point anteriorly, exhibiting mesaxonic asymmetry. Divarication angle between II and III is larger (68°) than III–IV (40°). Divarication between digits II and IV is 108°. No evidence of webbed toes is preserved. Digital pads impressions are recognizable in digit III and IV respectively; whereas no pads are preserved in digit I and II.

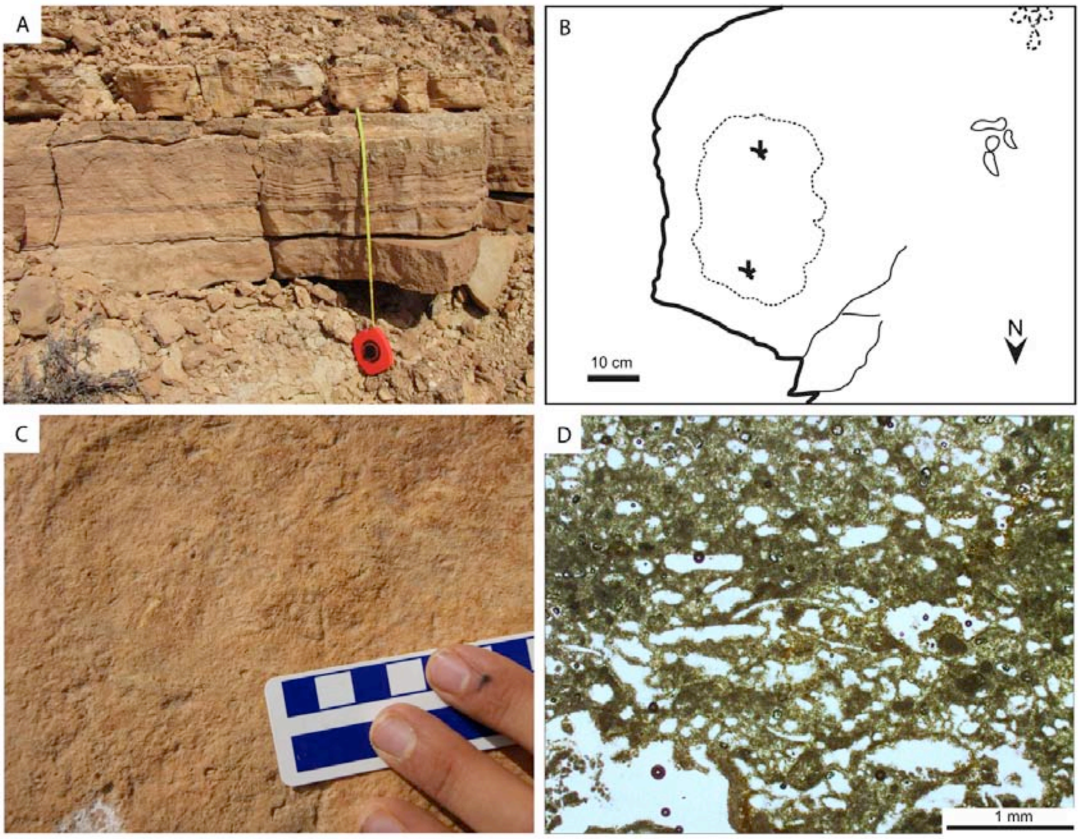

Figure 3 — *In situ* track-bearing surface. A) Track-bearing layer showing the stromatolitic laminations. B) Drawing of the track-bearing surface indicating the position of the mold of figure 4 and two theropod tracks occurring in the same slab. C) Trampled surface with small bird track. Scale in cm. D) Thin sections of the trampled layer showing laminoid fenestral fabric.

The two additional footprints are preserved on the same horizon and show features and size comparable to the one described above (see Table 1 for measurements), although they their preservation is worse. MGGC 21849B presents only the impressions of digits I, II and the first portion of digit III because the track is partially overstepped by MGGC 21849A (Figs. 4B, 5).

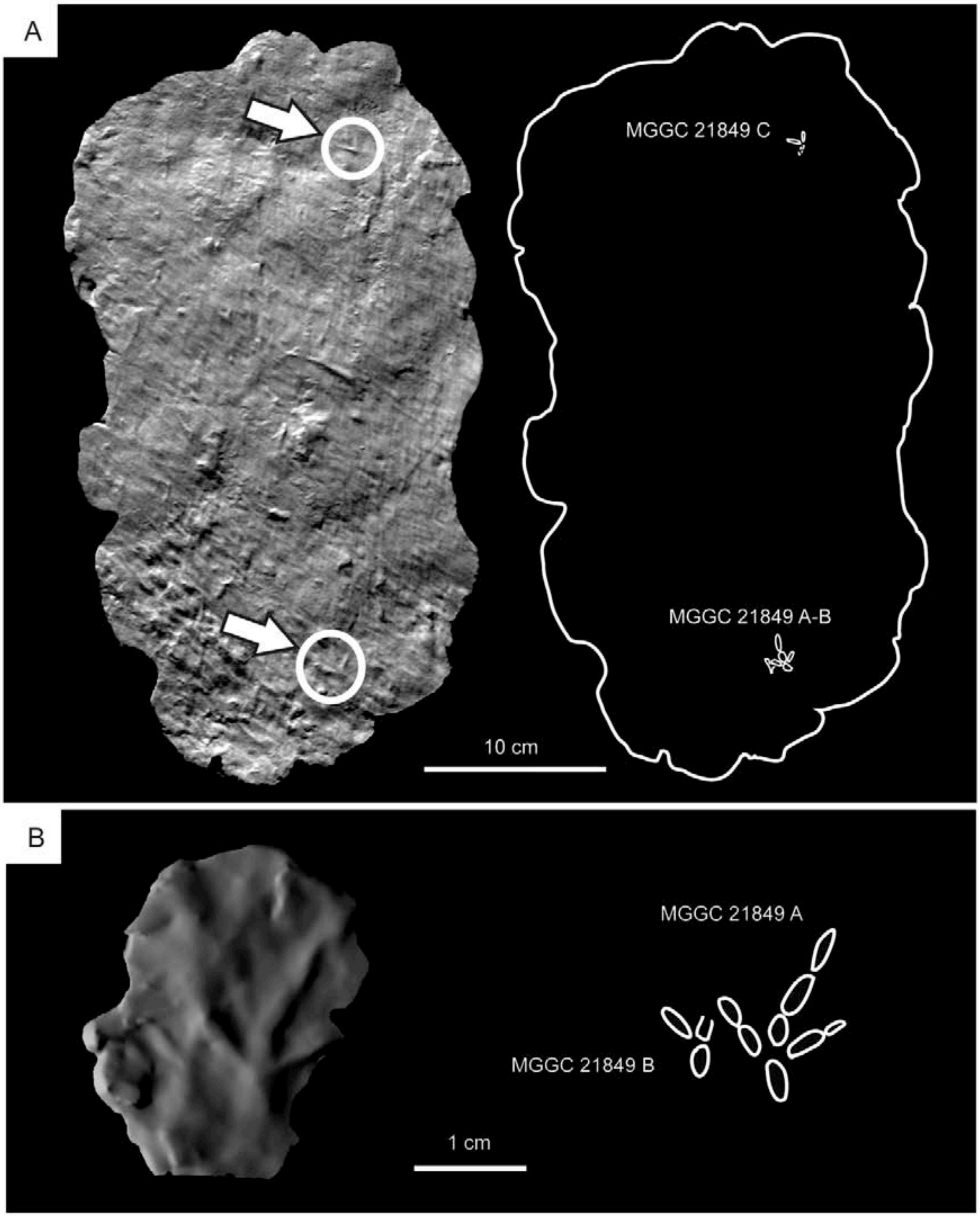

Figure 4 — Three dimensional (3D) models from molds. A) 3D model and simplified drawing of the molded area of the tracks-bearing surface (MGGC 21849). B) 3D model and detailed outline drawing of the best-preserved tracks (MGGC 21849 A-B).

3.5 Discussion

Fundamental criteria for the identification of fossil bird footprints are: (1) similarity to modern bird tracks; (2) small size; (3) slender digit impressions with indistinct differentiation of pad impressions; (4) wide divarication angle (110°–120° or more) between digits II and IV; (5) a posteriorly directed hallux impression; (6) slender claw; (7) distal curvature of outer (II and IV) claws away from central axis of foot and (8) track density (Lockley et al., 1992). McCrea and Sarjeant (2001) also used the foot length:width ratio (FL/FW) in order to distinguish bird from dinosaur tracks. FL/FW ratio in bird tracks is generally less than 1.0, much lower than theropod tracks. More recently De Valais and Melchor (2008) reviewed characters for the identification of bird tracks in the fossil record, emphasizing the character of slender digit impressions and the similarity with modern bird tracks. On the other hand, Falk et al., (2011) pointed out that the majority of these criteria were subjective, and only the divarication angle between toes II and IV has proved to be useful.

The tracks here described are characterized by: (1) significant similarity to modern shorebird tracks; (2) small size; (3) slender digit impressions with preserved pad impressions; (4) wide divarication angle (108°) between digit II and IV; (5) posteriorly directed hallux impression, and (6) FL/FW ratio of 1.06. The first five features of the tracks described here are in accordance with criteria (1)-(5) proposed by Lockley et al. (1992), although pad impression are usually not present in fossil bird tracks they have sometimes been reported (Lockley et al., 2006; Anfinson et al., 2009). The FL/FW ratio of 1.06 is larger than the average for bird tracks. The discrepancy, however, may be a reflection of the preservation, the type of medium or the behavior of the trackmaker (Elbroch and Marks, 2001). According to Falk et al. (2011) the divarication angle of digits II-IV is 108°, whereas the same angle in theropod dinosaur is always < 100°. Therefore, based on the discussed criteria and the strong similarity with modern bird tracks, we conclude that the Tunisian tracks are bird tracks.

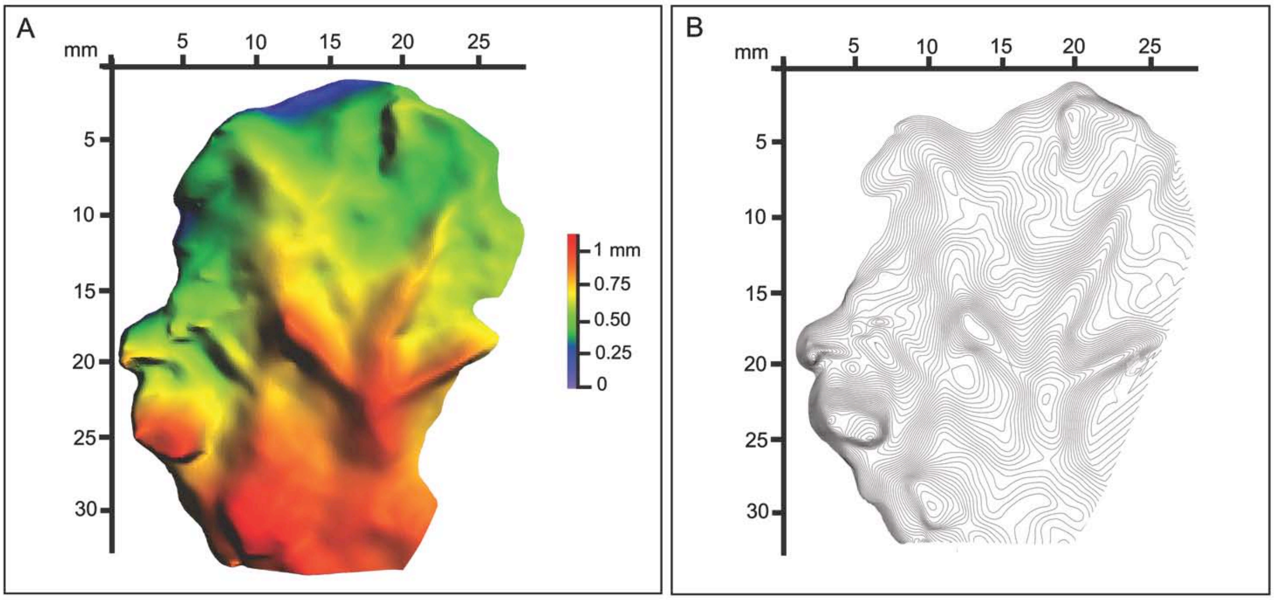

Figure 5 — 3D model of MGGC 21849 A-B produced from dense points cloud data acquired from the mold with ViaLUX scanner with a resolution of 0.2 mm. A) Color-coded surface. B) Contour lines of MGGC 21849 A-B; lines equidistance: 0.05 mm.

The possibility of comparing Mesozoic with younger Cenozoic bird track is still a controversial subject, as the Mesozoic fossil bird record is still far from complete and Mesozoic ichnotaxa are few compared to Cenozoic ones (Lockley and Harris, 2010). Considering the reduced dataset presented in this study, we consider more conservative a comparison restricted to Mesozoic taxa. Mesozoic bird ichnogenera are characterized by distinctive characters, such as webbed footprints in *Goseongornipes, Ignotornis, Hwangsanipes, Sarjeantipodus* and *Uhangrichnus,* (Mehl, 1931; Yang et al., 1995; Lockley et al., 2004; Lockley et al., 2006a;); absence of hallux impressions in *Aquatilavipes, Archeornithipus, Barrosopus, Yacoraitichnus* and *Tatarornipes* (Currie, 1981; Alonso and Marquillas, 1986; Fuente Vidarte, 1996; Coria et al., 2002; Falk et al., 2010; Fiorillo et al., 2011; Lockley et al., 2011); and zygodactyl morphology in *Shandongornipes* (Li et al., 2005). Considering the differences in morphology with the Tunisian specimens, we exclude these taxa from a comparison. On the contrary, ichnogenera that display morphologic similarities with the Tunisian tracks include *Gruipeda, Koreanaornis, Jindongornipes* and *Pullornipes* (Kim, 1969; Lockley et al., 1992; Lockley et al., 2006b; De Valais and Melchor, 2008), sharing an anisodactyl shape, unwebbed tracks and the presence of hallux impressions. *Gruipeda* is usually regarded as a Cenozoic taxon, but recently De Valais and Melchor (2008), assigned Early Jurassic tracks to this genus. *Gruipeda* and *Pullornipes* are nearly symmetric tracks, characterized by wide divarication angles (both 115° in average), and the absence of digital pads (Lockley et al., 2006b; De Valais and Melchor, 2008). For these reasons we exclude further taxonomic comparison with the Tunisian tracks. *Jindongornipes* tracks show a marked asymmetry and pad impression, but hallux impression is more prominent that in the Tunisian tracks and it presents wider divarication angles, ranging from 125° to 150° (Lockley et al., 1992). Tracks described here share more characters with the genus *Koreanaornis*. The most important criteria that define *Koreanaornis* are: small size, (average tracks are 30 mm long and 35 wide), wider divarication angle between digit II–III, compared to III–IV and presence of digital pads, metatarsal and hallux impression are not frequent in *Koreanaornis* although hallux impression has sometimes been reported (Lockley et al., 1992; Falk et al., 2010). In Lockley et al. (2006a) the Koreanornipodidae ichnofamily is described as characterized by small subsymmetric tracks (2.5–3 cm), slender digit impression, divarication angle ranging from 90° to 115°, occasionally small hallux posteromedially directed and digital pad impressions. The Tunisian tracks are similar in general morphology to *Koreanaornis hamanensis* (Kim, 1969), even if some differences occur; in addition, they show hallux impression connected to the metatarsal pad and continuous with others digit impressions together with digital pad impressions. Despite the fact that these features can be related to the state of preservation, they have never been reported in *K. hamanensis*. Given the morphological difference between the tracks described here and those defining *Koreanaornis hamanensis*, we refrain from assigning the Tunisian tracks to that species. Due to the scarcity of material and the absence of a trackway, the Tunisian specimens do not provide enough data to support the identification of a new genus or species. However, considering the morphological features of the footprints we assign the Tunisian tracks to the ichnogenus *Koreanaornis* (Kim, 1969), although the attribution to a ichnogenus is tentative owing to the scarce data available.

Comparison between extant and Mesozoic bird tracks is a complex subject, as the fossil record related to bird evolution is certainly not yet complete. Nevertheless several Mesozoic bird tracks show high similarities with modern birds (Lockley et al., 1992; Anfinson et al., 2009; Falk et al., 2010; Fiorillo et al., 2011) and similarities with modern bird tracks are one of the most significant features in distinguishing Mesozoic bird tracks from dinosaurian ones (Lockley et al., 1992). Modern bird tracks are not formally classified, yet modern field guides (Elbroch and Marks, 2001; Brown et al., 2003) separate tracks firstly on the base of their morphology and secondarily in size categories. Bird track manuals commonly indicate six length-related categories, which are: minute (0-25 mm); small (26-50 mm); medium (51-75); large (76-100 mm); very large (101-125 mm) and enormous (>125 mm). Size is currently considered as a diagnostic feature for distinguishing modern bird tracks (Murie, 1954; Elbroch and Marks, 2001), but this is not true for ichnotaxonomy. Even if size alone is not a significant criterion in classifying avian ichnotaxa, we think that this parameter may result more relevant than expected to discriminate fossil bird tracks. For instance, De Valais and Melchor (2008) suggested that only footprints 50% larger or smaller from the average size of an ichnospecies should fall in the same ichnospecies and, thus, they suggested introducing size as a valid ichnotaxabase at the ichnospecific level. However, size is still considered invalid for extablishing ichnotaxa or differentiating ichnospecies (Bertling et al., 2006). On the other hand, ratios of length-to-wide of various track or trace fossil morphologies may have valid use in defining or refining ichnotaxa (e.g. Platt et al., 2010; Falk et al., 2011). Comparing the mean foot length and width of taxa morphologically similar to the Tunisian tracks, some differences in size are evident (Fig. 6). Tracks here described result the smallest of the fossil bird track record, being 50% smaller of *Koreanaornis*, and are more likely to fall into the minute size class (< 20 mm long) proposed by Brown (2003), whereas other ichnotaxa pertain to the small size class. Differences in size may be related to ontogeny as well as phylogeny; however, ontogeny is not a significant cause for variation in track sizes in modern shorebird. In fact, metatarsal growth quickly decreases after hitching, avoiding vulnerability to predators (Tjørve et al., 2009; Tjørve and Tjørve, 2010); as a result changes in foot size are minimal from chicks to adult. Data available for the Tunisian tracks are not enough to propose a new ichnotaxon or to prove a statistically significant difference, but we think future studies should extend this subject. In particular, further data may indicate whether growing rate in fossil bird can be responsible for significant differences in fossil track, or if discrepancies in size should also be ascribed to differences in species.

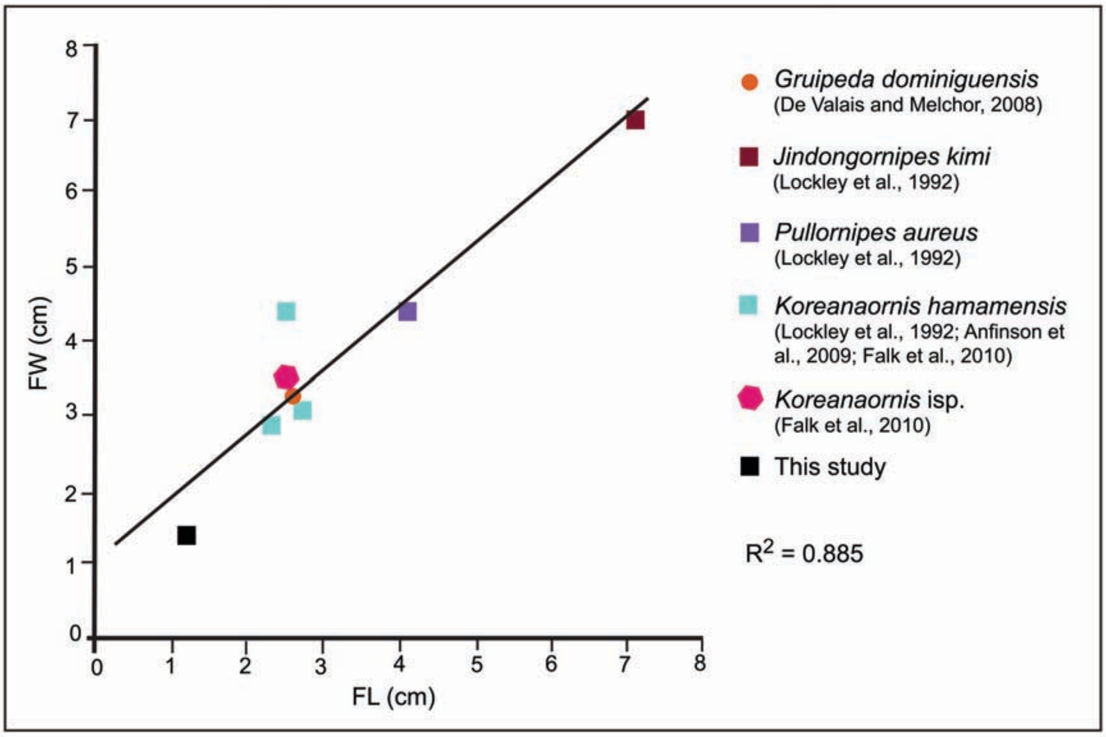

Figure 6 — Bivariate plot of mean foot length and width of avian taxa discussed in the text.

3.5 Paleoecological implications

The discovery of bird and dinosaur tracks in the Zebbag Formation indicate that during the deposition of the Kerker Member tidally driven fluctuations in sea level resulted in subaerial exposure of vast sector of the coastal area, creating an ecological niche for shorebirds. The abundance of evaporitic deposits, the presence of microbial mats, and dolomitization evidenced from the analyses on the thin-sections, support an arid climate, similar to the present day coastal sabkhas. During the Cenomanian southern Tunisia was located just a few degrees north of the equator (Wilson and Norris, 2001) and the region experienced a semiarid climate, warmer and more humid than present (Russel and Paesler, 2003).

Tracks referred to the ichnogenus *Koreanaornis* have already been compared with modern shorebirds (Lockley et al., 1992, 2006a; Lockley and Rainforth, 2002; Falk et al., 2010). Modern birds, in fact, are common in areas with important food resource, as tidal flats and coastal environments. In particular similarities in both size and general track morphology are observed between the Tunisian tracks and those of modern shorebirds of the family Scolopacidae, specifically with the members of the genus *Actitis* (i.e., sandpipers). This is a successful and widespread group of shorebirds, with a worldwide distribution and adaptation to a variety of environments, including a number of species found in coastal shallow water (Richards, 1988). The depositional setting observed at Jebel Boulouha is comparable with the modern Tunisian coastal wetland; despite the scarcity of paleontological data on the Kerker deposits, the presence of shorebird tracks potentially gives an example for the presence of shorebirds in analogue paleoenvironments and present-day environments.

3.6 Conclusions

The Tunisian tracks represent the first occurrence of birds in the Cenomanian of Africa, as well as the smallest of their kind ever found in the fossil record. The distinctive morphology of the Tunisian tracks may be indicative of a new taxon, but the small sample size limit their classification to the ichnogenus *Koreanaornis*, extending the global distribution of this genus, previously known only from Asia and North America (Kim, 1969; Lockley et al., 1992; Anfinson et al., 2009). Size and morphology of footprints described here share several similarities with modern bird tracks and with respect to categorization of bird tracks in use in modern guides, they can be ascribed to the minute class size. Although size is not considered a valid criterion for ichnological classification we think that further studies should discuss the relation between growing rates, ratios of track features and ichnological classification for fossil birds.

Finally the occurrence of vertebrate tracks, both theropod dinosaurs and birds, indicates the presence of emerged land in southern Tunisia not only during the Aptian–Albian but also during the Cenomanian. The presence of bird tracks also provides additional information on the largely unknown biodiversity in the fossil record of North Africa during the Late Cretaceous. In addition, considering discussed sedimentological data, tracks described here support the interpretation of *Koreanaornis* tracks in Africa as being a shorebirdlike avian that inhabited environments similar to those of modern African sandpipers.

Table 1 — Track measurements expressed in mm. FL, foot length; FW, foot width; AoD, angle of divarication between digits (degrees).

Specimen	FL	FW	Digit I	Digit II	Digit III	Digit IV	AoD. II-IV	AoD II-III	AoD III-IV	AoD I-II
MGGC 21849A	14.3	13.5	3.3	6.2	12.5	7.5	108	68	40	150
MGGC 21949B	-	-	2.8	-	-	5.0	?108	67	-	145
MGGC 21849C	10.4	-	-	-	9.8	7.3	-	-	43	-

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CHAPTER 4 - First report of mammal-like tracks from the Cretaceous of North Africa (Tunisia)

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ABSTRACT

This paper describes Cretaceous mammal-like tracks from southern Tunisia. The tracks, referred to the Cenomanian Kerker Member of the Zebbag Formation, are the first mammal-like footprints reported from the Cretaceous of North Africa. The good preservation of the two tracks and their distinctive morphology support their attribution to a mammalian trackmaker, although the limited available data prevents attribution to a specific ichnotaxon. Morphologically, the Tunisian tracks resemble those of modern Mustelidae, however, based on mammalian faunas in the Cretaceous of Africa, they probably have affinity with members of Multituberculate family. Theropod dinosaur and bird tracks occur on the same track-bearing layer. The sediments are interpreted as an arid tidal flat environment, suggesting that African mammals might have shared their environment with a diverse fauna of larger animals.

4.1. Introduction

The origin of mammals is still poorly understood, and only limited skeletal remains are known from the Mesozoic of Asia (e.g. Hu et al., 1997; Wang et al., 1998; Ji et al., 1999; Lopatin and Averianov, 2007), North and South America (Jaillard et al., 1993; Cifelli et al., 1999; Kielan-Jaworowska and Cifelli, 2001; Rougier et al., 2011) and Africa (Nessov et al., 1998; Hahn and Hahn, 2003). Similarly mammal tracks are exceptionally rare occurrences in the Mesozoic fossil record. Only a handful of true mammal tracks are reported from the Mesozoic of Argentina, Brasil, Canada, Europe and southern Africa (Casamiquela, 1964; Ellenberger, 1970; Sarjeant, 1975; Olsen and Galton, 1984; Sarjeant and Thulborn, 1986; Leonardi, 1994; Lockley et al., 1996; Schultz-Pittman et al., 1996; McCrea and Sarjeant, 2001; Standford and Lockley, 2002; Lockley and Foster, 2003; Gierliński et al., 2004).

Although Tunisian Cretaceous bonebeds have yielded a diverse vertebrate fauna (Benton et al., 2000; Srarfi et al., 2004; Fanti et al., 2012), mammals have not previously been reported from the Cretaceous of Tunisia. This paper describes small, well-preserved pentadactyl tracks from a recently discovered vertebrate tracksite at the Jebel Boulouha locality in southern Tunisia (Fig. 1). The J. Boulouha presents a diverse assemblage of non-avian dinosaur and bird tracks from late Cenomanian deposits (Contessi and Fanti, 2012a, b). Here I report the first discovery of Cretaceous mammal-like footprints in Africa. The available track and body fossil record is used to define the affinity of the possible tracemaker and implications of paleoenvironments in mammal-like tracks distribution is discussed.

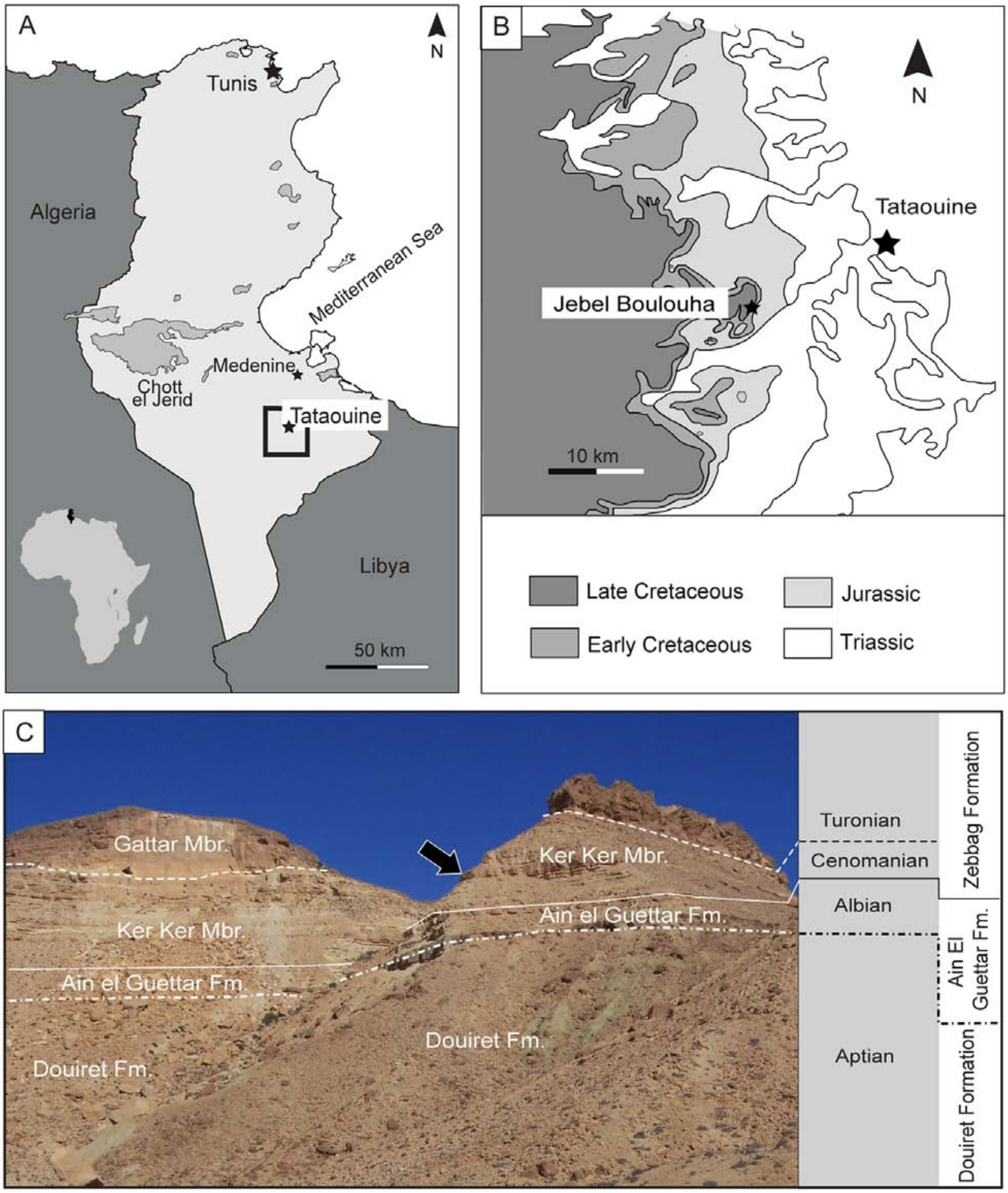

Figure 1 - Locality map of the study area. A) Map of Tunisia, the black box indicates the Tataouine area. B) Locality map showing Mesozoic outcrops in the studied area. C) Field picture and schematic stratigraphic column. Black arrow indicates the track-bearing layer.

4.2. Geological settings

Cretaceous sediments cropping out at the Jebel Boulouha locality belong to the Douiret, Aïn el Guettar and Zebbag formations (Fig. 1, 2). Vertebrate remains, including fishes, turtles, crocodiles and dinosaurs, are reported only from Aptian Douiret Fm. (Benton et al., 2000; Srarfi et al., 2004; Fanti et al., 2012), whereas the tracks occur in the Kerker Member of the younger Zebbag Formation (Kerker and Gattar mbrs.) (Ben Ismaïl, 1991; Fanti et al., 2012). The Kerker Member has been dated as late Cenomanian on the basis of the occurrence, in the northern part of the Tataouine Basin, of the ammonite *Neolobites medeninensis* (Busson, 1967). Sediments of this Member consist of alternating marls and carbonates deposited in a lagoonal to shallow marine environment (Bodin et al., 2010). Rare gastropods and some bivalves *tempestite* layers are the only fossils that occur in the Zebbag Formation.

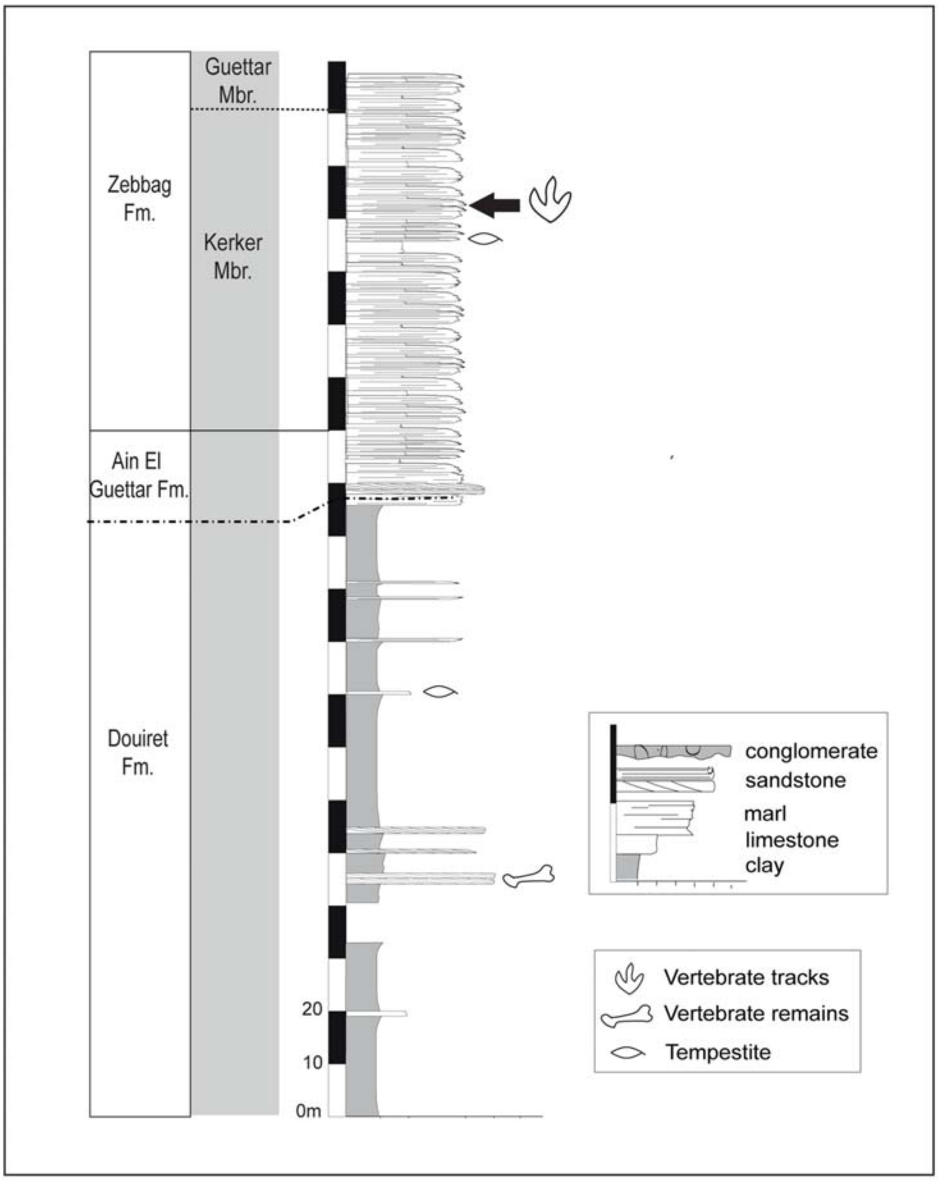

Figure 2 –Lithostratigraphic column of the Cretaceous outcrop at the Jebel Boulouha locality. Black arrow indicates the track-bearing layer.

4.2.1. Tracksite description

A set of tracks was discovered on an isolated and uncollected block of fine sandstone (Fig. 2 A–B), referable to a defined layer located 15 meters below the top of the Kerker Member (Figs. 1, 2). The track-bearing layer is characterized by a light to yellowish, fine-grained and biolaminated sandstone, showing early dolomitization and birdseye structures in thin section. The track-bearing surface presents a characteristic structure associated with the drying out of ancient microbial mats (Flügel, 2010; Fig. 3A-B). This feature, together with the early dolomitization, is indicative of arid tidal flat environments, and may have aided in the preservation of the tracks (Marty et al., 2009; Petti et al., 2011). Deeply impressed, non-avian theropod tracks occur on the block (Contessi and Fanti, 2012b), suggesting a high water content in the sediment. As all tracks in the track bearing-layer are preserved as a negative relief and display mud rims, they are interpreted as true tracks (*sensu* Thulborn, 1990).

4.3. Material and methods

Field data presented in this study were collected between February 2010 and March 2011. A mold of the two tracks was made using SILICAL 110 silicone rubber. A fiberglass cast of the mold was also produced and deposited at the Museo Geologico Giovanni Capellini in Bologna (Italy) (accession number MGGC 21855). Measurements were taken from the mold using a caliper and parameters used to describe tracks follows Leonardi (1987) and Thulborn (1990).

A three dimensional (3D) model was produced from molds for a more objective representation of the tracks. Data used to generate 3D models were acquired with a laser scanner (Zsnapper portable, ViALUX®) with a 0.2 mm resolution at the Visualization Laboratory at the Huffington Earth Sciences Department of Southern Methodist University in Dallas (Texas, USA). The scanning, image data processing and manipulation were done using Meshlab 1.3.0® (rendering of the scan) and Surfer 10® (for contour-line and depth-color image analysis).

4.4. Systematic description

Class Mammalia
Ichnogenus uncertain

Horizon and locality. Kerker Member of the Zebbag Formation, Cenomanian. Jebel Boulouha locality, Tataouine region. GPS: N32°51'72"; E10°20'16" (Figs. 1, 2, 3).

Description. Small (less than 3 cm long), robust (short and relatively large), pentadactyl and semidigitigrade manus and pes impressions of a quadrupedal trackmaker. Footprints are almost as wide as long with manus impression (26 mm wide) smaller than pes (33 mm wide). Digits traces are separated by hypex. In pes digits II and IV are subequal in length (about 12 mm) and straight, whereas digit III that is slightly curved and longer (18 mm). Central digits are slightly divergent, typically 30°. Digit I is shorter (9 mm in length), more divergent (40°) and the metatarsal-phalangeal joint is in a lower position compared with other digits. Similarly, in the manus impression the inner digit (I) is shorter and the central digits are subequal in length (10 mm), although digit III is slightly longer (12 mm) and straight. In the manus digits impressions are slender than pes, averaging 3.7 mm in width, compared to 5.5 mm in pes impression. Manus digits are slightly divergent (about 27°) with the exception of digit III that diverges from digit IV at higher angle (34°). In both manus and pes digit I shows two pad impressions, digits II-III-IV reveal three pad impressions, whereas digit V pads are not clearly preserved. Such pad impressions are consistent with mammalian phalangeal formula of 2:3:3:3:3 (Leonardi, 1987). No claw marks are displayed, although all digits are sharper distally.

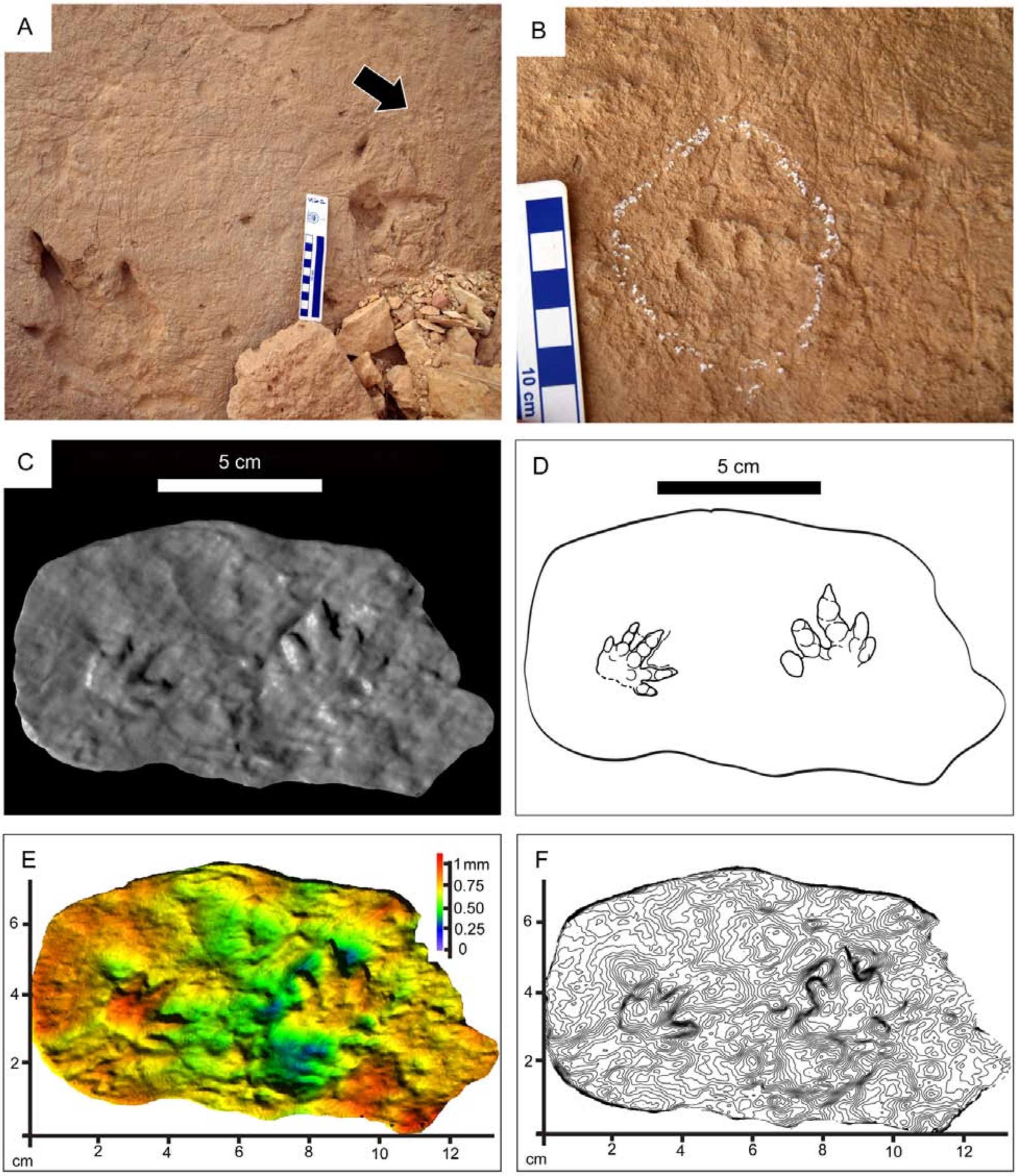

Figure 3 – Mammal tracks from the Jebel Boulouha locality. A) Field picture of the track-bearing block, black arrow indicates the position of the tracks described here. B) Detail of the isolated tracks on the block surface. C) Three dimensional model of the silicone mold. D) Line drawing of the tracks. E) Color-coded map from three dimensional (3D) model of the tracks silicone mold. F) Contour-line map, with 0,1 mm of equidistance, from 3D model of the tracks silicone mold.

4.5. Discussion

4.5.1. Systematic discussion

The two tracks are similar in the overall morphology and, although the relative position of the two footprints is not consistent with walking kinematics (Fig. 3), little differences in the track size and digit width suggest the interpretation of the tracks as manus and pes impressions. As they are the only impressions of this kind on the track-bearing slab, they are likely to be made by the same individual, although there is no direct evidence for this.

Four characteristics can be used to assign tracks to Mesozoic mammals (Leonardi, 1987; Lockley et al., 2004): appropriate size (digits up to 1,5 cm long), pentadactyl manus and pes impressions, digits phalangeal formula of 2:3:3:3:3 and morphology, showing straight slightly divergent central digits and shorter and more divergent lateral ones, together with faint traces of pad impressions. Five digits in the manus impressions are also features of lacertilian tracks (e.g., *Rhynchosauroides*), although such tracks are characterized by curved and slender digits, and increase in length from digit I to IV (Lockley et al., 2004; Avanzini et al., 2010). Footprints of other small reptiles, such as crocodilians are excluded because characterized by pentadactyl manus, tetradactyl pes impressions, slender digits, and greater (about 180°) interdigital angulation between digits I and V (Lockley and Meyer, 2004; Avanzini et al., 2007). The Tunisian tracks are small in size, have straight central digits, shorter lateral ones, and pad impressions are consistent with mammalian phalangeal formula of 2:3:3:3:3; therefore they can be tentatively referred to a mammal trackmakers.

Despite their unique features, there are few reports of Mesozoic mammal tracks and several are controversial and of dubious taxonomic value (Knoll, 2004; Lockley et al., 2004; De Valais, 2009). Ellenberger (1974) named several mammalian footprints from the Upper Triassic-Lower Jurassic of southern Africa, including the ichnogenera *Eopentapodiscus* and *Aristopentapodicus*. Casamiquela in 1961 named *Ameghinichnus*, from small prints of a quadruped with subequal-sized manus and pes from the Middle Jurassic of Argentina. The other references to *Ameghinichnus* come from the Late Triassic and the Lower Jurassic of the United States (Olsen, 1980; Olsen and Rainforth, 2001; Hunt and Lucas, 2007), the Lower Jurassic of southern Africa (Ellenberger, 1970; 1974; Olsen and Galton, 1984) and the Lower Jurassic of Poland (Gierliński et al., 2004). De Valais (2009) considered *Ameghinichnus* as a senior synonym of the ichnogenus *Eopentapodiscus*. Jurassic ichnogenera include also *Pooleyichnus* (Sarjeant, 1975), who was recorded from the Bajocian of the United Kingdom. The material consists of a single print of a small (about 5 cm long) animal with well-developed claws and mammalian phalangeal formula.

Cretaceous specimens include *Brasilichnium*, who was named by Leonardi (1981), and revised by Fernandes and Carvalho (2008). It is a trackway of a small size, pentadactyl and quadrupedal mammal from the Lower Cretaceous of Brazil. This ichnogenus was also reported from the Late Triassic of U.S. (Hunt and Lucas, 2007; Lockley, 2011) and the Lower Jurassic of Brazil. *Duquettichnus* (Sarjeant and Thulborn, 1986) was described from the Lower Cretaceous (Aptian-Albian) of Canada. The prints show syndactyly of the digits II and III of pes: a feature is further known only from living marsupials, however, the validity of this taxon has been questioned (McCrea and Lockley, written communication 2012). Finally, Lockley and Foster (2003) reported *Schadipes* from the Campanian and Maastrichtian of the U.S., a small, slender-toed, tetradactyl and pentadactyl tracks, with central digits (II-IV) subequal in length, and only slightly divergent.

All Cretaceous mammal tracks reported so far are characterized by pentadactyl pes and tetradactyl manus impressions (Sarjeant and Thulborn, 1986; McCrea and Sarjeant, 2001; Standford and Lockley, 2002; Lockley and Foster, 2003). Such tracks are thus not comparable with the Tunisian material, as tracks here described show pentadactyl manus impression. On the contrary, some Jurassic tracks show small pentadactyl hind and front feet (Casamiquela, 1964; Ellenberger, 1972; 1974; Leonardi, 1994). *Ameghinichnus* tracks show some differences with the Tunisian ones: the manus and pes impressions are similar in size, digits are subequal length, the total divarication angle is wider than in the Tunisian tracks and *Ameghinichnus* does not show digit pads impressions. South African tracks described by Ellenberger (1972, 1974) are the closest geographically to Tunisia, and share several morphological features with the tracks described here. The ichnogenera *Eopentapodiscus* and *Aristopentapodicus* (Ellenberger, 1974), like Tunisian tracks, show pentadactyl, semi-digitigrade front and hind feet, mammalian phalangeal formula, clear impression of the metacarpo-phalangeal joints and sharp distal edges. However, there are a few differences with the Tunisian tracks: the divarication angles are slightly different and digit III in the pes does not show a marked difference in size. Finally, *Pooleyichnus* sp. (Sarjeant, 1975) shows well-developed claws not present in the material described here.

Given the differences between the Tunisian tracks and the mammal track record, and considering the scarcity of data available, the Tunisian tracks do not support the assignation to any ichnotaxa, although based on their general morphology and size, they can be confidently attributed to Mammalia.

4.5.2. Affinity of the trackmaker

Basal mammals were small and quadrupedal, according to the track record, showing pentadactyl manus and pes, subequal in size (De Valais, 2009). Casamiquela attributed *Ameghinichnus* to the marsupials, but Bonaparte (1978) disagreed with this because there were not enough postcranial remains to assign the trackmaker to a particular mammalian clade. Lockley and Foster (2003) indicate that morphologically the tracks from the Upper Cretaceous of U.S. resemble those of some modern rodents. However rodents are not present in the Cretaceous (McKenna and Bell, 1997), and based on the dominant mammalian elements of faunas, the tracks probably belong to another mammalian group, such as marsupials, who were suggested as the Cretaceous mammalian trackmakers in Nord America by Sarjeant and Thulborn (1986).

Pentadactyl patterns are also typical of the pes of the ancient rodent-like mammals multituberculates, triconodnts and therians (eutheria and matheria) and, despite the differentiation in these three groups, it is likely that there was a lack of significant divergence in foot structure (Lockley and Foster, 2003). Until recently very few Cretaceous mammal feet have been recovered. Complete skeletons of Cretaceous rodent-like mammal genera have been described only from China: *Zhangheotherium* (Hu et al., 1997), *Jeholodens* (Ji et al., 1999) and *Eomalia* (Ji et al., 2002). Despite the small size, both skeletal remains and tracks of fossil and modern rodents and mice-like animals lack the fifth digit impression in the manus, which appears in the Tunisian tracks. The tracks described here are therefore more likely to belong to some other mammalian group. It is outside the scope of this paper to mention all the species that might be potential trackmakers to the Tunisian tracks. Despite the Cretaceous finds in Asia (e.g. Hu et al., 1997), the mammal record in the late Cretaceous of North Africa is limited to an isolated vertebra from Libya (Nessov et al., 1998) and teeth from Morocco, which have been referred to a generic multituberculate (Hahn and Hahn, 2003); thus the possibilities of matching Tunisian tracks to a trackmaker are strictly limited.

In modern mammals a semi-digitigrade and pentadactyl manus, with clear impression of the metacarpal-phalangeal joints is a common feature of Mustelidae (Murie, 1954). Carnivoran evolution is still a controversial topic, although the first carnivorans are only known from the Paleocene, and are believed to have evolved from late Cretaceous eutherians (Flynn et al., 2010). The Mustelidae first appear in the Late Eocene (Sarjeant and Langston, 1994; Goswani, 2010), thus, despite the morphological similarities, these Tunisian tracks can not be referred to a mustelid trackmaker.

4.6. Paleoecological implications

The shortage of mammalian footprints reported from the Mesozic is normally interpreted as a consequence of their small size and poor preservation potential (Sarjeant, 2000). However, mammal tracks are actually relatively common in the Lower and Middle Jurassic of southern Africa and Argentina. Perhaps the reason for their relatively frequent occurrence is related to the paleoenvironments where they lived. Mammal tracks are found in the highlands and arid regions in the Mesozoic of Argentina and Brazil, whereas dinosaur and other archosaurs lived in the valleys, plains and more vegetated coastal areas (Leonardi, 1994). Lockley and Foster (2003) mentioned that in the Cretaceous of North America mammal tracks were associated with fertile and well-vegetated area with diverse ichnofaunas. In the African site reported here the presence of a microbial mat is interpreted as indicative of arid tidal flat environments, where theropod dinosaurs and birds tracks also occurs. Despite the lack of information on body fossils, this new ichnological data, not only show how mammals were adapted to coastal environments, but they also show how they shared the same habitat with a diverse fauna of larger animals.

4.7. Conclusions

Mammal tracks from Jebel Boulouha, in south Tunisia, represent the first ichnological record of mammals in the Cretaceous of Africa. The scarcity of data available on the Tunisian tracks prevents the attribution to any specific ichnotaxon, although the pentadactyl front and hind feet, together with digital pads and metacarpal-phalangeal impressions are distinctive features for a mammalian trackmaker.

Given the scarcity of mammal reports in the Cretaceous, this finding provides important new information on mammal distribution. As the Cretaceous mammals skeletal record in Africa is limited to a few remains of Multituberculata in Morocco and Libya, and diagnostic information on the foot morphology of these Cretaceous mammals are still lacking, the attribution to the Tunisian tracks to a trackmaker is still tentative.

Finally, the J. Boulouha site presents a relatively diverse ichnofauna comprising theropod dinosaurs, birds, and mammal-like tracks in an arid tidal flat environment. This ichnoassociation occurs in the same environment as South American mammals, suggesting that Cretaceous mammals might survive in arid and extreme environment with larger theropod dinosaurs, already known to be relatively frequent inhabitants of arid tidal flats.

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CHAPTER 5 – Late Albian/Cenomanian dinosaur tracks from Tunisia: new constraints on the paleobiogeography of the Mediterranean platforms during mid-Cretaceous

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Manuscript under review for Palaeogeography, Palaeoclimatology, Palaeoecology

ABSTRACT

New dinosaur tracks discovered at the Chenini site, near Tataouine (southern Tunisia), and referred to the Oum ed Diab Member (late Albian) of the Aïn el Guettar Formation are described here. Isolated tracks as well as manus/pes couples of a quadrupedal dinosaur are assigned to *Apulosauripus federicianus*. This hadrosaurian ichnospecies was originally described in the Upper Cretaceous carbonate platform of southern Italy, and this discovery represents the first report of *A. federicianus* in Africa.

The occurrence of *A. federicianus* in Tunisia also represents the first evidence of the presence of similar ichnofauna in the Upper Cretaceous of both northern Africa and carbonate platforms of the Mediterranean area. Supporting these new data, a Cenomanian theropod, ichnofauna, recently described from southern Tunisia, is here compared with coeval theropod tracks from the Italian and Croatian carbonate platforms. This comparison documents several shared morphological features, suggesting possible affinities of the trackmakers. The Tunisian vertebrate ichnofauna also supports the hypothesis of a subaerial connection linking the carbonate platforms of the Mediterranean area to the northern margins of Africa in the mid-Cretaceous.

5.1. Introduction

In the last decade the increasing number of dinosaur skeletal remains and tracksites discovered in Europe has provided important paleobiogeographic constraints for reconstructing the geodynamic history of the peri-mediterranean carbonate platforms during the mid-Cretaceous. Dinosaur skeletal remains from the Cretaceous of Spain and France share several common elements with their African counterparts, such as spinosaurid theropods, ornithopods, and titanosaurid and rebacchisaurid sauropods (Le Loeuff, 1991; Sereno et al., 1998; Milner, 2003; Pereda Suberbiola et al., 2003; Rauhut et al., 2003; Sereno et al., 2004; Royo-Torres et al., 2006; Smith et al., 2006; Krause et al., 2007; Canudo et al., 2009). Several dinosaur tracksites, displaying a diversified ichnoassociations, have been discovered in carbonate platforms of Italy and Croatia (Dalla Vecchia, 2000; Nicosia et al., 2000a, 2000b; Nicosia et al., 2007; Petti et al., 2008a; Sacchi et al., 2009). These discoveries opened a debate on the paleobiogeography role of carbonate platforms in the Mediterranean area during mid-Cretaceous, and the possible existence of subaerial connections with the northern African margin (Bosellini, 2002; Nicosia et al., 2007; Petti et al., 2008b; Sacchi et al., 2009; Zarcone et al., 2010). Despite an increasing number of studies on Jurassic vertebrate tracksites from Africa (Ellenberger, 1972; Lingham-Soliar and Broderick, 2000; Belvedere et al., 2010; Mudroch et al., 2011), reports on Cretaceous dinosaur tracks are restricted to few poorly preserved tracks from Morocco, Sudan and Tunisia (Ambroggi and De Lapparent, 1954; Demathieu and Wycisk, 1990; Contessi and Fanti, 2012a, b). As a result, in the literature, all paleobiogepgraphic reconstructions suggesting a subaerial connection in the mid-Cretaceous are based on few stratigraphic data and ichnological data from the Mediterranean carbonate platforms, and no comparison with African ichnofaunas are available so far (Bosellini, 2002; Petti et al., 2008b; Sacchi et al., 2009; Zarcone et al. 2010).

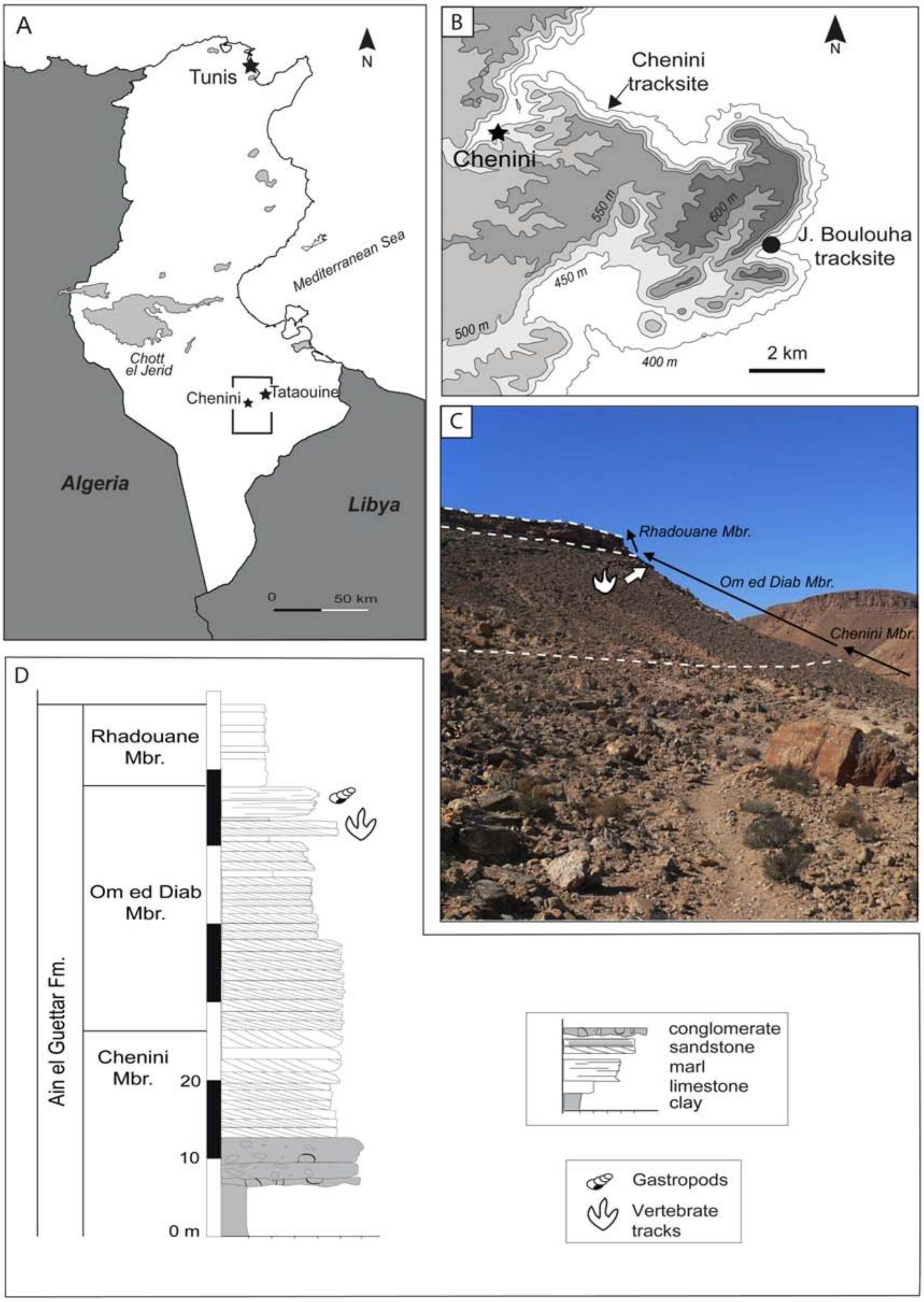

Figure 1 – Geologic and stratigraphic settings. A) Tunisian map showing the position of the study area. B) Topographic map of the Chenini locality. C) Chenini outcrop, arrow indicates the track-bearing layer. D) Stratigraphic log of the Chenini section.

Due to its relative position close to the Mediterranean carbonate platforms during mid-Cretaceous, Tunisia plays a primary role in the paleobiogeographic reconstructions platforms in the Mediterranean area, and has been hypothesized as the possible area of connection between Africa and Adria (Bosellini, 2002; Zarcone et al., 2010). Southern Tunisia is well known in the literature for its rich and diverse Lower Cretaceous fossil record, including fish, sharks, turtles, crocodiles, pterosaurs, sauropods, non-avian theropods and rare ornithopods (De Lapparent, 1960; Benton et al., 2000; Srarfi et al., 2004; Fanti et al., 2012). Relevant to this study, three Cretaceous vertebrate tracksites have been discovered in the Tataouine region during recent field work (Contessi and Fanti, 2012b).

The purpose of this paper is to describe new dinosaur footprints recently discovered at the Chenini locality and to analyze the previously described Tunisian ichnofauna in the framework of the paleobiogeography of the mid-Cretaceous Mediterranean carbonate platforms.

5.2. Geological settings

The mid-Cretaceous sediments in the study area are characterized by marine, to shallow marine deposits in which the general environment of littoral platform, with limited periods of emersion, prevailed (Busson, 1967; Busson, 1972; Bouaziz et al., 2002; Bodin et al., 2010). At the Chenini tracksite only three Cretaceous units crop out: the Chenini, Oum ed Diab and Rhadouane members of the Aïn el Guettar Formation (Fanti et al., 2012) (Fig. 1). The basal Chenini Member is characterized by coarse conglomeratic beds at the base, that fine upward to cross-stratified sandstones. At the measured section, the transition to the overlying Oum ed Diab Member is marked by a coarse- to fine-grained sandstone, displaying herring-bones and flaser structures. Towards the top, the Oum ed Diab Member is characterized by sandstone layers interbedded with marl to carbonate beds, rich in bivalves and gastropod remains. This 15 meters thick succession is capped by the carbonate deposits of the overlying Rhadouane Member.

The track-bearing layer is located five meters below the top of the Oum ed Diab Member (Fig. 1). This Member has been dated as middle Albian on the basis of stratigraphic correlations and its fossil content (Bodin et al., 2010). The overlying Rhadouane Member has been dated as late Albian-early Cenomanian on the base of the occurrence of the ammonite *Knemiceras* (Bodin et al., 2010; Fanti et al., 2012; Fig. 1). Considering the stratigraphic position of the track-bearing level, it is here interpreted as late Albian in age. The tracks occur in massive siliclastic sandstone with rare shell fragments. A number of tracks have been found on isolated blocks below the *in situ* layer, and referred to the same layer (Fig. 2). The depositional environment of the track-bearing bed is here interpreted as nearshore environment, supported by the presence of shell fragments and the occurrence, a few meters below, of the ichnotrace *Diplocraterium*, representative of shallow-marine, high energy nearshore deposits (Seilacher, 2007). Vertebrate tracksites in southern Tunisia occur in similar lagoonal to near shore environments (Contessi and Fanti, 2012b) where tracks are seldom found together with microbial mats, typical of lagoonal and arid environments (Noffke, 2010; Petti et al., 2011).

5.3. Material and methods

Field data in Tunisia were collected between February 2010 and March 2011. Tracks described here were measured *in situ* and named as follows: site name initials; number indicating the track-bearing block; capital letter indicating the single track - when more than one occur on the same block, and lower case letter indicating manus or pes impression (see Table 1). Molds were taken of selected footprints using a silicon-molding compound (SILICAL 110). Fiberglass replicas of tracks cited in this paper are deposited at the Museo Geologico Giovanni Capellini (Bologna, Italy) under inventory numbers MGGC 21848 (CH4A), MGGC 21850 (BL12B), MGGC 21851 (BL20) and MGGC 21862 (BL25A). Three dimensional (3D) modeling was used in order to provide a more objective representation of tracks (Fig. 3). Molds of Tunisian tracks were scanned, with the NextEngine laser scanner (0.2 mm of resolution). Cast of *A. federicianus* type ichnospecies from the Altamura site (Bari, Southern Italy), deposited at the University of Roma La Sapienza (Rome, Italy), and molds of theropod tracks from Istrian sites, deposited at the Monfalcone Museum (Gorizia, Italy), were scanned too for comparison with the Tunisian tracks (Figs. 4, 5). Data processing was carried out using Next Engine ScanStudio HD Pro® (alignment of the scans), Surfer 10.0® (color and contour line-coded maps) and Meshlab (model rendering). Standard track and trackway parameters used here include footprint length (FL) and footprint width (FW) (*sensu* Leonardi, 1987).

Institutional abbreviations: MGGC (Museo Geologico Giovanni Capellini)
Other abbreviations: CH (Chenini); BL (Boulouha); PR (Premantura Promontory); SLD (San Lorenzo Di Daila); FL footprint length; FW footprint width.

5.4. Systematic paleontology

Ichnogenus *Apulosauripus* Nicosia et al., 2000b
Apulosauripus federicianus Nicosia et al., 2000b
Figs. 2, 3

Material. Six manus-pes couples, five isolated manus and two isolated pes on uncollected blocks (Table 1). Cast of CH4 manus-pes couple (MGGC 21848).

Description. Pes impressions average 22 cm in length and 21 cm in width, whereas manus impressions average 13 cm in length and 14 cm in width. The best manus/pes couple (CH4) shows tridactyl manus and pes impressions (Fig. 3). Manus impression is placed forward and medially with respect to pes impression. Both manus and pes are slightly wider than long, the digits are short with rounded hooves, and roughly equal in length. Digit III in the hind foot is more prominent than the others, and in the central part of the pes a transverse ridge separate the heel from the digit impressions. The manus impression shows three asymmetrical lobes. The lobe corresponding to digit II is wider, shorter and closer to the pes impression than the medial one, which corresponds to the longer digit impression.

5.5. Systematic discussion

Ornithopods tracks are historically the oldest dinosaur tracks known. Their discovery dates back to the 19th century, when they were generally referred as Iguanodon. In recent years the discovery of ornithopod and hadrosaur tracks worldwide has led to a number of specific names (Alonso, 1980; Leonardi, 1984; Sarjeant et al., 1998; Zhang et al., 2006). Unfortunately, most of the names attributed to hadrosaur tracks have been incorrectly assigned (Lockley et al. 2003). According to Lockley et al. (2003), only four ichnogenera should be accepted as ornithopod tracks: *Amblydactylus* (Sternberg, 1932), *Caririchnium* (Leonardi, 1984), *Iguanodontipus* (Sarjeant et al., 1998) and *Hadrosauropodus* (Lockley et al., 2003).

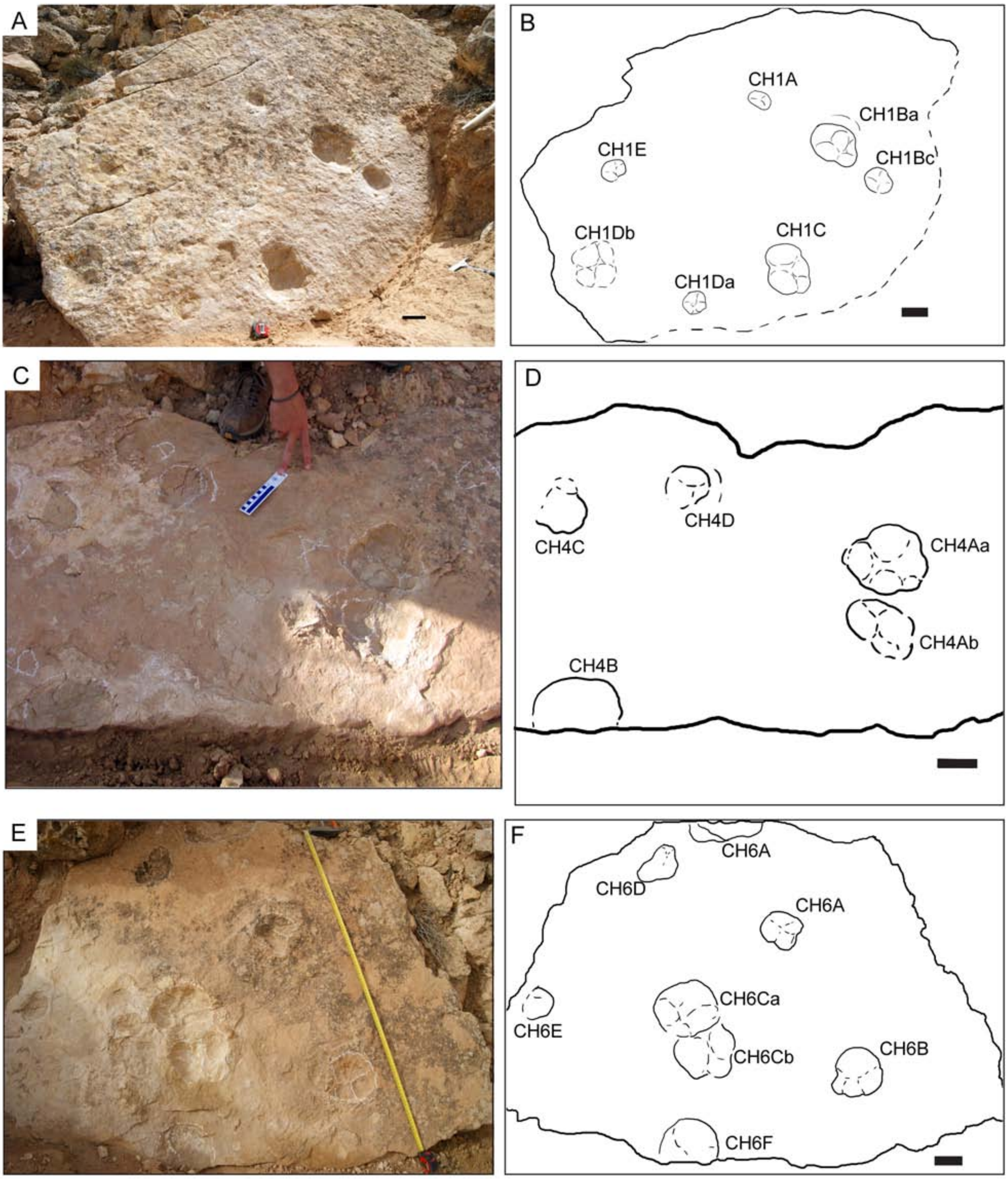

Figure 2 - The *in situ* track-bearing surface. A) Picture of the *in situ* CH1 block. B) Schematic drawing of the CH1 block. C) Picture of the *in situ* CH4 block. D) Schematic drawing of the CH4 block. E) Picture of the *in situ* CH6 block. F) Schematic drawing of the CH6 block. Scale bar 10 cm.

The first ichnogenus is referred to hadrosaurian tracks from the Aptian-Albian of western Canada (Sternberg, 1932; Currie and Sarjeant, 1979), and it is characterized by the sporadic impression of manus, elongate digits in pes impression and high divarication angles between outer digits. *Caririchnium*, from the Lower Cretaceous of Brazil (Leonardi, 1984), is characterized by the absence of manus impressions and wide divarication angles between outer digits. *Iguanodontipus* is named from large ornithischian tracks from the Lower Cretaceous of England (Sarjeant et al., 1998). Lastly, *Hadrosauropodus* (Lockley et al., 2003) presents bilobed heel impression, symmetrical tracks and subtriangular manus impression, about one third of pes width. All these listed ornithopod ichnotaxa present some differences from tracks here described, such as elongate digit impressions, bilobed heel impression and sporadic and small manus impression, preventing further comparisons with the Tunisian material. The ichnospecies *A. federicianus* was described by Nicosia et al. (2000b) from the Santonian beds of the Altamura tracksite (Puglia, southern Italy). According to Nicosia et al. (2000b) tracks ascribed to *A. federicianus* are characterized by tridactyl manus and pes impressions, with manus impressions almost half the size of pes. Digits in both manus and pes are sub-equal in length, generally short and U-shaped in outline. A transversal ridge in the pes separates the heel from digits impressions. In the trackway, manus impressions are placed anterior-medially in relation to pes and pace angulation is low in both manus and pes, averaging 91° and 100° respectively. Although *A. federicianus* was not mentioned in Lockley et al. (2003) ornithopod tracks list, it is here considered a valid ichnotaxon, as it shares the same characters and temporal distribution of other ornithopod tracks.

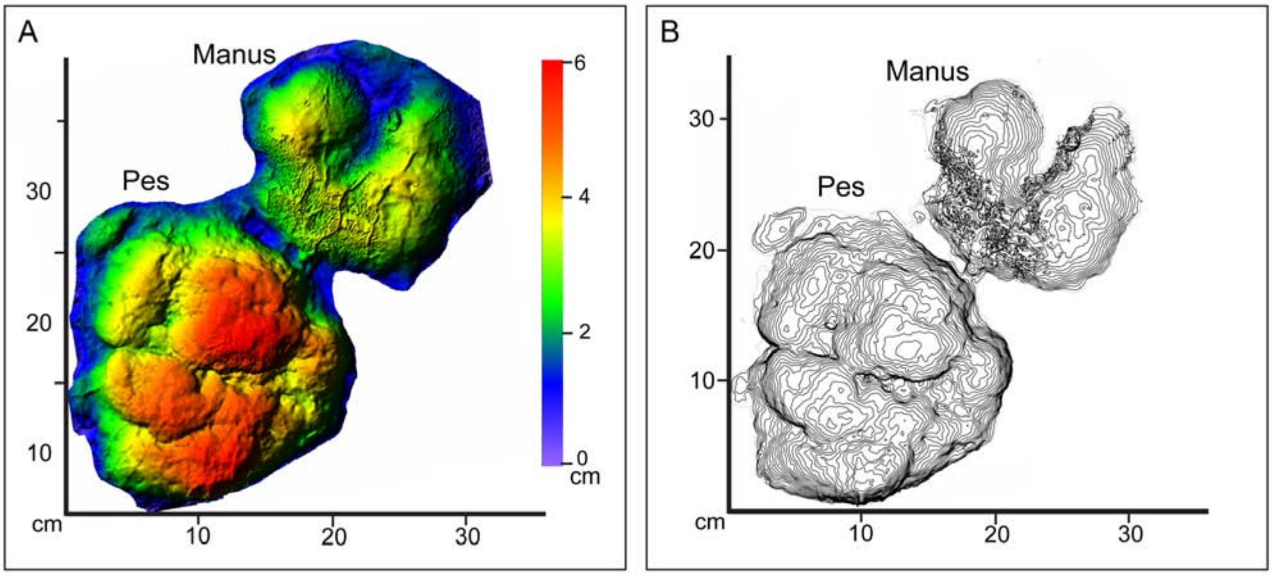

Figure 3 – Three dimensional model of mold MGGC 21848 (CH4) of the best-preserved manus-pes couple (CH4). A) Color coded map. B) Contour lines map with 0.1 cm of equidistance.

A. federicianus tracks were originally referred to a hadrosaurian trackmaker on the basis of the tracks morphology and the discovery of the hadrosauroid *Tethyshadros insularis* in the Upper Cretaceous of the Dinaric Platform (Nicosia et al., 2000b; Dalla Vecchia, 2009). Gierliński et al. (2005) proposed an ankylosaurian affinity for the *Apulosauripus* ichnogenus, based on the large manual prints (larger than other quadrupedal ornithopods), the greater width of the trackway and the absence of inward rotation in the pes impressions. On the contrary, Petti et al. (2010) excluded ankylosaurs as the probable trackmakers, as ankylosaurs with tridactyl hands are not yet known from the skeletal fossil record. Basal hadrosauroids firstly appeared in the Turonian (Rozhdestvensky, 1977; Weishampel et al., 2004; McDonald et al., 2006), whereas hadrosaurs are commonly found in the Campanian-Maastrichtian of Europe, China and North America (Horner et al., 2004; Weishampel et al., 2004; Dalla Vecchia, 2006; Godefroit et al., 2008). Closest relatives to hadrosaurs in Africa are the more primitive ornithopods *Ouranosaurus*, from the lower Cretaceous of Niger (Taquet, 1976), and few poorly preserved ornithopods teeth from the Albian deposits of the Om ed Diab Member in southern Tunisia (Benton et al., 2000; Srarfi et al., 2004; Fanti et al., 2012).

The Tunisian tracks from the Chenini locality share several morphological features with the *A. federicianus* ichnospecies (Fig. 4; Table 1), according to Lockley (2007) ichnotaxa are usually discriminated by morphologies and not age-differentiate, therefore on the basis of morphological similarities the Tunisian footprints are assigned to the *A. federicianus* ichnospecies. Considering the Turonian age of youngest hadrosaurs, Tunisian tracks cannot be referred to an hadrosaur trackmaker. More likely, *A. federicianus* tracks could be referred to a basal, and older, ornithopod, with a foot structure similar to hadrosaurs.

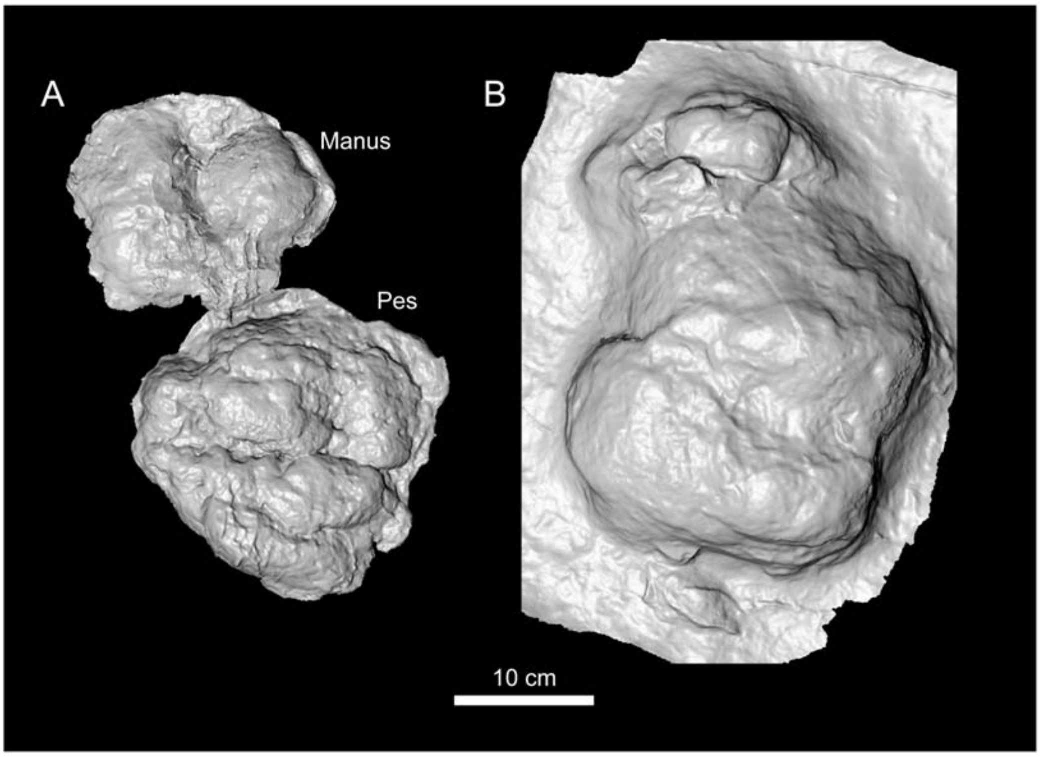

Figure 4 - Comparison between Tunisian MGGC 21848 (CH4) and Italian *Apulosauripus federicianus*. A) 3D model of MGGC 21848 (scanned from mold, model with reversed normals) B) 3D model of cast of *A. federicianus* ichnoptype.

5.6. Cretaceous dinosaur tracks from the Mediterranean carbonate platforms

The presence of *A. federicianus* in the Cretaceous of Tunisia extends the relevance of dinosaur ichnofaunas in the framework of the Mediterranean carbonate platforms and the northern African margin, opening the field for further comparisons between dinosaur tracks.

Dinosaur tracksites have been largely documented in the Mediterranean mid-Cretaceous platforms (Dalla Vecchia, 2002; Mezga et al., 2006; Nicosia et al., 2007; Petti et al., 2008a, 2008b). Tracksites dominated by small to mid-sized theropods and sauropods are relatively common in the Adriatic Dinaric and Lazio-Abruzzi-Campania platforms (Mezga and Bajraktarević, 1999; Dalla Vecchia, 2000; Dalla Vecchia et al., 2002; Mezga et al., 2006; Petti et al., 2008b; Nicosia et al., 2007), whereas a more diverse ichnoassociations, including theropod, ornithischian and sauropod tracks characterize tracksites in the Apulian platform (Nicosia et al., 2000a, b; Petti et al., 2008a; Sacchi et al., 2009).

Although the Tunisian track record is still limited to four tracksites, a varied ichnofauna has been recently described from Cretaceous deposits in the Tataouine area (Contessi and Fanti, 2012b). Crocodile tracks occur on the same Albian-early Cenomanian Chenini site where the *A. federicianus* tracks came from, turtle tracks are preserved at the Cenomanian Ksar Ayaat locality, and theropod, bird and mammal tracks occur at the late Cenomanian Jebel Boulouha tracksite (Contessi and Fanti, 2012a, b; Contessi, in press).

5.6.1 Ichnofaunal correlations

As it results from these discoveries, theropod tracks occur in coeval deposits in both Tunisia and the Mediterranean carbonate platforms, and a comparison between these two ichnofaunas can be carried out. Due to the derived structure of the foot, theropod tracks are difficult to compare, although peculiar morphological features can help to distinguish different morphotypes (Nicosia et al., 2007). Theropod tracks preserved at the J. Boulouha tracksite are characterized by: (1) averaging 22 cm in length; (2) slender digits impressions; (3) clear pad impressions with, occasionally, claw marks; (4) longer digit III, and digits II and IV subequal in length; (5) base of digits IV placed slightly back in relation to other digits; (6) divarication angle between digits II-III lower than between III-IV; and (7) mean total divarication angle of 52°. Similarly, the theropod tracks from the early Aptian of the Apulian platform (Sacchi et al., 2009), the Cenomanian of central Italy (Nicosia et al., 2007) and Istria (Mezga and Bajraktarević, 1999; Dalla Vecchia et al., 2000; Dalla Vecchia et al., 2001) share the morphological features (1)-(7) of tracks described from the J. Boulouha site (Fig. 5).

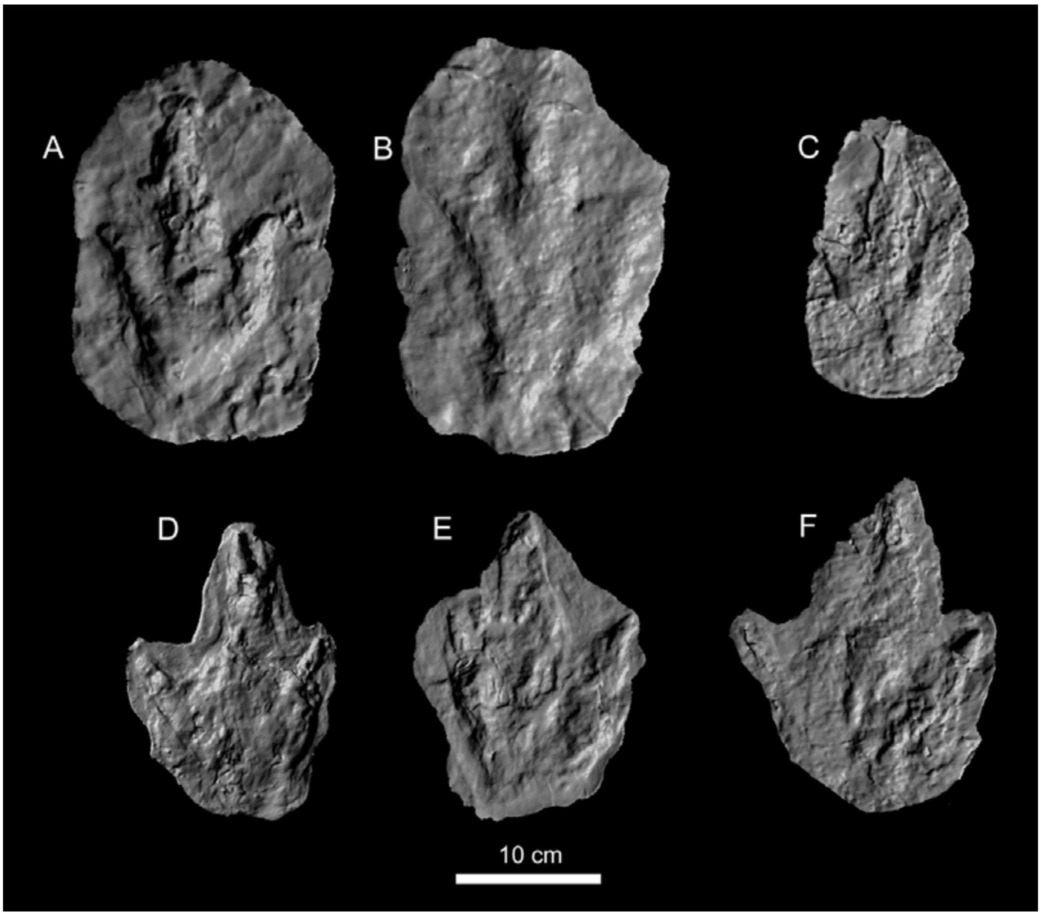

Figure 5 - Comparison between 3D model of Cenomanian Tunisian theropod tracks and coeval theropod tracks from the Adriatic Dinaric platform, all scanned from molds. A-C theropod

tracks from Croatia (see Dalla Vecchia et al., 2001 for a detailed description): A) Cervar I; B) PR T2-2; C) SLD T14-10. D-E theropod tracks from the J. Boulouha locality (Contessi and Fanti, 2012b): D) BL 20; E) BL 12B; F) BL 25A.

The comparison between theropod tracks from Tunisia and those from the Dinaric, Apulian and Lazio-Abruzzi-Campania carbonate platforms indicates similarities in size and morphological features of individual tracks, suggesting that they could have been made by similar trackmakers.

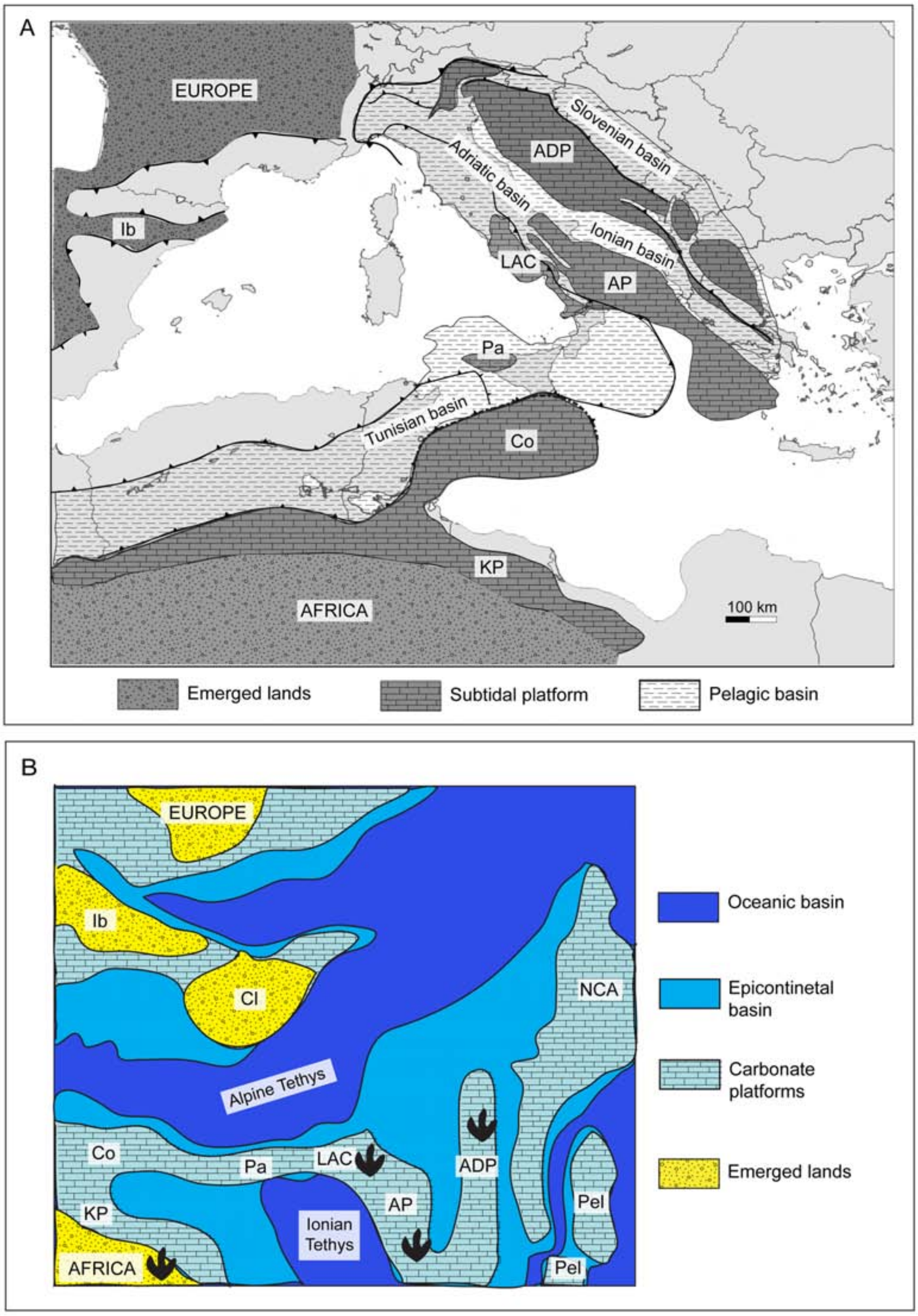

Figure 6 - Domains and paleogeographic maps of the Mediterranean area during Cenomanian. A) Distribution of the Cretaceous Mediterranean carbonate platforms, (after Zapaterra, 1994,

modified and redrawn). B) Paleogeographic map of the Central Mediterranean during Cenomanian (modified after Zarcone et al., 2010). ADP = Adriatic Dinaric Platform; AP = Apulian Carbonate Platform; Cl = Calabria; Co = Constantine Platform; KP = Kasserine Platform; Ib = Iberia; LAC = Lazio-Abruzzi-Campania Carbonate Platform; MP = Malta Carbonate Platform; NCA = Northern Calcareous Alps; Pa = Panormide Carbonate Platform; Pel = Pelagonian.

5.6.2 Paleobiogeographical considerations

Varied ichnofaunas from the Mediterranean carbonate platforms are found in arid nearshore environments analogous to Tunisian ones (Mezga and Bajraktarević, 1999; Dalla Vecchia et al., 2000; Nicosia et al., 2007; Sacchi et al., 2009). Studies on Cretaceous dinosaurs tracks in central and southern Italy show how the presence of a diverse fauna, composed by mid- to large-sized animals, cannot be explained with the reduced food availability in an isolated, relatively small, island platform scenario (Nicosia et al., 2007; Sacchi et al., 2009). According to Nicosia et al. (2007) and Sacchi et al. (2009) the presence of this diverse ichnofauna, in a relatively extreme environment, such as carbonate platforms, could only be explained with the existence of a link with an emerged landmass. Recent studies have documented for the first time the presence of a diverse ichnofauna, including turtles, crocodiles, ornithopod, avian and non-avian theropod dinosaurs in lagoonal to nearshore environments in the Cenomanian of the northern African margin (Contessi and Fanti, 2012a, b), and the discovery of *A. federicianus* hadrosaur tracks described here add new data on the faunal diversity of the late Albian/Cenomanian of Tunisia. Although the Tunisian sedimentologic data describes the environment as an arid and warm lagoon, or nearshore (Bodin et al., 2010; Contessi and Fanti, 2012b), it is likely that this record represents only a fragment of a more diverse ecosystem, linked to the African continent, which could better explain the existence of this varied vertebrate fauna. Similarly, the presence of a diverse dinosaur ichnofauna, comparable to the Tunisian one, in the Apulian, Dinaric and Lazio-Abruzzi-Campania platforms could be explained hypothesizing a subaerial connection between the Mediterranean carbonate platforms and the African landmass during mid-Cretaceous (Fig. 6).

5.7. Conclusions

Dinosaur tracks from the Chenini locality in southern Tunisia have been described and assigned to the ichnospecies *Apulosauripus federicianus* (Nicosia et al., 2000b) on the basis of their morphological features. This ichnospecies has been originally described from Santonian deposits in southern Italy, and previously referred to an hadrosaur trackmaker (Nicosia et al., 2000b; Petti et al., 2010). As hadrosaurs are not known from the Cretaceous Tunisia, nor North Africa, and the first members of this family appear only in the Turonian (Rozhdestvensky, 1977), it is more likely that *A. federicianus* tracks were the result of convergence in the foot morphology between more basal African ornithopod and younger hadrosauroid.

In addition, *A. federicianus* tracks and previously described vertebrate tracks from the mid-Cretaceous of Tunisia have been discovered in arid lagoonal to nearshore paleoenvironments, similar to those in which coeval vertebrate tracks from the carbonate platforms in the Mediterranean area have been found. Data presented here indicates several similarities in the theropod ichnofaunas from Tunisia and the Dinaric and Lazio-Abruzzi-Campania platforms, suggesting that the tracks could have been made by similar trackmakers that inhabited similar warm nearshore environments. The presence of similar ichnofaunas of both southern Tunisia and the Mediterranean carbonate platform represents the first ichnological evidence supporting the hypothesis of a possible subaerial connection between the Mediterranean platforms and the northern African margin during the late Abian/Cenomanian.

Table 1. Parameters of footprints at the Chenini site: FL and FW expressed in centimeters.

Specimen	manus/pes	FL	FW
CH 1A	**manus**	14,2	12,5
CH 1Ba	**pes**	30	28
CH 1Bb	**manus**	17	16
CH 1C	**pes**	26	21
CH 1Da	**manus**	11	11
CH 1Db	**pes**	21	-
CH 1E	**manus**	12	14
CH 4Aa	**pes**	18	20
CH 4Ab	**manus**	12,2	15,2
CH 4B	**manus**	12	10
CH 5Aa	**pes**	23	17
CH 5Ab	**manus**	14	16,5
CH 6A	**manus**	13,7	15,2
CH 6B	**manus**	14	15,2
CH 6Ca	**pes**	15	21
CH 6Cb	**manus**	15,5	20
CH 6D	**manus**	13	16,5
CH 6E	**manus**	-	11
CH 6F	**pes**	-	20,5
Mean	**pes**	22	21
Mean	**manus**	13	14

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GENERAL CONCLUSIONS

This research project proposes a stratigraphic and paleontological revision of the mid-Cretaceous outcrops of the Tataouine basin, in south Tunisia. Both traditional techniques, such as stratigraphy and taxonomy, and modern tools, such as laser scanning and stable isotopes have been used. Unfortunately, isotopes dating resulted imprecise, due to the mineralogical characteristics of the samples and the extreme difficulties in calibration, resulting data have therefore not been considered here. Seventeen reference sections were measured, and litho- and cronostratigraphic units were described in term of geometry, sedimentology and paleontological characteristics. All vertebrate layers were sampled, recording their stratigraphic occurrence and lateral variability, and resulting data were combined to document facies distribution and variations in the faunal assemblages. Studied vertebrate remains are found in two stratigraphic intervals: the Barresian, lower Douiret Formation and the Albian Oum ed Diab Member of the Aïn el Guettar Formation. Fossil taxa include: fishes (*Lepidotes* sp., *Rhinobatos* sp., *Lissodus* sp., *Lepidotes* sp., *Mawsonia* sp., *Ceratodus* sp., *Neoceratodus* sp., and pycnodontiformes), sharks (*Hybodus* sp., *Prihybodus arambourgi*,), turtles, crocodiles (*Sarcosuchus imperator*, *Hamadasuchus* sp. and *Araripesuchus* sp.), pterosaurs and dinosaurs (*Spinosaurus* sp., *Carcharodontosaurus* sp., abilisauridae and ornithopods). Siliclastic deposits of coastal environment characterize the lower Douiret Formation and fossils from this interval are mainly representatives of freshwater taxa. The Chenini Member of the "C*ontinental Intercalaire*", which has been referred in the literature as the main fossil-bearing interval, is here interpreted as barren of vertebrate remains, which otherwise have be referred to the overlying Oum ed Diab Member. The fluvial sandstones of the Chenini Member, in fact, consist of a conglomerate deposited in an environment similar to present day drainage system and they are barren of fossils, with the exception of rare actinopterygian remains. The fossil-bearing intervals are now interpreted as transgressive conglomerates and used as lithostratigraphic marker of the overlying Oum ed Diab Member. This member is characterized by a transition from tidal flats to foreshore deposits, which is also confirmed by the diverse fossils content, varying from freshwater dominated taxa, such as *Neoceratodus* sp., *Mawsonia* sp., pycnodontiformes, and land vertebrates remains, such as *Sarcosuchus imperator*, *Spinosaurus* sp. and ornithopods to exclusively marine taxa as *Rhinobatos* sp., *Lissodus* sp. and *Lepidotes* sp.. In addition, the Rhadouane Mb., previously referred to the Zebbag Fm., is interpreted here as a minor marine transgression laterally equivalent of the Oum ed Diab Mbr in the northern part of the Tataouine basin, and therefore assigned to the lower Aïn el Guettar Formation.

The second part of this thesis concentrates on the study of the newly discovered Tunisian vertebrate tracksites. Four track-bearing localities were found in the Tataouine basin. The Beni Ghedir tracksite, Middle Jurassic in age, is dominated by tridactyl tracks referred to mid-sized theropods. The preservation of tracks prevented any detailed taxonomical study. Differently, isolated tracks and small trackway segments have been recovered at the upper Albian/lower Cenomanian Chenini site. Tracks are assigned here to a generic crocodile and to the ichnospecies *Apulosauripus federicianus*. Lastly, two upper Cenomanian tracksites were discovered at the Ksar Ayaat and Jebel Boulouha localities. In the first site, a set of 52 tracks are referred to a pleurodian turtle. The J. Boulouha site yielded more than ninety tridactyl tracks referred to a generic mid-sized theropod, three small bird tracks, assigned to the

Koreanaornis ichnogenus, and two tracks referred to a mammalian trackmaker. The track-bearing layers are found in siliclastic sandstones or carbonate successions characterized by early dolomitization, bird eye structures and the presence of microbial mats. Paleoenvironments have been interpreted as a nearshore to lagoonal settings, dominated by carbonatic deposition. These discoveries represent the first record of the presence of dinosaur and other vertebrates in the Upper Cretaceous of Tunisia. Moreover, this study documents the first record from Africa of Cretaceous mammal tracks and the ichnogenera *A. federicianus* and *Koreanaornis*. *A. federicianus* was originally referred to an hadrosaur trackmaker. However, as hadrosaurs appear only in the Turonian, *A. federicianus* tracks should more likely be referred to more basal ornithopod, which might had a certain convergence in the foot morphology with younger hadrosaurs.

The presence *A. federicianus* in Tunisia and the Apulian platform is the first evidence of a possible connection between African and peri-Mediterranean ichnofaunas. The Tunisian vertebrate track record has therefore been compared with tracks form the mid-Cretaceous Italian and Croatian carbonate platforms in order to investigate further relations. In particular, three-dimensional models acquired by laser scanning the Tunisian theropod track molds have been compared with 3D models of Italian and Croatian theropods track molds. This comparison indicates some affinity in size and general morphology of the footprints, in addition to the similar lagoonal to near shore environments in which all theropod tracks were recovered. These new data suggest that, during mid-Cretaceous, a similar ichnofauna might have inhabited the northern African margin and the carbonate platforms of Italy and Croatia, supporting the hypothesis of the existence emerged lands connecting Africa to the southern Mediterranean platforms, which might explain the presence of large animals, such as dinosaurs, in the isolated settings of the Italian and Croatian carbonate platforms.

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Curriculum Vitae

Michela Contessi was born on 30th July in Ravenna, Italy. She attended the Dante Alighieri linguistic high school in Ravenna and after graduation she began studying Geoscience at the Alma Mater Studiorum University in Bologna. She graduated in October 2009 with a first class Honors degree. In January 2010 she began the PhD in Earth Science of which this thesis is the result.

Publications not included in the thesis, and meetings attended during this three years PhD are listed here:

PUBBLICATIONS:

- Contessi, M., Fanti, F., Hassine, M., Aljane, H., Handoura, M., 2011. Les empreintes des dinosaures dans la région de Tataouine. 4ème Colloque National du Patrimoine Géologique, Résumés et livret guide de l'excursion. Tabarka, Tunisia. Office National des Mines. pp. 9.
- Fanti F., Contessi M., Nigarov A. and Esenov P., New data on two large dinosaur tracksites from the upper Jurassic of eastern Turkmenistan (central Asia). Manuscript under review for Ichnos.
- Fiorillo A.R., Contessi M., Kobayashi Y., McCarthy, P, in press. Theropod tracks from the Lower Cantwell Formation (Late Cretaceous) of Denali National Park, Alaska, USA with comments about theropod diversity in an ancient high-latitude terrestrial ecosystem. In: Lockley, M.G., Lucas, S.G. and Spielmann, J.A., eds., 2013, Tracks of Western North America. New Mexico Museum of Natural History and Science, Bulletin 5?.

INTERNATIONAL MEETINGS:

- Contessi M., Fanti F. and Hadjane H., "New dinosaur dominated tracksites in the Late Jurassic and Early Cretaceous of southern Tunisia". Poster at the Society of Vertebrate Paleontology (S.V.P.) meeting, Las Vegas (U.S.A.), 1-6 November 2011.
- Fanti F., Contessi M. and Nigarov A., "New data on two large dinosaur tracksites from the Middle Jurassic of eastern Turkmenistan, central Asia". Poster at the Society of Vertebrate Paleontology (S.V.P.) meeting, Las Vegas (U.S.A.), 1-6 November 2011.
- Contessi M., Cantelli L., Fanti F., Gabbianelli G. and Mohsen H., "Southern Tunisia as an example of international partnership in cultural and geological heritage conservation **"**. Poster at the European Geological Union (E.G.U.) meeting, Vienna (Austria), 22-27 April 2012.
- Contessi M., Fanti F., Nigarov A. and Esenov P., "New data on dinosaur megatracksites from the Koitendag region, Lebap province, eastern Turkmenistan." Oral presentation at the International Meeting on The Turkmen Nature: Undiscovered Miracles of the Koytendag, Turkmenabat, Turkmenistan, 23-29 May 2012.
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