

Original Article

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Depositional model of the Eocene El Kohol Formation (Central Saharan Atlas, Algeria): integration of facies analysis, palaeontology and petrography

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Abstract

The present study documents the lithostratigraphy, biostratigraphy, facies evolution and depositional environments of the Eocene El Kohol Formation exposed on the southern flank of the Central Saharan Atlas (Algeria), through the integration of lithological characteristics, fossil and ichnofossil assemblages, and microfacies analysis. The succession is subdivided into two formal members: the Marly El Kohol Member, comprising a lower marlstone-dominated interval, and the Siliciclastic Kheneg ed Dis Member, representing an upper sandstone-dominated succession. The boundary between these members is marked by a transition from pale, carbonate-rich deposits to darker clastic sediments.

Field observations and microscopic analyses have enabled the recognition of sixteen facies types (Ft1–Ft16), which are interpreted in terms of depositional environment and grouped into four main facies associations (FA1–FA4): (FA1) an inland lake environment; (FA2) a palustrine environment, characterized by carbonate deposition in freshwater to brackish conditions with subaerial exposure and paedogenic modification; and alluvial settings comprising (FA3) fluvial channel and (FA4) floodplain deposits.

Palaeontological analyses have produced new micropalaeontological data for the region, including charophytes (*Sphaerochara parvula*, *Nodosochara* [*Turbochara*] sp., *Gyrogonia* sp., *Harrisichara* cf. *leptocera*, *Lamprothamnium papulosum*, *Peckichara torulosa* var. *varians*, *Raskyella* cf. *sahariana* and *Nitellopsis* cf. [*Tectochara*] *dutemplei*), ostracods (*Neocyprideis meguerchiensis*, *Paracypris*? sp. 1, *Paracypris*? sp. 2 and *Thalassocyprida*? sp. 1) and actinopterygian fish microremains (primarily from polypterids and alestids). Additionally, fragmentary remains of the terrestrial proboscidean *Numidotherium koholense* have been recovered. Ichnological analysis of the succession identified five ichnotaxa: *Ophiomorpha* isp., *Palaeophycus* isp., *Skolithos annulatus*, *Skolithos linearis* and *Thalassinoides horizontalis*.

This study contributes to refining the regional and North African understanding of the spatial extent and palaeoenvironmental evolution of the Eocene succession and helps to complete the ichnological and palaeontological records of the Eocene in the area.

1. Introduction

The Eocene succession of the Central Saharan Atlas (Djebel Amour, Algeria) has been the focus of geological mapping and research since the early 20th century (e.g. Flamand, 1911; Menchikoff, 1946; Cornet, 1949, 1952; Jodot, 1953; Galmier, 1972; Bassoullet, 1973). Over the past four decades, the Djebel El Kohol locality in Algeria has yielded significant palaeontological discoveries, with Mahboubi's fieldwork playing a crucial role in assisting palaeontologists in describing new mammal species. Crochet (1984) described *Garatherium mahboubii* from Early Eocene deposits, although its initial classification as a marsupial was later contested by Gheerbrant (1995), who reinterpreted it as a member of the Adapisoriculidae, an enigmatic group of early Palaeogene placentals. Mahboubi *et al.* (1986) reported two new mammal species:

Seggeurius amourensis and *Numidotherium koholense*. Notably, Crochet (1988) documented the earliest known *Creodonta* (*Kohalia atlasense*), and Buffetaut (1989) described a new sebecosuchian crocodyliform, *Eremosuchus elkoholicus*, based on fragmentary remains.

Microfossils, particularly charophytes and ostracods, were subsequently studied by Mebrouk *et al.* (1997, 2011, 2013) and Mebrouk and Feist (1999). In 1997, Mebrouk *et al.* identified 21 charophyte species in lower Eocene deposits of the Saharan Atlas and the northwestern Saharan Hammada, including six new taxa – *Raskyella sahariana*, *Harrisichara meguerchiensis*, *Peckisphaera bessediki*, *Gyrogonia caudata*, *Peckichara atlasensis* and *Neochara ameuriorum*. These were later described and illustrated by Mebrouk and Feist (1999), based on specimens collected from sites such as Oued Meguerchi (several kilometres west of Djebel El Kohol), Gours Lazib and Glib Zegdou. Further studies by Mebrouk *et al.* (2011, 2013) reported non-marine ostracods from lower Ypresian deposits in Djebel Amour, including two newly described species – *Neocyprideis meguerchiensis* and *Perissocytheridea algeriensis* – found alongside *Hemicyprideis* and *Limnocythere*.

Despite their excellent exposures, previous studies of this Eocene sedimentary succession have not integrated ichnological content, detailed facies analyses or comprehensive palaeoenvironmental interpretations. An integrated study of the continental Eocene outcrops of the Central Saharan Atlas (Algeria) is critical for understanding the palaeogeographic, environmental, and tectonic evolution of North Africa during the Palaeogene. These deposits preserve valuable records of non-marine sedimentary environments, including fluvial, lacustrine and palustrine systems, which are essential for reconstructing palaeoclimatic conditions and basin development in a region shaped by the early Alpine orogeny. Documenting and characterizing these outcrops improves regional stratigraphic correlations, refines palaeoenvironmental models at both local and North African scales and advances our understanding of biotic evolution through new fossil discoveries, thereby helping to fill critical gaps in the continental palaeontological record of the Eocene.

2. Geological background

Algeria is divided into three major geographical domains, each with distinct geological characteristics: from north to south, these are the Tellian domain, the Atlasic domain (Saharan Atlas) and the Sahara. The Tellian and Saharan Atlas domains correspond to two major southwest–northeast (SW–NE)-trending orogenic systems that developed as a result of the convergence between the African and Eurasian plates by the Late Cretaceous. They form part of the larger Maghrebide orogenic chain (Fig. 1a). The Atlas system consists of a series of intracontinental doubly plunging fold-and-thrust belts, including the Saharan Atlas and Aurès ranges in Algeria, the High and Middle Atlas in Morocco and the Tunisian Atlas Mountains (Fig. 1a).

The Saharan Atlas is a weakly deformed intracontinental range that extends over 700 km in a SW–NE direction, between the Moroccan High Atlas and the Aurès Range. To the south, it is bordered by the Saharan Basin – a flat, tectonically stable region with low-magnitude Phanerozoic deformation (Frizon de Lamotte *et al.* 2013). The southern margin of the Saharan Atlas is defined by the South Atlas Fault (SAF) system, a discontinuous series of faults (Jacobshagen, 1992). This mountain chain originated from an aborted Mesozoic rift that was later uplifted and moderately shortened during the Late Cretaceous–Cenozoic. It is traditionally

subdivided into three main subranges (Ritter, 1902): the Ksour Mountains (Western Saharan Atlas), the Djebel Amour (Central Saharan Atlas, the focus of this study; see Fig. 1b), and the Ouled Nail Mountains (Eastern Saharan Atlas).

Continental Eocene strata are widely exposed across the Saharan Atlas and the Sahara, particularly within narrow fold structures of the Central Saharan Atlas (e.g. Djebel El Kohol, Kheneg ed Dis, near Oued Meguerchi and Rhellal El Maya; Fig. 1c), on the plateaus of the northwestern Sahara (e.g. the Hammadas of Oum es Sebaa and Merdija, Gour Lazib, Glib Zegdou, Tizi N'Daguine and Gour Mohani) and in the Low Sahara (e.g. Tilmas Tezegguirine and Hassi el Biod). The present study focuses on an area located a few tens of kilometres south of the town of Brezina, on the northern flank of the Djebel El Kohol and Kheneg ed Dis area (Fig. 1b, c). This N–S-trending anticline lies at the southern margin of the Central Saharan Atlas, between latitudes N38°06'–N38°46' and longitudes E38°00'–E38°25'. It consists primarily of Upper Cretaceous marine strata and continental deposits ranging from the Eocene to the Pliocene (Figs. 1c, 2a), all deformed during the Atlasic phase of the Alpine orogeny, triggered by the late Eocene collision between the African and Eurasian plates (Angrand & Mouthereau, 2021). The folded Eocene continental succession at Djebel El Kohol and Kheneg ed Dis lies stratigraphically between the lower Turonian limestone substratum – corresponding to the *Rhondjaia Formation* (Bassoullet, 1973) – and the overlying Oligo-Miocene claystones and sandstones, commonly referred to as the '*Terrains des Gour*' (Flamand, 1911) or the *Hammada d'El Guerar Formation* (Flandrin, 1952).

3. Materials and methods

During a field campaign conducted in December 2022, three stratigraphic sections of the Eocene succession exposed between the periclinal closure of Djebel El Kohol and the Kheneg ed Dis area (Fig. 1c) and were measured along an approximately 10 km W–E transect. These sections were described and sampled, with detailed documentation of lithological variations, bed geometry, colour, grain size, allochemical components, textural features, key sedimentary structures, and fossil and trace fossil occurrences. These data allowed for the identification and description of individual facies, interpretation of depositional processes, and the grouping of cogenetic and contemporaneous facies into facies associations (FAs).

Thirty-nine representative samples were collected from key lithofacies – including limestones, marlstones, claystones and sandstones – for laboratory analysis, which included washing, slabbing and detailed examination. Nine thin sections were prepared for petrographic analysis to evaluate compositional constituents, textures, grain size, siliciclastic content and microfossil abundance. Diagenetic features and microfacies were also assessed. Carbonate textures were classified following Dunham (1962), as modified by Embry and Klovan (1971), while siliciclastic deposits were categorized according to Pettijohn *et al.* (1973). Thirty soft rock samples (marlstones and claystones) were soaked in water for several days, then disaggregated using a high-pressure water jet and sieved through a graded mesh sequence (300 µm, 250 µm, 180 µm and 125 µm). The residues were dried, steam-cooked and examined under a Euromex Dzet Optika ST-40-2L binocular stereomicroscope at the Faculty of Nature and Life Sciences, Mustapha Stambouli University of Mascara (Algeria), for microfossil identification. Selected specimens (ostracods,

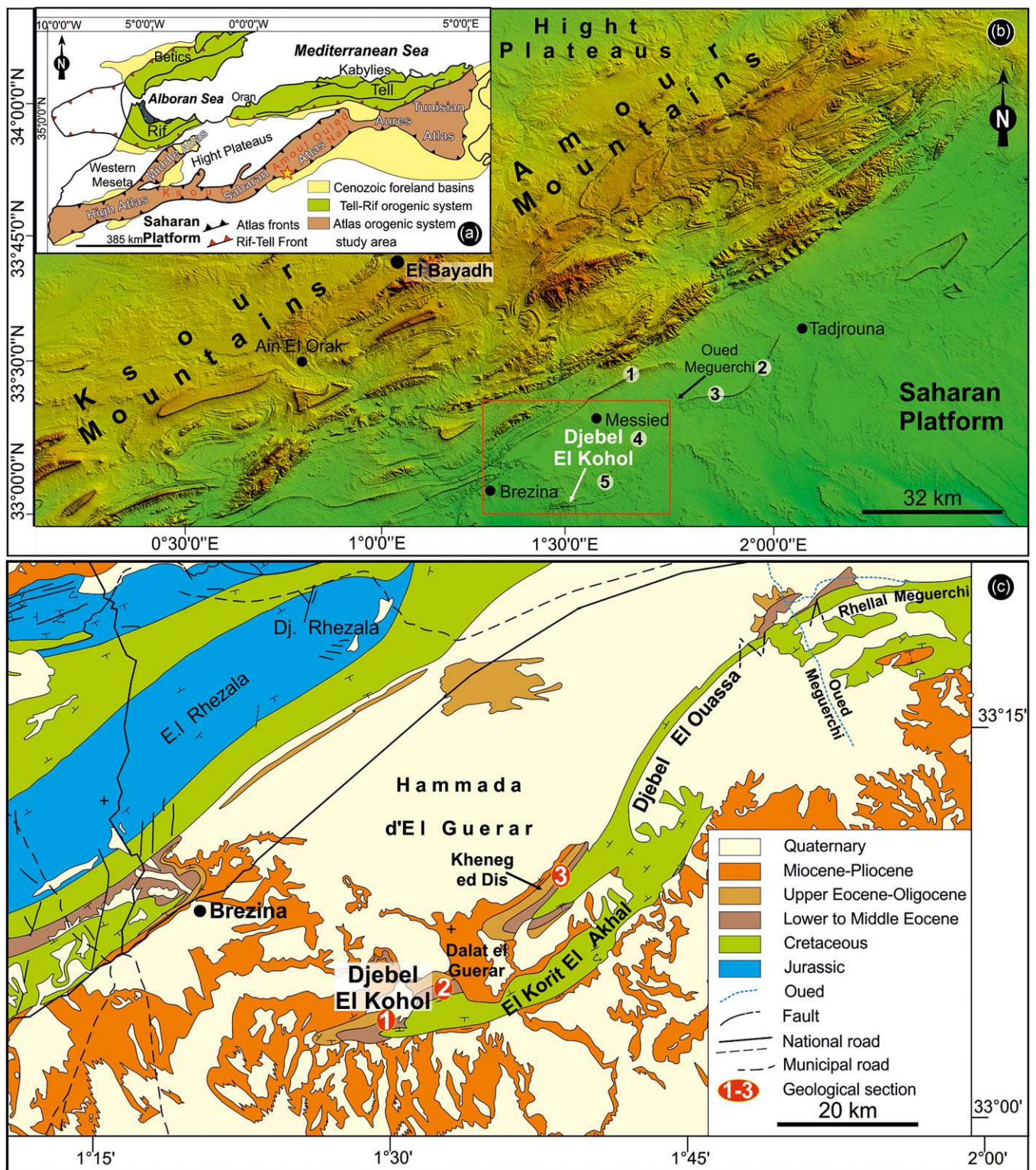


Figure 1. Geographic and geological framework of the study area. (a) Structural map of northwestern Africa (Maghreb) showing the main orogenic systems (the yellow star indicates the study area). (b) Satellite image indicating the location of the study area within the Djebel Amour (1- Djebel Messied, 2- Rhellal El Maya, 3- Rhellal Meguerchi, 4- Djebel El Ouassa, 5- Kheneg ed Dis). (c) Extract from the 1:50,000 geological map of Brezina, highlighting the position of the studied sections.

charophytes and fish remains) were mounted on stubs with double-sided carbon tape, carbon-coated and imaged using a Quanta 200 scanning electron microscope (SEM) at the Centres Científics i Tecnològics (CCiTUB), Universitat de Barcelona

(Spain). All fossil material is curated at the Laboratoire de Géomatique, Écologie et Environnement, Mustapha Stambouli University of Mascara (Algeria), under the collection acronym LGEE-Eoc-Koh.

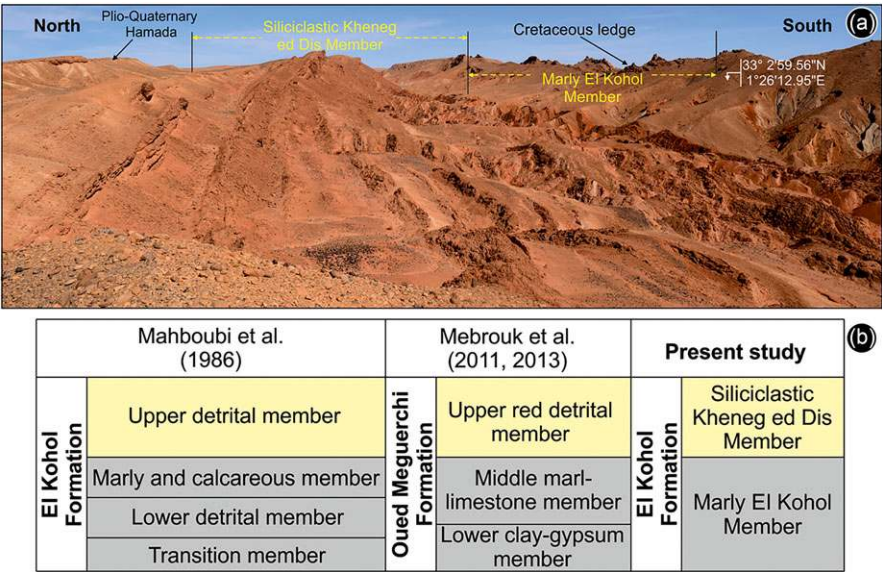


Figure 2. (a) Panoramic view of the main outcrops at Djebel El Kohol, illustrating the sharp contact between the Marly El Kohol Member and the overlying Siliciclastic Kheneg ed Dis Member (Central Saharan Atlas, Algeria). (b) Stratigraphic classification of the Eocene strata on the southern flank of Djebel Amour.

4. Results

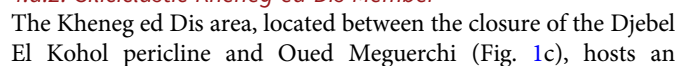
4.a. Stratigraphy

The geological importance of the Djebel El Kohol region was recognized early in the history of Saharan Atlas research by pioneering geologists (e.g. Flaman, 1911; Menchikoff, 1946; Cornet, 1949, 1952; Jodot, 1953). The first comprehensive stratigraphic framework of the Eocene succession was established by Mahboubi *et al.* (1986), who assigned the entire sequence to the El Kohol Formation and subdivided it into four members: the transition member, the lower detrital member, the marly and calcareous member and the upper detrital member. Subsequently, Mebrouk *et al.* (2011, 2013), with Mahboubi as co-author, proposed a revised nomenclature scheme for stratigraphically equivalent deposits located several kilometres eastward, formally designating them as the Oued Meguerchi Formation. This revised framework subdivided the succession into three members: a lower transitional clay-gypsum member, a middle limestone-mudstone member, and an upper red detrital member. However, neither Mahboubi *et al.* (1986) nor Mebrouk *et al.* (2011, 2013) provided detailed descriptions of the boundaries between these members, and our recent fieldwork did not allow their consistent recognition in outcrops (see Fig. 2a). Therefore, in the present study, we propose a slightly modified stratigraphic framework based on detailed analysis of three measured sections that span nearly continuous exposures from the western periclinal closure of the Djebel El Kohol anticline to the Kheneg ed Dis area. Within this updated context, the historically mammal-bearing El Kohol Formation (Mahboubi *et al.* 1986) is subdivided into two formal units. The Marly El Kohol Member, comprising the lower marlstone-dominated interval, and the Siliciclastic Kheneg ed Dis Member, representing the overlying sandstone-dominated succession (Figs. 2, 3). These members exhibit lateral continuity along the northern flank of the Djebel El Kohol anticline and are separated by prominent erosional discontinuity, characterized by abrupt facies shifts from pale carbonate-rich strata to darker clastic deposits.

4.a.1. Marly El Kohol Member

The type locality of the Marly El Kohol Member is situated on the northern flank of Djebel El Kohol, near the closure of the Djebel El Kohol pericline, approximately 10 km southeast of the town of

Brezina in El Bayadh province (Fig. 1). This unit forms a broad valley between the prominent Upper Cretaceous limestone ledge and the overlying Siliciclastic Kheneg ed Dis Member (Figs. 2–4) and is notable for yielding the historically significant mammalian fauna of the Central Saharan Atlas. The base of the Marly El Kohol Member rests with angular unconformity upon the lower Turonian limestone ledge of the upper Rhoundjaia Formation. This lowermost interval, 1.5–3 m thick, consists predominantly of reddish gypsiferous marl, locally overlain by thin, reddish to ochre sandstone channels. These bodies exhibit sharp erosional bases, extend laterally for several metres, and display planar and rippled laminations. Rare, poorly preserved freshwater gastropod moulds, including *Potamides* and *Ampullaria*, have been identified within these sandstones. The remainder of the succession is dominated by grey to greenish marlstone. In the central and eastern parts of the outcrop, the marl is interbedded with discontinuous, nodular to massive, cream- to beige-coloured lithified limestone beds (Ko3, Ko6, Ko14, Ko15' and Ko16), ranging from 0.20 to 1.30 m in thickness (Figs. 3, 4b, 4c). The marlstones form metre-scale packages, massive or displaying crude horizontal lamination. Washed residues from selected marly horizons have yielded charophyte gyrogonites, non-marine ostracods and opercula of the freshwater gastropod *Bithynia*. Vertebrate remains, including mammalian bones and teeth, actinopterygian fish elements and indeterminate freshwater turtles, have also been recovered from certain marly levels (e.g. Ko3, Ko4, Ko15 and Ko15' in Figs. 3, 4c). Microfacies analysis reveals mudstone to wackestone textures containing ostracod shells, cyanobacterial/algal microstructures, oncoids and scattered fine-grained quartz. Bioturbation, brecciation and rhizoliths are commonly observed at the upper contacts of some limestone beds, while the basal contacts show no evidence of subaerial exposure. Freshwater pulmonate and other gastropods are frequently encountered within certain limestone beds, notably Ko14. In contrast, the western part of the section lacks calcareous beds, and the marlstones attain their maximum thickness (Figs. 3, 4a). Based on the associated charophyte assemblages (see below), the Marly El Kohol Member is chronostratigraphically assigned to the lower Ypresian (early Eocene). The temporal framework established by magnetostratigraphic studies of the mammal-bearing strata (Ko15' equivalent) as reported by Costeur *et al.*



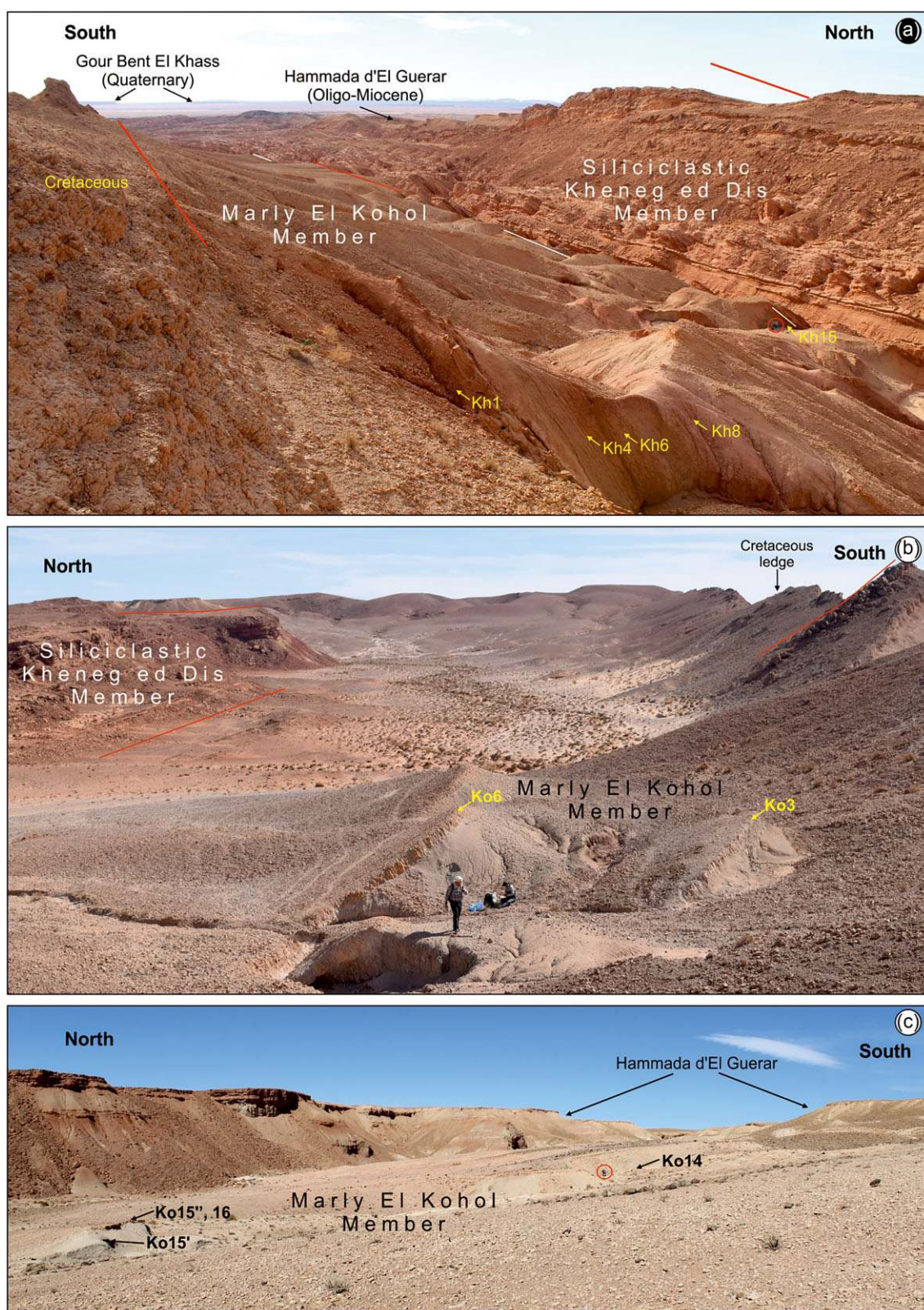


Figure 4. Panoramic views of the studied Eocene succession in the Djebel El Kohol region (Central Saharan Atlas, Algeria). (a) Outcrop near the western periclinal termination of the Djebel El Kohol. (b) General view of the middle part of Djebel El Kohol section. (c) Outcrop in the Kheneg ed Dis area. Scale in (a) and (c) is provided by a person encircled in red (height = 1.65 m).

extensive outcrop of the upper part of the Eocene El Kohol Formation and serves as the type locality for the Siliciclastic Kheneg ed Dis Member. This unit forms a broad, dark-coloured,

decametre-thick ledge that lies stratigraphically between the Marly El Kohol Member and the overlying Hammada d'El Guerar Formation (Figs. 2–4).

The Siliciclastic Kheneg ed Dis Member is readily distinguishable from surrounding deposits due to its distinctive dark colouration and sedimentary characteristics. It displays lateral continuity over several kilometres, with no significant thickness variation and no significant pinch-outs. The lower boundary is a sharp erosional unconformity separating the basal siliciclastic deposits from the Marly El Kohol Member. The upper boundary is marked by an angular disconformity beneath the pale-coloured sandstones and clays of the Hammada d'El Guerar Formation. Lithologically, the Siliciclastic Kheneg ed Dis Member consists primarily of alternating reddish channelized and tabular sandstone beds interbedded with decimetre- to metre-thick intervals of greenish and reddish claystone and silty claystone. The sandstone beds exhibit lateral continuity over distances up to 500 m, though individual beds may vary in thickness and sedimentary structures over short distances.

The lower part of the member is clay-dominated, comprising red mudstone interbedded with fine-grained sandstone. These sandstones are typically structureless or exhibit small-scale trough cross-lamination, planar cross-lamination, horizontal lamination and ripple-laminated tops. Stratigraphically upward, the member becomes increasingly sandstone-dominated, forming cyclic fining-upward sequences. These include laterally and vertically discontinuous conglomerate and pebbly sandstone bodies, trough and planar cross-stratified sandstones, ripple cross-laminated and horizontally stratified sandstones, highly bioturbated sandstones and occasionally deformed beds transitioning into undeformed sandstone layers of similar composition and texture. At the outcrop scale, these sandstone bodies are generally tabular, although lateral wedging is common, with interfingering fine-grained sediments. They display locally erosional bases with flute casts and tool marks.

Conglomerate beds exhibit scoured bases, sharp upper contacts, and restricted lateral continuity, generally only a few metres wide in outcrop. These beds grade upward and laterally into sandstone and range in thickness from 0.3 to 1.2 m. They display matrix- to clast-supported fabrics, with reddish-brown mudstone and polygenic carbonate clasts ranging from 0.5 to 10 cm in diameter. The colour of these deposits varies from reddish-brown to mottled purple.

Macrofossils are rare, limited to occasional moulds of terrestrial pulmonate gastropods (*Strophocheilidae* indet.). Due to the dominance of siliciclastic lithologies, no microfossils have been recovered from this member. Nevertheless, based on its stratigraphic position above the lower Eocene Marly El Kohol Member and its sedimentological characteristics – consistent with the tectonic inversion and orogenic development of the Atlas System – the Siliciclastic Kheneg ed Dis Member is chronostratigraphically assigned to the lower-middle Eocene.

4.b. Facies analysis and depositional environments

The studied Eocene El Kohol Formation consists primarily of carbonate and siliciclastic deposits, with minor evaporitic sediments occurring at the base of the succession. Sixteen representative sedimentary facies types (Ft1–Ft16) have been identified and grouped in four distinct lithofacies assemblages (facies associations FA1 to FA4), each corresponding to a specific depositional environment: (1) Inland lake environment (FA1); (2) Palustrine environment (FA2); (3) Alluvial environments, represented by floodplain (FA3) and fluvial channel (FA4) deposits. Descriptions and interpretations of the facies types and their associated FAs are provided below and summarized in Table 1.

4.b.1. Types of sedimentary facies

4.b.1.a. Facies Ft1: ostracod limestone

Description. This facies is best exposed in the central and eastern outcrops of the Marly El Kohol Member. It consists of compact, tabular beds ranging from cream to grey in colour and varying in thickness from 0.30 to 1.3 m, which can be traced laterally for tens of metres. The beds are predominantly of wackestone texture and contain thin, monospecific, non-marine ostracod shells, both articulated and disarticulated. Subordinate clotted micritic textures and cyanobacterial/algal microstructures are also present (Fig. 5a, b). Bioturbation structures and coarse silt-sized (40–60 µm) detrital quartz grains are occasionally observed in petrographic thin sections.

Interpretation. The wackestone texture, combined with the presence of both articulated and disarticulated non-marine ostracod shells, suggests deposition in a low-energy, nearshore lacustrine environment. The scarcity of clastic detritus further indicates that these carbonates were deposited in settings protected from significant terrigenous input. This microfacies is consistent with the lacustrine freshwater microfacies type (LMF 8) described by Clausen (1990) and Flügel (2010).

4.b.1.b. Facies Ft2: cyanobacterial/algal limestone

Description. This facies is developed in the eastern part of the study area within the Marly El Kohol Member, immediately overlying the mammal-bearing marlstone interval. It consists of compact and well-cemented limestones, ranging in colour from cream to dark grey, forming tabular beds of 0.4–1.0 m thick. Microfacies analysis reveals a cyanobacterial/algal boundstone characterized by a thrombolite-like clotted microstructure and abundant fine-grained bioclasts (Fig. 5c). Additional features include desiccation cracks and scattered fine-grained quartz grains.

Interpretation. Macrofossils and charophyte debris are notably absent in the laminated intervals. Nevertheless, a lacustrine origin is inferred based on the presence of thin lamination and fine-grained bioclasts. The occurrence of algal laminae, desiccation cracks, and the lack of facies indicative of high-energy shoreline (e.g. grainstone) or deeper open-lake (e.g. wackestone) environments collectively suggest deposition in a low-energy, shallow lacustrine setting with intermittent subaerial exposure and periodic desiccation. This interpretation is consistent with comparable facies described in similar palaeoenvironmental contexts (Platt & Wright, 1991; Alonso-Zarza *et al.* 1992; Armenteros *et al.* 1997).

4.b.1.c. Facies Ft3: oncoid limestone

Description. This facies occurs in the middle part of the Marly El Kohol Member. Macroscopically, it comprises grey to green, compact, well-cemented limestone beds (0.30–0.60 m thick) containing mammal bones, freshwater gastropods (*Elimia* sp.), coprolites and scattered quartz grains. Thin-section analysis reveals an oncoid wackestone/floatstone microfacies dominated by abundant porostromate and agglutinated oncoids (Fig. 5d–e). Additional components include non-marine ostracods, cyanobacterial/algal structures, root-related features (rhizoliths), and evidence of bioturbation (Fig. 5e–f). The matrix consists of dense to clotted micrite with numerous fine-grained bioclasts. Some samples display vuggy porosity infilled with silt (Fig. 5e–f).

Interpretation. The fossil assemblage of facies Ft3 indicates deposition within a shallow, freshwater lacustrine setting.

Table 1. A summary of facies and facies associations of the Eocene El Kohol Formation (Algeria)

Facies types	Brief description	
Ft1. Ostracod limestone	Limestone beds (0.30–1.3 m thick) exhibit wackestone texture, dominated by thin, monospecific non-marine ostracod shells (articulated and disarticulated), with subordinate clotted micrite and cyanobacterial/algal microstructures.	
Ft2. Cyanobacterial/algal limestone	Tabular limestone beds (0.4–1.0 m thick) exhibit algal boundstone microfacies with desiccation cracks and dispersed fine-grained quartz.	
Ft3. Oncoid limestone	Limestone beds (0.30–0.60 m thick) displaying an oncooid wackestone to floatstone microfacies, characterized by abundant porostromate and agglutinated oncoids, scattered non-marine ostracods, cyanobacterial/algal structures and root-related features (rhizoliths).	
Ft4. Peloidal-intraclastic limestone	Pseudonodular limestone beds (0.05–0.20 m thick) with a dense micritic matrix, containing dark subspherical clasts, micritic peloids, rhizoliths and evidence of brecciation.	
Ft5. Massive marlstone	Massive to rarely parallel-laminated intervals (2–60 m thick) contain fish and turtle remains, mammalian teeth, charophyte gyrogonites, non-marine ostracods and freshwater gastropod opercula (e.g. <i>Bithynia</i>), with no evidence of subaerial exposure.	
Ft6. Mammal-rich marlstone	Massive marlstone beds (1.5–2.8 m thick) rich in charophytes and numerous <i>Numidotherium koholense</i> specimens.	
Ft7. Gypsiferous marlstone	Discontinuous reddish marlstone beds (1.5–3 m thick) with abundant discoidal and radial gypsum crystals, lacking fossil content.	
Ft8. Clastic mudstone (claystone and silty claystone)	Reddish-brown to greenish-grey claystone, barren of fossils or organic matter, with occasional laminated siltstone-claystone couplets, desiccation cracks and flame-structured, meniscus-filled burrows.	
Ft9. Sandstone with even-parallel stratification	Well-sorted fine- to medium-grained sandstone (10 cm to >1 m thick) with tabular geometry, horizontal laminae, asymmetrical ripple marks and bioturbation including <i>Skolithos</i> and unidentified horizontal to inclined burrows.	
Ft10. Sandstone with soft-sediment deformation	Fine- to medium-grained sandstone beds (25–90 cm thick) exhibit soft-sediment deformation features such as small-scale slumps and irregular load casts.	
Ft11. Trough cross-stratified sandstone	Fine- to medium-grained channelized sandstone beds (15 cm to >70 cm thick) display trough cross-stratification, repeated fining-upward trends, erosional bases and sharp upper contacts.	
Ft12. Planar cross-stratified sandstone	Fine- to medium-grained sandstone beds (0.10–1 m thick) show planar cross-stratification, sharp basal contacts and occasional ripple marks.	
Ft13. Burrowed sandstone	Fine-grained sandstone beds (0.5–1.1 m thick) display dense vertical burrows of non-marine <i>Skolithos linearis</i> , with minor traces of <i>Thalassinoides</i> , <i>Palaeophycus</i> and <i>Ophiomorpha</i> .	
Ft14. Structureless sandstone	Massive fine- to medium-grained sandstone beds (0.2–1.2 m thick) with sharp erosional bases; mostly structureless, locally bioturbated with <i>Skolithos</i> and <i>Ophiomorpha</i> trace fossils.	
Ft15. Structureless pebbly sandstone	Discontinuous, massive sandstone beds (0.15–0.8 m thick) with coarse to pebbly grains, well-sorted subrounded to well-rounded clasts, sharp erosive bases and flat tops.	
Ft16. Structureless conglomerate	Channelized, lenticular conglomerate beds (<2 m thick) with scoured contacts, ranging from clast- to matrix-supported.	
Facies association	Facies types	Depositional setting
FA1	Ft1, Ft2 and Ft5 to Ft7	Open lacustrine
FA2	Ft3 and Ft4	Palustrine
FA3	Ft8 to Ft16	Fluvial channel
FA4	Ft8 and Ft11 to Ft13	Floodplain

Lacustrine oncooids typically develop in nearshore zones of lakes where moderate wave or current energy facilitates their formation by rolling or agitation, with detrital grains or shell fragments acting as nuclei for growth (Lanès & Palma, 1998; Hargrave *et al.* 2014).

The presence of rhizoliths, bioturbation structures and freshwater fauna further supports deposition in a marginal lacustrine environment with periodic subaerial exposure and colonization by vegetation.

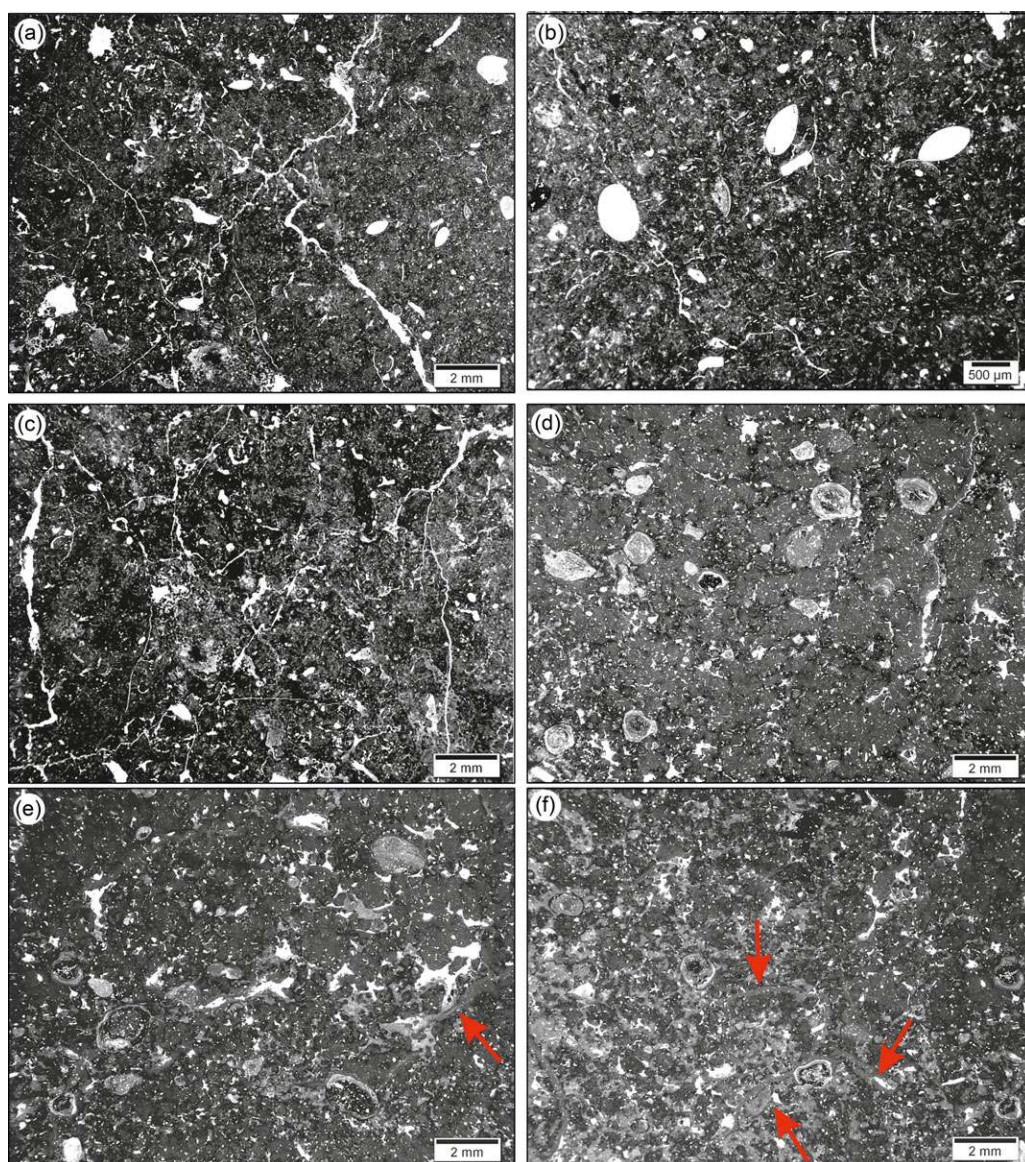


Figure 5. Microfacies (plane-polarized light photomicrographs) from the Eocene Marly El Kohol Member (Algeria). (a) and (b), Ostracod wackestone: numerous fine-grained bioclasts (articulated or disarticulated ostracods), clotted micrite, and cyanobacteria/algal-derived structures. (c) Microbial/algal boundstone: thrombolite texture with clotted fabric, fine-grained bioclasts and spar-filled shrinkage cracks. (d–f) Oncolite wackestone with diverse oncolites (porostromate/agglutinated), disarticulated ostracods, algal structures, and root-related features (rhizoliths; red arrows). The matrix includes dense/clotted micrite with vadose silt in voids.

4.b.1.d. Facies Ft4: peloidal-intraclastic limestone

Description. This facies is observed in the lower part of the Marly El Kohol Member and crops out in the central part of the study area. It consists of cream-coloured, pseudonodular limestone beds (0.05–0.20 m thick) arranged in decimetric units. Microscopic examination reveals a dense micritic matrix containing isolated, dark, subspherical clasts and rounded to angular micritic peloids (Fig. 6a, b). Carbonate grains exhibit regular to irregular micritic or microsparitic laminae (Fig. 6a, b). Root-related structures (rhizoliths) are common and appear as tubular, branched voids left by decayed roots, now infilled with microspar (Fig. 6c–e). Diagenetic features include vadose micritic cement and blocky calcite cement, the latter often filling microkarst cavities (Fig. 6d–f). Evidence of brecciation, intense root activity, and dissolution is also widespread (Fig. 6b, e).

Interpretation. The presence of subaerial exposure features – such as rhizoliths, brecciation and microkarstification – alongside peloidal grains indicates deposition in marginal lake settings within a palustrine environment (Moreau *et al.* 2024). Shallow-water conditions are supported by the occurrence of rootlet-related porosity (likely associated with emergent or submerged vegetation) and vadose

diagenetic signatures. This facies thus reflects sedimentation in a sublittoral zone of low-energy, low-gradient carbonate lakes. The proposed depositional environment is consistent with established interpretations of palustrine systems in open lacustrine basins (Freytet & Plaziat, 1982; Allen & Collinson, 1986; Platt, 1989; Bohacs *et al.* 2000; Moreau *et al.* 2024). Within the sedimentary succession, this facies type, characterized by cyclic occurrences of brecciation, microkarst features, and root mark structures, is interbedded with subaqueous sediments (see Fig. 6c).

4.b.1.e. Facies Ft5: massive marlstone

Description. Marlstone deposits constitute the dominant lithology of the Marly El Kohol Member. They appear as light grey to greenish, massive or rarely parallel-laminated intervals ranging from 2 to 60 m in thickness and are occasionally interbedded with limestone beds (Ft1 to Ft4; see Fig. 7a) and sandstone beds (Ft14). Certain intervals contain common to abundant vertebrate remains, including fragments of fish and turtles and mammalian teeth (Fig. 7b, c), as well as charophyte gyrogonites, articulated non-marine ostracod valves and opercula of freshwater gastropods (e.g. *Bithynia*). Notably, no subaerial exposure features have been observed in this facies.

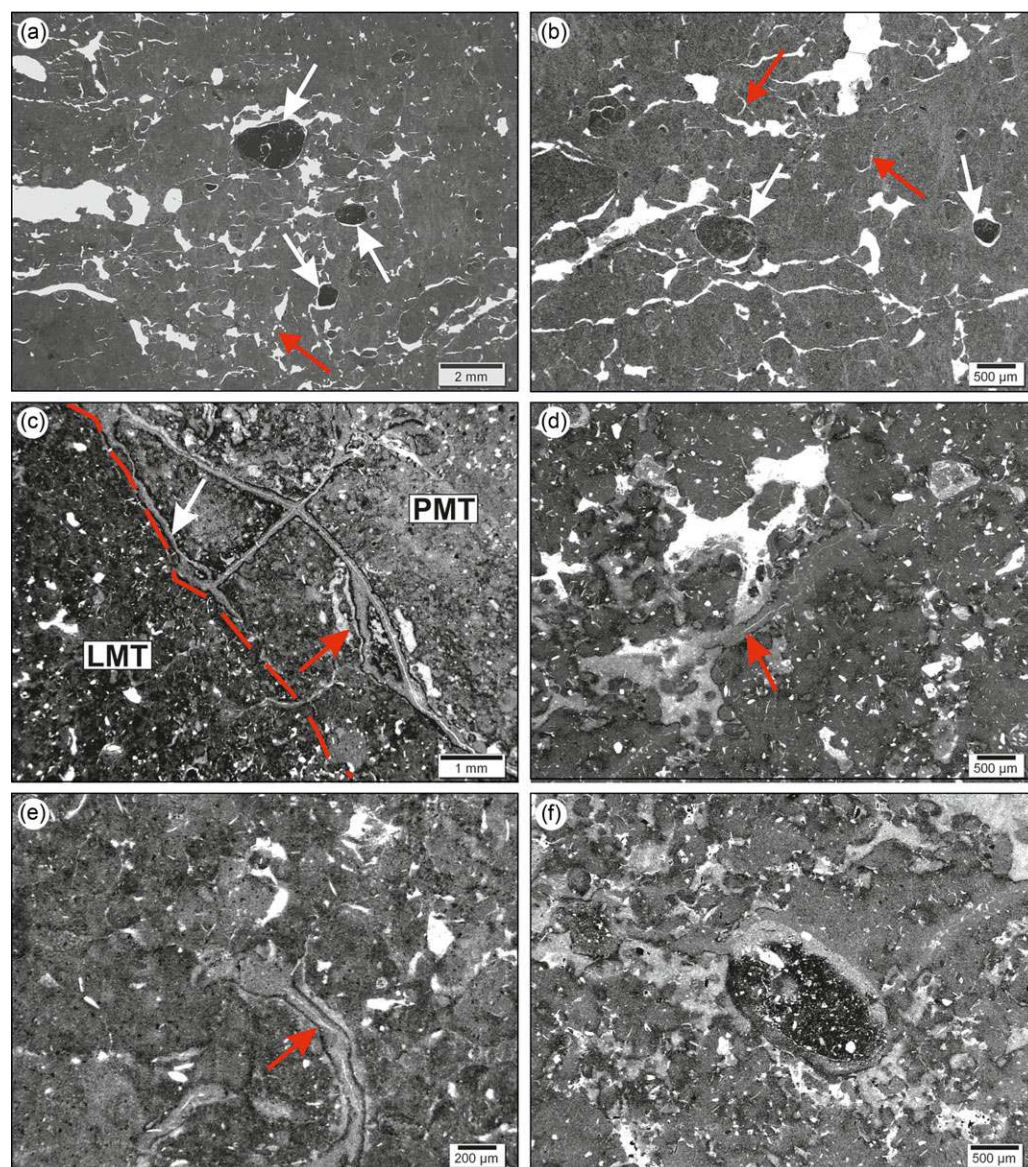


Figure 6. Microfacies (plane-polarized light photomicrographs) from the Eocene Marly El Kohol Member (Algeria). (a) and (b), Lime mudstone with circumgranular cracks (white arrows) around micritic nodules, spar-filled shrinkage cracks and branching voids (red arrows; interpreted as root moulds). (c–f), Secondary (paedogenic) carbonates with clotted micritic, root traces, in situ brecciation and pervasive vadose micritic cement. (c) Dashed red line indicates contact between lacustrine (LMT; Ft2) and palustrine (PMT) microfacies types.

Interpretation. This marly facies is interpreted as recording deposition in a low-energy aquatic environment characterized by the simultaneous accumulation of fine-grained terrigenous clastic material and carbonate mud. The presence of non-marine ostracod tests, charophyte remains and Bithyniidae gastropods indicates a freshwater lacustrine to palustrine setting (Glöer, 2002; Wesselingh & Wilke, 2015). The occurrence of articulated ostracod valves – whose fragile carapaces typically disarticulate after death – suggests overall calm, shallow-water conditions punctuated by intermittent high-energy events (e.g. currents capable of reworking and transporting bioclasts, such as fish and turtle remains). Comparable marly facies are well-documented in the Lower Cretaceous of the Cameros Basin, Spain (Platt, 1989, 1995; Platt & Pujalte, 1994; Quijada *et al.* 2014), where they have similarly been interpreted as open lacustrine deposits.

4.b.1.f. *Facies Ft6: mammal-rich marlstone*

Description. This facies is well developed in the upper part of the Marly El Kohol Member, particularly in the eastern part of the studied area. It consists of a grey to greenish, structureless

marlstone interval ranging from 1.50 to 2.8 m in thickness (Fig. 7d). Fossil content includes abundant charophyte remains and numerous specimens of *Numidotherium koholense*, one of Africa's earliest and most primitive known proboscideans.

Interpretation. Although *Numidotherium koholense* has been interpreted as exhibiting terrestrial adaptations (Mahboubi *et al.* 2014), its association with charophyte remains within this facies suggests deposition in a lakeshore setting. The coexistence of terrestrial mammal fossils and aquatic algae is consistent with marginal lacustrine environments that experienced periodic subaerial exposure or proximity to vegetated lake margins.

4.b.1.g. *Facies Ft7: gypsiferous marlstone*

Description. This facies occurs exclusively in the lower part of the studied succession, immediately overlying the erosional surface that marks the base of the Marly El Kohol Member. It is represented by discontinuous, reddish marlstone intervals, 1.5–3 m thick, containing abundant discoidal and radial gypsum crystals. Fossil remains are entirely absent.

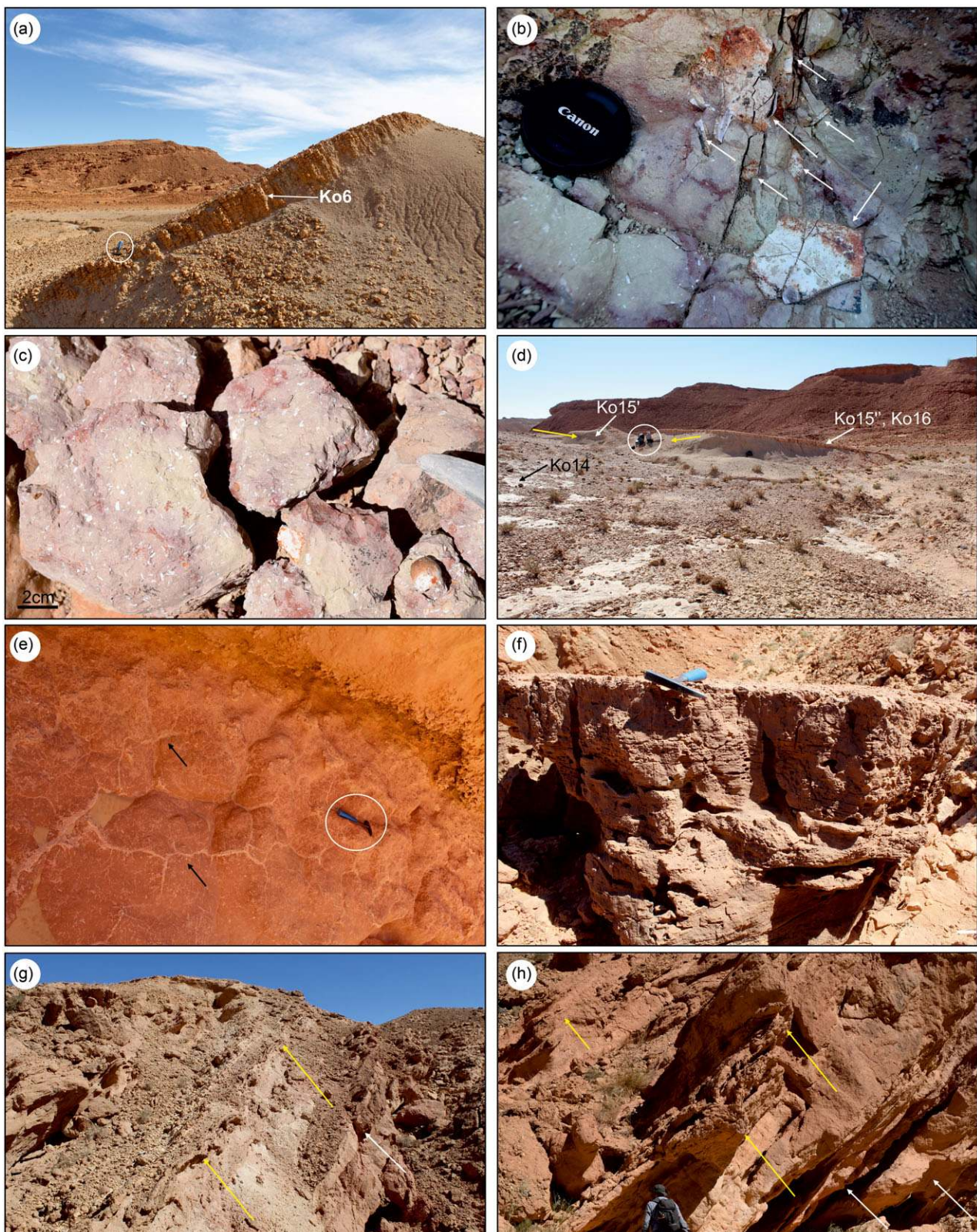


Figure 7. Field photographs from the Eocene El Kohol Formation (Algeria). (a) Pseudonodular limestone bed interbedded within the massive marlstone facies; (b) and (c), Fossiliferous greenish marlstone (Ko15), rich in fish debris and turtle shell fragments (arrows); (d) Horizon of green marlstone yielded *Numidotherium koholense* remains; (e) Reddish mudstone with mud cracks (arrows); (f) Sandstone with even-parallel stratification (Ft9); (g) and (h), Soft-sediment deformation in sandstone beds (yellow arrows) transitioning into undeformed layers (Ft10). White arrows show irregular base surfaces (channels). Scale: hammer (28 cm), lens cap (7 cm).

Interpretation. Deposition of this facies reflects calm-water conditions that promoted the settling of fine-grained suspended sediments. The occurrence of gypsum within the marlstone indicates arid climatic conditions and deposition in an evaporative lacustrine (playa) environment, characterized by alternating precipitation of sulphate minerals and fine-grained carbonate mud. Gypsiferous marlstone facies are commonly documented within saline mudflats on the margins of modern playas (Hardie *et al.* 1978; Handford, 1982).

4.b.1.h. *Facies Ft8: clastic mudstone (claystone and silty claystone)*

Description. This facies is composed predominantly of reddish-brown to dark-brown claystone, with some lateral horizons exhibiting greenish-grey colouration and lacking fossils or organic matter. It is interbedded with sandstone beds and dominates the lower part of the Siliciclastic Kheneg ed Dis Member, forming weathered slopes. It shows both lateral and vertical transitions into sandstone facies. Most of the mudstones are massive, although occasional laminated siltstone-claystone couplets occur. Locally, desiccation cracks (Fig. 7e) and flame-meniscus-filled burrows are observed. Carbonate nodules, ranging from a few millimetres to several centimetres in diameter, are sporadically present and show variability in shape and distribution density.

Interpretation. The observed lateral and vertical transitions into sandstone facies suggest that the clastic massive mudstone facies formed through the settling of clay and silt from suspension on an alluvial plain. Deposition likely took place under subaqueous, lower-flow-regime currents, representing overbank deposits or abandoned channels. The laminated siltstone-claystone couplets probably record individual flood events that overtopped levees (Allen, 1965), with each couplet corresponding to a single flood event outside the main channels. The overall absence of preserved sedimentary structures may result from post-depositional compaction or bioturbation. Desiccation cracks on depositional surfaces indicate episodes of subaerial exposure, while the presence of carbonate nodules points to paedogenic processes, comparable to caliche development in semiarid regions. The reddish colouration reflects well-drained, oxygenated soil conditions (Driese & Ober, 2005).

4.b.1.i. *Facies Ft9: sandstone with even-parallel stratification*

Description. This facies is present especially throughout the Siliciclastic Kheneg ed Dis Member. It consists of well-sorted, fine- to medium-grained sandstone with a tabular geometry, characterized by continuous horizontal laminae (Fig. 7f) expressed as subtle colour and grain-size variations. Bed thickness ranges from 10 cm to over 1 m, and the bases are typically sharp. Asymmetrical ripple marks occasionally occur on upper bed surfaces. Some beds display vertical transitions from structureless to parallel-laminated textures. Unidentified horizontal to slightly inclined burrows preserved in concave epirelief on ripple-marked sandstone surfaces, along with occasional *Skolithos*, are observed.

Interpretation. The persistent horizontal lamination, good sorting and lack of significant vertical grain-size variation suggest deposition under stable flow conditions. Weakly erosional to non-erosional basal contacts indicate unchanneled settings. Facies Ft9 likely represents an upper-flow-regime plane bed developed on sandbar tops (Miall, 1977). *Skolithos* ichnofossil is a common component of fluvial and other continental deposits (e.g.

Netto, 2007; Hasiotis, 2010; Melchor *et al.* 2012), where insects (e.g. midge larvae) are inferred to be the primary trace makers. Ripple-marked surfaces and occasional bioturbation may reflect shallowing-upward trends or waning flow conditions. Similar deposits have also been interpreted as unconfined flow deposits on a floodplain (North & Davidson, 2012).

4.b.1.j. *Facies Ft10: sandstone with soft-sediment deformation*

Description. Facies Ft10 occurs in the middle part of the Siliciclastic Kheneg ed Dis Member. It consists of fine- to medium-grained sandstone forming 25–90-cm thick intervals interbedded with other sandstone facies. Bedding is occasionally disrupted by soft-sediment deformation, including small-scale, asymmetrical and irregular load casts measuring a few centimetres, observed at the interfaces between sandstone beds and claystone layers. Additionally, contorted and deformed laminae are present, forming small-scale slump structures (Fig. 7g, h) that range from a few decimetres up to 1 m in size. These slumps exhibit folds with varying degrees of deformation.

Interpretation. Soft-sediment deformation structures (SSDSs) typically develop in unconsolidated sediments prior to lithification. A variety of processes can generate such deformation. Slumps generally require relatively steep slopes, although they can also form on gradients as low as 1° (Mills, 1983). Seismic activity has been linked to the occurrence of slumps and slides even in low-gradient settings (Rossetti & Góes, 2000). Load structures can result from differential density loading (Allen, 1981) and from sediment liquefaction in response to gravitational instability between layers (Owen, 1987). Hilbert-Wolf *et al.* (2016) describe SSDSs in Cretaceous braided fluvial deposits (SW Tanzania) as gas-escape structures genetically linked to seismic shocks. Rana *et al.* (2016) report SSDSs in Late Pleistocene–Holocene fluvial deposits, demonstrating consistent relationships among the types of SSDSs, the deformed facies and the associated overloading processes.

4.b.1.k. *Facies Ft11: trough cross-stratified sandstone*

Description. This facies is observed sporadically in the basal part of the Marly El Kohol Member and more frequently at various stratigraphic levels within the Siliciclastic Kheneg ed Dis Member. It consists of fine- to medium-grained sandstone beds exhibiting trough cross-stratification, with individual beds ranging in thickness from several centimetres up to 70 cm. The beds are channelized (Fig. 8a, b) and are commonly associated with planar cross-stratified and planar-stratified sandstones. Facies Ft11 exhibits, in some cases, repeated fining-upward trend (Fig. 8b, c). Palaeocurrent directions obtained from cross-strata indicate a dominant southwestward axial flow. The lower and upper contacts of facies Ft11 are erosional and sharp, respectively, with the adjacent units.

Interpretation. This facies reflects sediment transport by unidirectional currents and deposition by migrating subaqueous dunes with sinuous crests (3D dunes and bars) under lower-flow-regime conditions (Miall, 1977, 1996; Hjellbakk, 1997). Each fining-upward succession may record deposition during waning flow (falling flood stage) or gradual abandonment of fluvial channels (Moretti & Ronchi, 2011).

4.b.1.l. *Facies Ft12: planar cross-stratified sandstone*

Description. This facies is present throughout the Siliciclastic Kheneg ed Dis Member. It consists of fine- to medium-grained sandstone, with bed thicknesses ranging from 0.10 to 1 m. The sandstone exhibits planar cross-stratification (Fig. 8d),

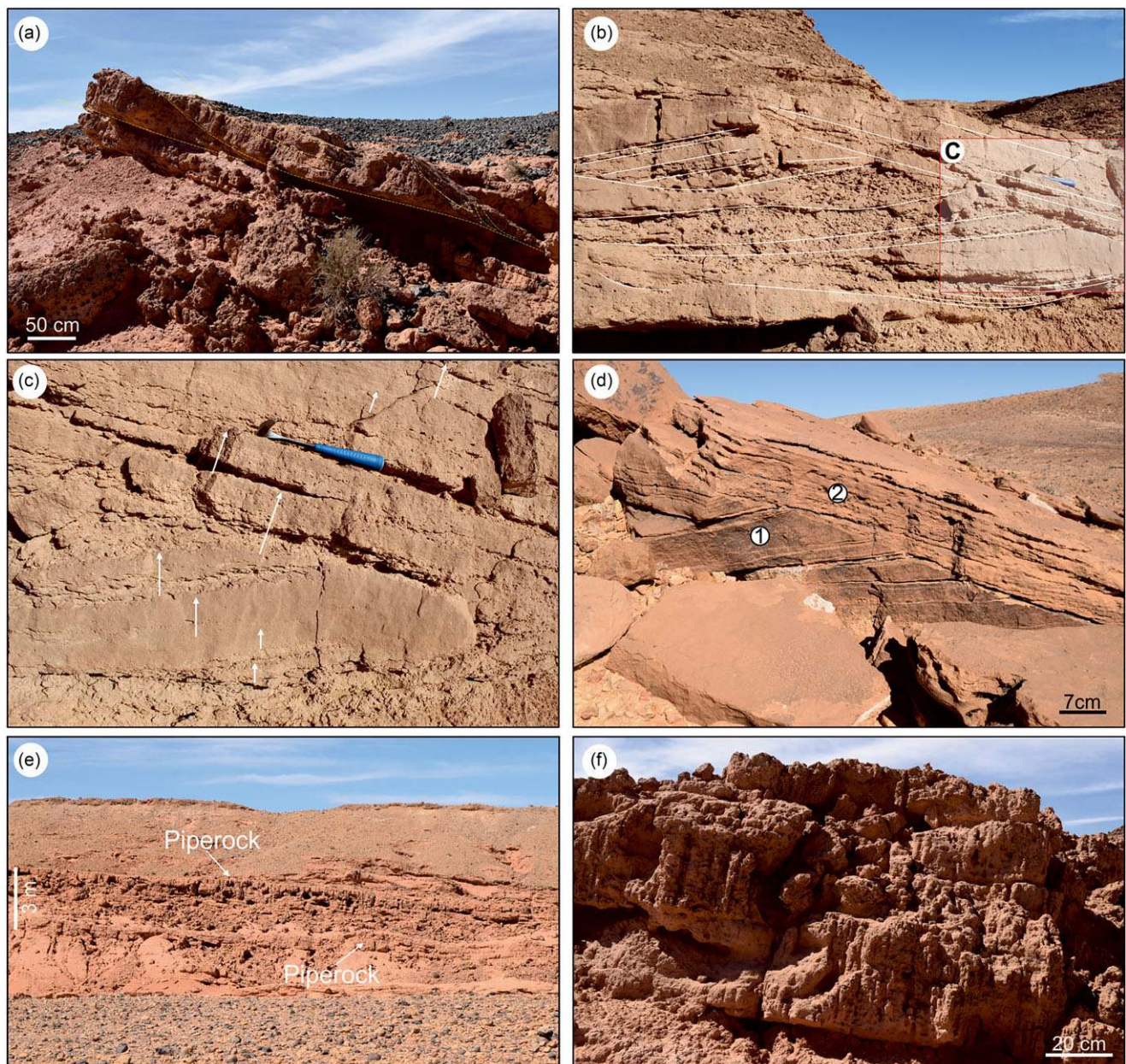


Figure 8. Field images of Eocene siliciclastic facies at Djebel El Kohol (Algeria). (a–c) Sandstone facies with trough cross-stratification (Ft11), erosional basal surfaces (a), and repeated fining-upward trends (arrows). (d) Planar cross-stratified sandstone (1) overlain by horizontally stratified sandstone (2); (e–f), Sandstone with dense *Skolithos*-dominated piperock ichnofabric (Ft13). Hammer (28 cm) shown for scale.

occasionally accompanied by subordinate ripple marks. Beds have sharp basal contacts and are commonly interbedded with red claystone (Ft8), sandstone with even-parallel stratification (Ft9) and trough cross-stratified sandstone (Ft11).

Interpretation. Planar-cross-stratification indicates lower-flow-regime conditions and is associated with 2D subaqueous sand dunes developed along transverse rather than longitudinal bars (Boggs, 2006). These features suggest deposition on floodplain areas or within channels during periods of low water level or waning flow (Hjellbakk, 1997).

4.b.1.m. Facies Ft13: burrowed sandstone

Description. This facies is best developed in the middle and upper parts of the Siliciclastic Kheneg ed Dis Member. It consists of

sandstone beds exhibiting an ichnoassemblage dominated by densely packed vertical dwelling burrows of the non-marine *Skolithos linearis* (Fig. 8e, f). Locally, minor occurrences of *Thalassinoides*, *Palaeophycus* and *Ophiomorpha* are also present. Individual beds of facies Ft13 range from 0.5 to 1.1 m in thickness, extend laterally for tens to hundreds of metres in outcrop, and display irregular bases with lateral gradation into the overlying sandstone facies. These beds are intercalated with red and green claystone.

Interpretation. Dense accumulations of *Skolithos linearis* are commonly referred to as piperocks. The term ‘piperock’ was first introduced by Peach and Horne (1884) to describe similar dense assemblages of *Skolithos* in the Lower Cambrian Eriboll Sandstone of Scotland. Piperocks are traditionally regarded as a classic

Cambrian ichnofabric indicative of shallow marine environments (e.g. Crimes & Anderson, 1985). However, occurrences in non-marine settings are rare and have been variably interpreted as a distinct ichnocoenosis within the *Scoyenia* ichnofacies (Bromley & Asgaard, 1979; Collinson, 1996; Fitzgerald & Barrett, 1986); as non-marine expressions of the *Skolithos* ichnofacies (Buatois & Mángano, 2004); or even as part of the *Coprinisphaera* ichnofacies (Melchor *et al.* 2002). Similarly, Woolfe (1990) interpreted Devonian piperocks in the Taylor Group (Antarctica) as fluvial deposits belonging to the *Scoyenia* ichnofacies, while Fitzgerald and Barrett (1986) attributed Permian occurrences in Antarctica to fluvial environments. In non-marine settings, *Skolithos* piperocks are typically attributed to colonization by arthropods – primarily insects and arachnids (e.g. Bromley & Asgaard, 1979; Buatois & Mángano, 2004) – due to their articulated appendages, which facilitate excavation and sediment mobilization.

4.b.1.n. Facies Ft14: structureless sandstone

Description. Facies Ft14 constitutes the dominant lithofacies in the upper part of the Siliciclastic Kheneg ed Dis Member. It is characterized by massive, fine- to medium-grained sandstone beds. Individual beds range from 0.2 to 1.2 m in thickness and commonly exhibit sharp, erosional basal contacts. Although these sandstones are largely structureless (Fig. 9a, b), some beds display biogenic features (Fig. 9b), including trace fossils such as *Skolithos* and *Ophiomorpha*, along with indistinct bioturbation near the upper surfaces.

Interpretation. The absence of discernible primary sedimentary structures is interpreted primarily as a consequence of bioturbation, which may have homogenized original depositional features. However, alternative processes such as rapid sedimentation or sediment liquefaction during or shortly after deposition (cf. Alfaro *et al.* 2002) may also account for the massive nature of these sandstones.

4.b.1.o. Facies Ft15: structureless pebbly sandstone

Description. Facies Ft15 occurs in the upper part of the Siliciclastic Kheneg ed Dis Member as discontinuous, massive and chaotically organized bodies of coarse- to pebbly-grained sandstone (Fig. 9c). The pebbles are generally well sorted, subrounded to well-rounded and composed predominantly of quartz, sandstone and limestone clasts. The matrix consists of red to greyish-brown sandstone. Individual beds range from 0.15 to 0.8 m in thickness, typically showing a sharp, erosive basal contact and a flat upper surface. Upward transitions into finer-grained sandstone are evident, indicating vertical grain-size gradation.

Interpretation. The coarse- to pebbly-grained sandstone bodies, with erosive bases and flat tops, are interpreted as channel-fill deposits. The presence of well-sorted pebbly sandstone suggests deposition as channel lag accumulations within a highly sediment-laden fluvial system (cf. Malaza *et al.* 2013). Facies Ft15 likely represents channel lag deposits formed during episodes of channel incision related to the initiation of new stream courses or seasonal high-flow events. The pebbly component may include reworked material derived from the erosion of older alluvial deposits. The upward fining trend into fine- to medium-grained sandstone indicates deposition under waning flow conditions and a transition to a more stable, lower flow regime.

4.b.1.p. Facies Ft16: structureless conglomerate

Description. Facies Ft16 (Fig. 9d–f) is predominantly observed in the upper part of the Siliciclastic Kheneg ed Dis Member. It is commonly associated with planar cross-stratified and trough

cross-stratified sandstones and consists of strongly channelized, lenticular conglomerate bodies characterized by sharply scoured lower and upper bedding contacts. These conglomerates are clast-supported with a sandstone matrix and include clasts reaching up to 70 cm in diameter (Fig. 9e, f). The clasts are subrounded to well-rounded, frequently imbricated, and consist primarily of limestone and chert fragments. Individual conglomerate bodies are typically less than 2 m thick. In addition to the clast-supported varieties, some beds are poorly sorted, matrix-supported conglomerates with chaotic internal structures and large clasts embedded in a finer-grained matrix, consistent with debris-flow deposits (Fig. 9d).

Interpretation. The clast-supported, massive conglomerate units were deposited by sediment gravity flows occupying channels, as indicated by their lack of internal structure and the nature of their erosional bounding surfaces (Miall, 1996). They likely represent small lensoid channel-lag deposits or longitudinal braided-bar facies of low-sinuosity streams (Rust, (1972; Miall, 1977). The coarse grain size suggests higher discharge and greater flow energy compared to the other siliciclastic facies described above. The absence of sedimentary structures, together with poor sorting and the mixture of fine and coarse material, indicates that the matrix-supported conglomerates were also deposited by gravity flows, most likely of debris-flow origin.

4.b.2. Facies associations

Based on palaeontological content, spatial variations in sedimentary facies and bed geometry, the sixteen recognized facies types can be grouped into four FAs, each representing a distinct depositional environment (Table 1, Figs. 10, 11).

4.b.2.a. FA1 – open lacustrine facies association. The FA1 association constitutes the dominant portion of the Marly El Kohol Member and includes five main sedimentary facies types alternating in beds and bed intervals: ostracod lime-wackestone (Ft1); cyanobacteria/algal boundstone (Ft2); massive marlstone (Ft5); mammal-rich marlstone (Ft6); and gypsiferous marls (Ft7). Within the sedimentary succession, open lacustrine facies are interbedded with palustrine facies (Fig. 6c). The biota (charophytes, freshwater ostracods, gastropods, fish and turtles), along with the microfacies characteristics, indicate deposition in a shallow, meso-oligotrophic freshwater lake. The bioclastic limestones (Ft2 and Ft5) likely formed in well-oxygenated littoral zones with low to moderate energy conditions, which favoured the proliferation of freshwater benthic biota and aquatic vegetation (Gierlowski-Kordesch, 2010; Soulié-Märsche *et al.* 2010; Vázquez-Urbez *et al.* 2013). Minor silt-sized quartz grains in the open lacustrine limestone facies suggest sporadic high-energy inflows. Additionally, fine-grained sandstone beds (Ft11) overlying the gypsiferous marls (Ft7) indicate episodic fluvial inputs.

The occurrence of the charophyte species *Lamprothamnium papulosum* – the most salt-tolerant extant member of the Characeae – in some marlstone samples (Ft5) suggests the development of ‘vegetated playa’ ecosystems. Although this euryhaline species can withstand a broad salinity range, including hypersaline conditions, it produces viable oospores and gyrogonites only at salinities between 20‰ and 40‰ (Soulié-Märsche, 1998; Soulié-Märsche *et al.* 2008). Furthermore, *L. papulosum* requires seasonal salinity fluctuations for successful reproduction and cannot persist in environments that are permanently fresh or saline (Soulié-Märsche, 1998). The abundance of *L. papulosum*

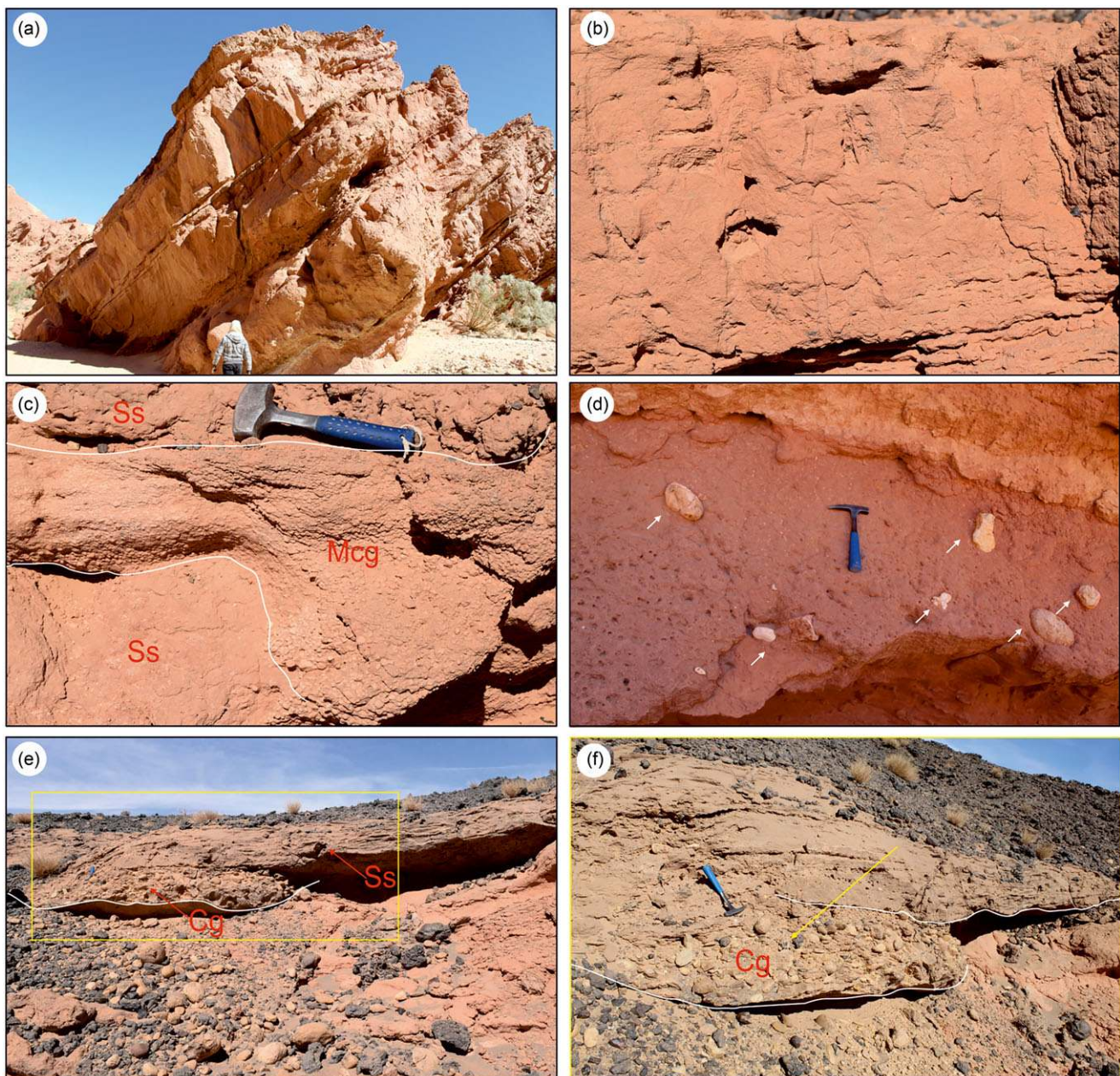


Figure 9. Field images of siliciclastic facies from the Eocene of Djebel El Kohol (Algeria). (a) Thick, massive sandstone beds; (b) Bioturbated structureless sandstone with *Skolithos*; (c) Lenticular, clast-supported pebbly sandstone (Ft15); (d) Debris-flow deposit (Ft16) with rounded to subrounded pebbles in sandstone matrix (arrows); (e–f), Channelized conglomerate (Ft16) interbedded with cross-stratified sandstone. Legend: Ss = sandstone; Mcg = microconglomerate; Cg = conglomerate. Hammer for scale (28 cm).

gyrogonites in certain intervals of the Marly El Kohol Member indicates salinity fluctuations, likely reflecting temporal rather than spatial variations in water salinity.

4.b.2.b. FA2 – palustrine facies association. This facies association dominates the basal 10–25 m interval of the eastern outcrops of the Marly El Kohol Member. It comprises limestone beds displaying two distinctive microfacies: oncoid wackestone (facies Ft3) and peloidal-intraclastic limestone (facies Ft4). These facies exhibit abundant evidence of subaerial exposure, including desiccation cracks, nodulization, oxidation, brecciation, root-related structures (rhizoliths), vadose silt and fenestral fabrics. Fauna is absent or limited to rare occurrences of ostracods and gastropods.

The subaerial exposure features indicate intermittent water presence in lacustrine systems or seasonal wetlands, characteristic of a palustrine environment (Freytet & Plaziatj, 1982; Platt, 1989; Platt & Wright, 1991; Freytet & Verrecchia, 2002; Alonso-Zarza & Wright, 2010). The palustrine domain was extensive under semi-arid climatic conditions, consistent with established models of palustrine carbonate formation (Freytet & Plaziatj, 1982; Wright & Tucker, 1991; Platt & Wright, 1992; Alonso-Zarza, 2003; Huerta & Armenteros, 2005; Alonso-Zarza & Wright, 2010). Comparable carbonate FAs have been documented in Cretaceous and Tertiary strata, primarily in France, Spain and the USA, and are associated with various tectonic settings (Armenteros *et al.* 1997). Most examples occur in continental depositional environments.

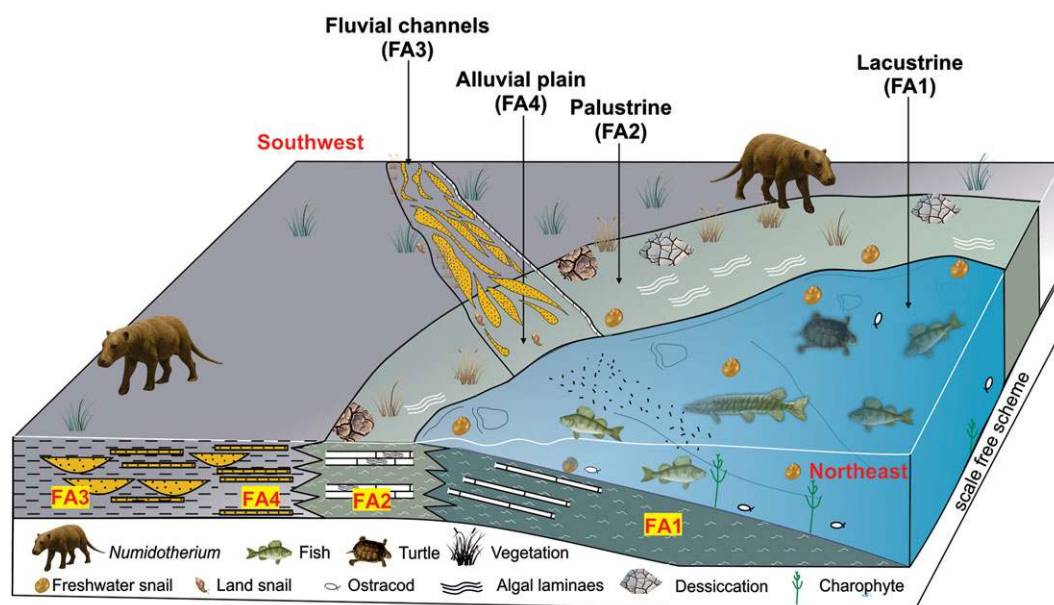


Figure 10. Depositional model illustrating the lacustrine-palustrine to alluvial environments of the Eocene succession at Djebel El Kohol (Algeria), based on facies types, associations and spatial distribution.



Figure 11. Scientific palaeoart of the Eocene El Kohol Formation (Algeria), created using IA tools (ChatGPT-4).

4.b.2.c. FA3 – fluvial channel facies association. This facies association forms the upper part of the Siliciclastic Kheneg ed Dis Member and is dominated by sandstone lithofacies (Ft9–Ft14), interbedded with greenish to reddish clastic mudstone (Ft8). Subordinate pebbly sandstone (Ft15) and conglomerate (Ft16) lithofacies are also present. Diagnostic features – including abundant erosional bases, channelized geometries, parallel and cross-bedding and fining-upward sequences – indicate deposition by bedload and streamflow processes (Ridgway & DeCelles, 1993; Miall, 1996, 2006; Suresh et al. 2007). This facies association is interpreted as representing sand-rich braided river deposits. The clast-supported, massive conglomerates and pebbly sandstones (Ft15–Ft16), interbedded with sandstone beds, are interpreted as products of mass-flow events and high-energy, channelized currents. These deposits likely represent small channel lags or longitudinal braided bars within low-sinuosity streams. Mottled textures indicate episodes of subaerial exposure and the development of palaeosols (Kraus, 1999).

4.b.2.d. FA4 – alluvial plain facies association. This facies association is present in the lower part of the Siliciclastic Kheneg ed Dis Member. It is characterized by thick-bedded, massive or laminated mudstone (Ft8) interbedded with siltstone and fine-grained sandstone beds (Ft11, Ft12 and Ft13), which range from 0.15 to 0.8 m in thickness and exhibit lateral continuity over several hundred metres. The mudstones are reddish-brown, with individual bed thicknesses varying between 0.2 and 5 m. The sandstones show no significant vertical grain-size variation. Sedimentary structures include abundant horizontal stratification and ripple cross-lamination, along with rare small-scale trough and planar cross-stratification, minor scour surfaces, symmetrical ripples and sporadic bioturbation. The bioturbation consists mostly of horizontal burrow structures, including *Palaeophycus* isp. and *Thalassinoides horizontalis*.

The heterolithic nature of this facies association suggests deposition from both traction (silt and fine sand) and suspension

(mud), reflecting fluctuating but generally low-energy currents (Terwindt, 1981). These deposits likely record multiple unconfined flows across an alluvial flood plain, with flow energy decreasing over time and laterally from proximal source areas towards the lacustrine margin. At the mouths of the distributary channels, floods became entirely unconfined, resulting in flow expansion and thinning. The associated velocity reduction led to decreasing grain size and lithofacies thickness with increasing distance from the source. This process is accompanied by a reduction in the proportion of ripple-laminated and cross-bedded deposits, indicating that suspension fallout became the dominant depositional mechanism (Fisher *et al.* 2008). Minor erosional surfaces reflect occasional high-energy flood events that caused localized erosion.

4.c. Palaeontological data

4.c.1. Charophytes

Up to nine fossil charophyte taxa have been identified in the non-marine deposits of the Marly El Kohol Member. The algae were recovered from nine samples, six of which (Kh04, Kh06, Kh08, Ko09, Ko13 and Ko15) yielded identifiable taxa (Figs. 12, 13).

Sphaerochara parvula (Reid & Groves 1921) Horn af Rantzien 1959 (Fig. 12a–d). This species is present in sample Ko13. The gyrogonites are very small, measuring ~330 µm in height (mean) and ~260 µm in width (mean). They exhibit a prolate shape, with an isopolarity index (height/width × 100) of 126. Eight to ten convolutions are visible in lateral view. The spiral cells are concave and lack ornamentation. Both the apex and base are slightly pointed, with the base displaying a pentagonal pore through which the basal plate is externally visible. *Sph. parvula* has a broad biostratigraphic range, occurring from the early Paleocene to the late Miocene in Europe and China (Riveline, 1986; Li *et al.* 2013, and references therein). However, it is particularly abundant in the late Eocene (Priabonian).

Nodosochara (Turbochara) sp. (Fig. 12e–h). Few specimens were found in sample Ko13. The gyrogonites are small, with a mean height of 488 µm and a mean width of 315 µm, displaying an ovoidal shape and an average isopolarity index of 155. Ten to eleven convolutions are visible laterally. The spiral cells are convex and ornamented with an irregular, thick midcellular crest. The apex is rounded and prominent, forming a cap-like structure adorned with nodular formations resembling a rosette. Spiral cells exhibit a distinct periapical narrowing. The gyrogonites have a tapering, pointed base with a small basal pore. Due to the limited number of specimens, a specific attribution could not be established. Species of *Nodosochara (Turbochara)* are commonly reported from the Eocene of China (Feist *et al.* 2005).

Gyrogona sp. (Fig. 12i–l). A few poorly preserved gyrogonites occur in samples Ko15 and Kh04. The gyrogonites are large, measuring 602 µm in height and 653 µm in width on average, and display an oblate spheroidal shape with a low isopolarity index of 92. Seven to eight convolutions are visible laterally. The spiral cells are normally convex and ornamented with a thick midcellular crest. The apex is flat, showing a well-marked periapical depression and prominent elongated apical nodules. The base is rounded. Due to the poor preservation and limited number of specimens, a clear taxonomic attribution is hindered, and open nomenclature has been retained. However, the gyrogonites of this population resemble those of the species *G. caelata*, a well-known taxon from the middle-late Eocene of Europe (e.g. the Headon beds in England; the Paris, Languedoc, Aquitaine and Provence basins in

France; the Ebro Basin in Spain; and the Transylvanian Basin in Romania; Sanjuan & Martín-Closas, 2014, and references therein). In Algeria, *G. caelata* has previously been reported by Mebrouk *et al.* (1997) in the Central Sahara (El Biod locality).

Harrisichara cf. leptocera Grambast 1977 (Fig. 12m–o). A few poorly preserved specimens were found in samples Kh04 and Ko09. The gyrogonites measure 702 µm in height and 561 µm in width on average, with an ovoidal to sub-ovoidal shape and an isopolarity index of 125 (mean value). Nine convolutions are visible laterally. The spiral cells are flat to concave and ornamented with regularly spaced, large tubercles. The apex is flat, lacking periapical modification, while the base is conical and elongated, forming a small column. The limited number of gyrogonites recovered from the Djebel El Kohol locality complicates a definitive taxonomic assignment within the genus *Harrisichara*. *H. leptocera* is known from the late Paleocene (Tanethian) to early Eocene (Ypresian) of the Paris Basin and the northern Pyrenees in France (Riveline, 1986, and references therein). Additionally, Mebrouk *et al.* (1997) previously reported this species in the Southern Oran High Plateaus (Hadjrat Zennad locality, Algeria).

Lamprothamnium papulosum (Wallroth) Groves, 1926 (Fig. 13a–e). Gyrogonites of this species were found in two samples from the Djebel El Kohol locality (Ko09 and Ko13). This taxon dominates the assemblage in sample Ko09. The gyrogonites are medium in size (average height of 606 µm and average width of 368 µm), elliptical in shape, with a mean isopolarity index of 164. Laterally, eight to nine convolutions are visible. The spiral cells are non-ornamented and may appear concave, flat or convex depending on the degree of calcification (Fig. 13b–d). The apex is flat and of the lamprothamnoid type (*sensu* Feist *et al.* 2005), displaying a periapical furrow that forms an apical groove (Fig. 13a). The base is generally rounded, with a shallow pentagonal basal pore, though this feature is poorly preserved in the studied population. This cosmopolitan brackish-water species has a wide biostratigraphic range, extending from the early Eocene (Demirci *et al.* 2023, and references therein). Mennad *et al.* (2021) have already reported this species in the Ksour Mountains (Oued Tafarahit site).

Neochara ameuriarum Mebrouk and Feist 1999 (Fig. 13f–h). This species occurs in samples Kh04, Kh06 and Kh09. The gyrogonites are medium-sized, averaging ~670 µm in height and ~554 µm in width, with an ellipsoidal-ovoidal shape and an isopolarity index of 120. Nine convex convolutions are visible laterally. The spiral cells exhibit strong periapical thinning and slight periapical narrowing. The apex is ornamented with large nodules forming an apical rosette, while the base is rounded and features a large funnel-shaped basal pore. The basal plate is externally visible. This species was originally described by Mebrouk and Feist (1999) and later documented by Mebrouk *et al.* (2013) from the early Eocene (Ypresian) of the Saharan Atlas, Algeria (Oued Meguerchi locality).

Peckichara torulosa var. *varians* (Grambast 1957) Sanjuan *et al.* 2020 (Fig. 13j–m). Several specimens have been recovered from samples Ko09, Ko13, Ko15 and Kh04. The gyrogonites are medium to large in size, with a mean height of ~709 µm and a mean width of ~633 µm, exhibiting a prolate spheroidal shape and an isopolarity index of 110. The spiral cells are predominantly convex and heavily ornamented with prominent tubercles as thick as the width of the spiral cells. The apex is flat, bearing thick and large nodules that form an apical rosette. At the periphery of the apex, the spiral cells show pronounced thinning and slight narrowing. The base is rounded, featuring a pentagonal pore within a small star-shaped

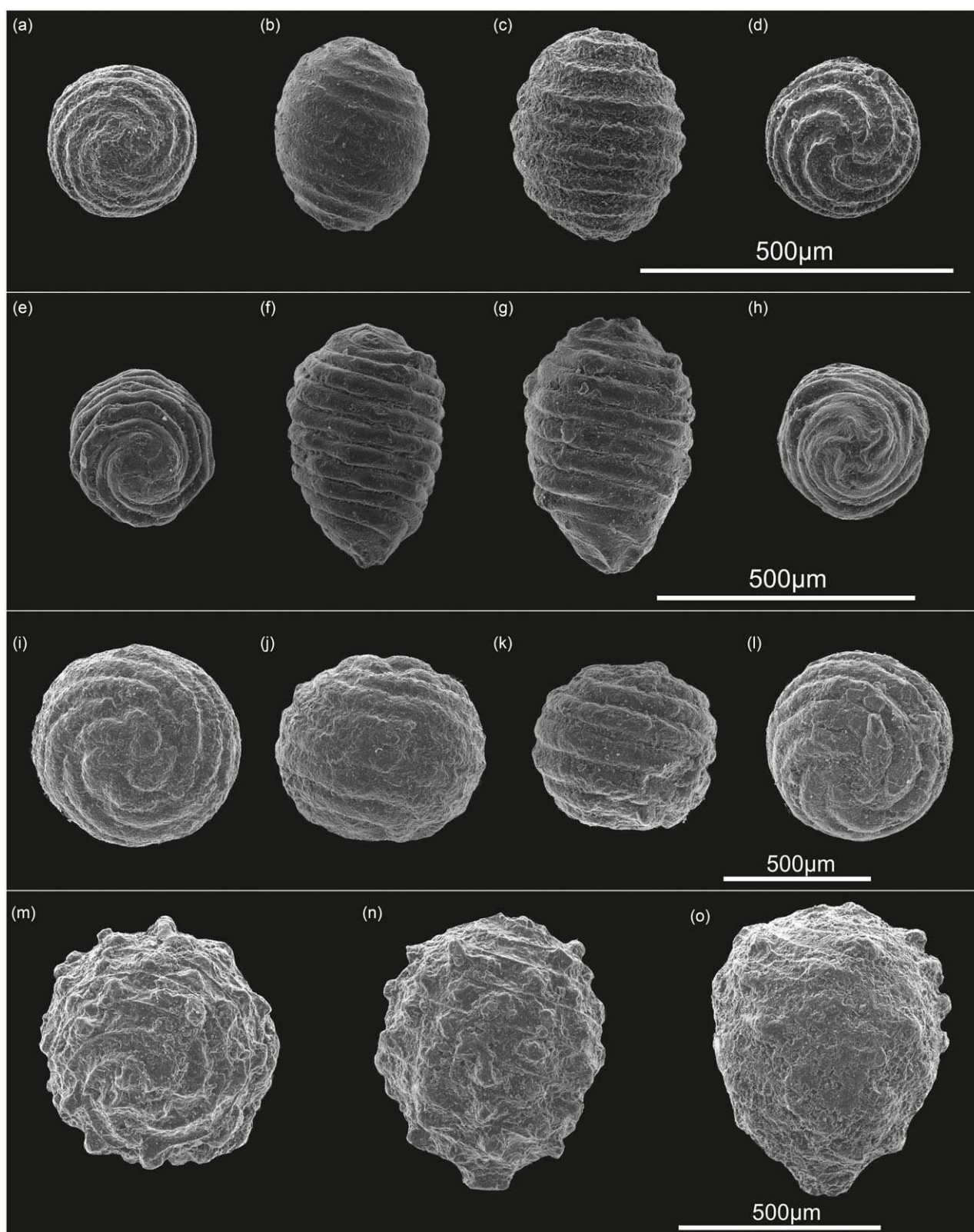


Figure 12. Charophyte assemblage from the Eocene of Djebel El Kohol anticline (Algeria). (a–d). *Sphaerochara parvula* (sample Ko13). (a) apical view, (b and c). lateral views, (d) basal view. (e–h) *Nodosochara (Turbochara)* sp. (sample Ko13). (e) apical view, (f and g) lateral views. (h) basal view. (i–l) *Gyrogona* sp. (samples Ko15 and Kh04). (i) apical view, (j and k) lateral views, (l) basal view. (m–o) *Harrisichara* cf. *leptocera* (samples Kh04 and Ko09). (m) apical view, (n and o). lateral views.

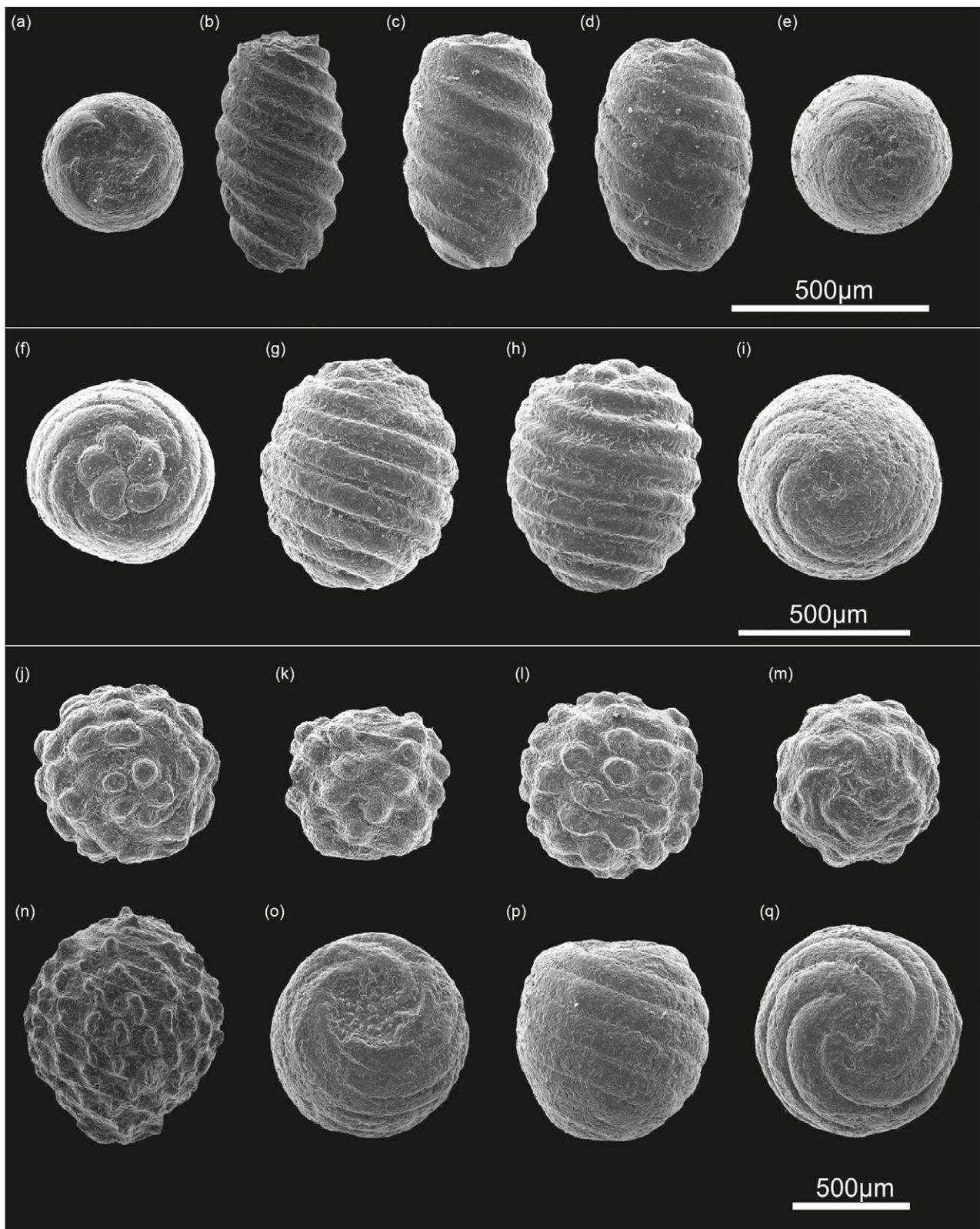
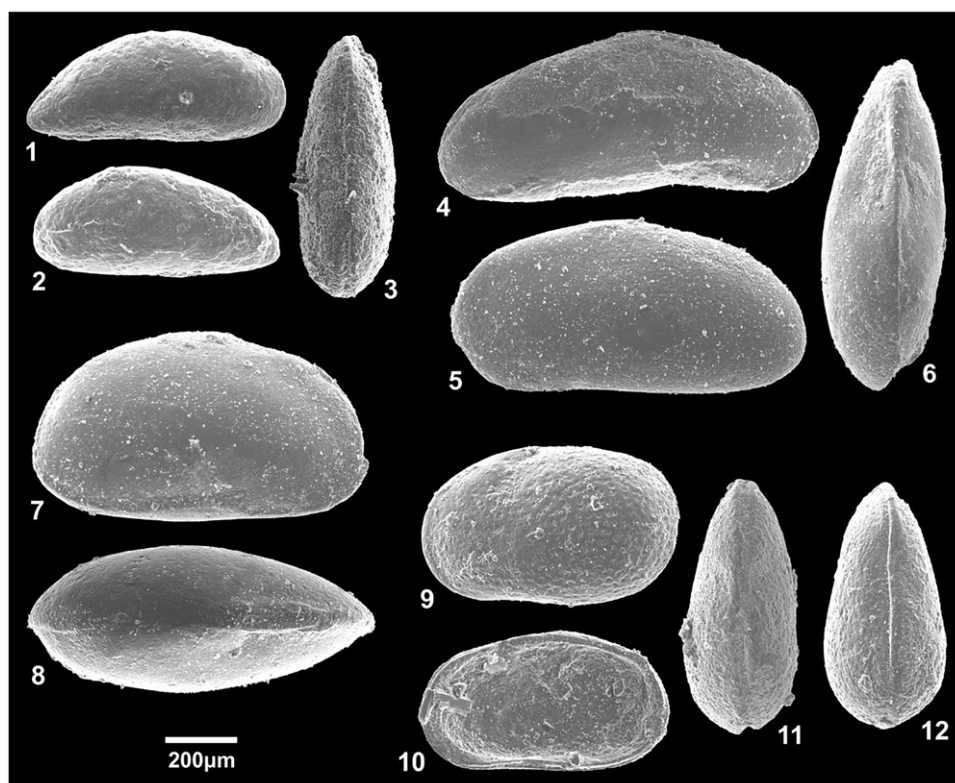


Figure 13. Charophyte assemblage from the Eocene of Djebel El Kohol anticline (Algeria). (a–e) *Lamprothamnium papulosum* (sample Ko09). (a) apical view, (b, c and d) lateral views showing different degrees of calcification; (e) basal view. (f–i) *Neochara ameuriarum* (samples Kh04, Kh06 and Kh09). (f) apical view, (g and h) lateral views. (i) basal view. (j–m) *Peckichara torulosa* var. *variens* (samples Ko15 and Kh04). (j) apical view, (k and l) lateral views, (m) basal view. (n) lateral view of *Nitellopsis (Tectochara)* cf. *dutempleii* (sample Ko15). (o–q) *Raskyella* cf. *sahariana* (sample Kh06). (o) apical view (germinated), (p) lateral view, (q) basal view.

Figure 14. Ostracod assemblage from the Eocene of Djebel El Kohol anticline (Algeria). (a–c) *Paracypris?* sp. 1 (sample Ko04): (a) right lateral view; (b) left lateral view; (c) dorsal view. (d–f) *Paracypris?* sp. 2 (sample Ko15): (d) right lateral view; (e) left lateral view; (f) dorsal view. (g, h) *Thalassocypris?* sp. 1 (sample Ko15): (g) right lateral view; (h) dorsal view. (i–l) *Neocyprideis meguerchiensis* (sample Ko04): (i, l) female: (i) left lateral view; (l) ventral view; (j, k) male: (j) right internal view; (k) ventral view.



pentagonal funnel. *P. torulosa* var. *varians* is known from the Paleocene to lower Eocene deposits in several European and Chinese basins (Sanjuan *et al.* 2020, and references therein).

Raskyella cf. *sahariana* Mebrouk & Feist, 1999 (Fig. 13o–q). A few germinated but poorly preserved specimens were found in sample Kh06. Gyrogonites are large, measuring ~860 µm in height and ~822 µm in width, and display an ovoidal shape with a low isopolarity index of 105. Nine non-ornamented convolutions are visible laterally. The apex is broad and flat, featuring a flower-like germination pore; in non-germinated forms, this pore is covered by an operculum. The base is rounded to slightly pointed, displaying a large basal pore situated within a funnel. This taxon has only been reported from the upper Ypresian–Lutetian of Algeria, specifically in the Gour Lazib and Glib Zegdou localities, Hammada du Dra (Mebrouk & Feist, 1999).

Nitellopsis cf. (*Tectochara*) *dutempleii* (Watelet) Grambast and Soulié-Märsche 1972 (Fig. 13n). Very few specimens were found in sample Ko15. The gyrogonites are large, measuring ~983 µm in height (mean average) and ~870 µm in width (mean average), and display a prolate spheroidal shape with an isopolarity index of 112. Ten convolutions can be distinguished laterally. The spiral cells are concave and well ornamented with elongated tubercles regularly arranged along them. The apex is nitellopsoid (*sensu* Feist *et al.* 2005), showing a periapical narrowing and thinning of the spiral cells. Gyrogonites display a pointed base. This taxon has been reported in the early Eocene of the Paris and Provence basins (France), the Mondego Basin (Portugal), and in the same locality of Djebel El Kohol in Algeria (Riveline, 1986; Mebrouk & Feist, 1999; Antunes and Colin, 2003; Aubry *et al.* 2005).

4.c.2. Ostracods

Four ostracod taxa have been identified in the lower Eocene Marly El Kohol Member (samples Ko04 and Ko15) (Fig. 14). Valves and

carapaces are generally poorly preserved, hindering taxonomic identification beyond the genus level. The observed assemblage is characteristic of transitional (brackish) waters, exhibiting very low species diversity and dominated by genera commonly associated with such palaeoenvironments. Among these, *Neocyprideis* is particularly abundant, resembling its occurrence in the lower Eocene of the Paris Basin (Apostolescu, 1956). The *Neocyprideis* sp. identified here is closely related to *Neocyprideis meguerchiensis* Mebrouk *et al.* 2011, previously recorded on the right bank of Oued Meguerchi. The observed variations in size and ornamentation between specimens from both areas are consistent with those expected in transitional, highly seasonal waters (Mebrouk *et al.* 2011, 2013). This faunal similarity with neighbouring regions of the Mediterranean realm is also observed in other microfossil groups from the Oued Meguerchi Formation (Mebrouk *et al.* 2013), such as charophytes, which have been similarly dated to the lower Eocene in the region (Mebrouk *et al.* 1997; Mebrouk & Feist, 1999).

Unlike the forms observed at the Oued Meguerchi, the pericidal termination of the Djebel El Kohol also contains possible representatives of *Paracypris* and *Thalassocypris* (Paracypridae).

4.c.3. Fish

Several sediment samples from the Marly El Kohol Member have yielded numerous fish microremains, consisting primarily of scales and teeth. Polypteriform fishes (Polypteridae indet.) are represented by numerous ganoid scales, which are rhombic in shape and less than 10 mm in length. The outer surface of the ganoid layer is smooth, with only a few small pits. Similar scales are commonly found in Cenozoic non-marine deposits from Africa (e.g. Otero *et al.* 2017: their fig. 4b). In addition, some small, subconical teeth with a short acroding cap may also belong to this indeterminate

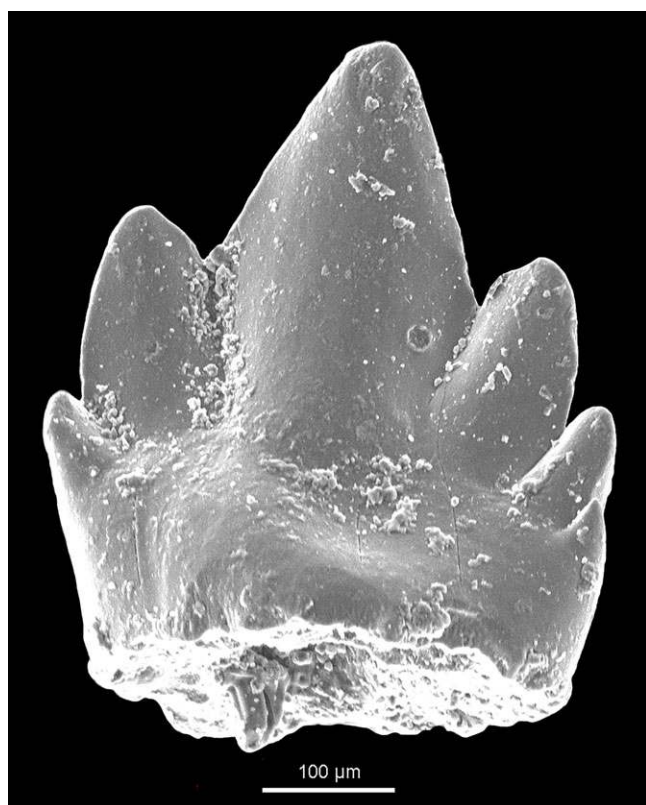


Figure 15. Multicuspid tooth of an alestid characiform fish (*Alestes/Brycinus* complex), from the Eocene of Djebel El Kohol anticline (sample Ko15).

polypterid. Among the teleosts, characiform fishes belonging to the family Alestidae appear in several samples. The teeth of three distinct taxa have been identified. The first taxon is assigned to the *Alestes/Brycinus* complex, characterized by minute multicuspoid teeth (Otero *et al.* 2009; Stevens *et al.* 2016). These teeth bear up to six cusps and can be either sharp or molariform, depending on their position in the jaws (Fig. 15). The second taxon is represented by slightly larger, more globulous, unicuspid teeth. These specimens resemble some teeth identified as *Sindacharax* sp. (Otero *et al.* 2009; their fig. 10a, b). The third alestid taxon is represented by lanceolate teeth assignable to the genus *Hydrocynus*. These show a labiolingually compressed crown with sharp mesial and distal carinae (Murray *et al.* 2010, 2014; Otero *et al.* 2009, 2015; Hammouda *et al.* 2016; Stevens *et al.* 2016). Additionally, a minute, elongated bicuspid tooth – with equally sized cusps – exhibits a dental morphology reminiscent of the characiform genus *Distichodus* (Otero *et al.* 2009, 2017; Argyriou *et al.* 2015) or of certain modern cichlids such as *Pseudosimochromis* and *Tropheus* (Yamaoka, 1983). Further material is required to securely identify this bicuspid-toothed taxon.

4.c.4. Other vertebrate remains

The Marly El Kohol Member has yielded abundant mammal remains (Ko15') in the eastern outcrops of Djebel El Kohol, near the Kheneg ed Dis area. These remains primarily belong to *Numidotherium koholense* Jaeger (in Mahboubi *et al.* 1986), one of the few known pre-Miocene proboscidean species. Sedimentological and taphonomical evidence suggests rapid deposition of this layer. During fieldwork, we identified several postcranial skeletal elements, two relatively complete skulls,

numerous maxillary fragments, partially to fully preserved mandibles, and isolated teeth, including upper incisors (Fig. 16).

Additionally, partial remains of turtle plates were recovered. The absence of a granular outer surface and the relatively thin nature of the plates suggest that they do not belong to a terrestrial form (i.e. Testudinidae) (Pérez-García *et al.* 2016). Given its fragmentary state, the scarcity of material, and especially the lack of diagnostically relevant features, a precise systematic attribution of the freshwater form(s) represented cannot be confidently established.

4.d. Ichnological data

The trace-fossil assemblage of the Siliciclastic Kheneg ed Dis Member is characterized by low diversity, comprising only five identified ichnotaxa. These include primarily vertical burrows, simple branched forms, and network structures. *Skolithos* is the most common ichnotaxon, occurring frequently and in high densities across multiple *Skolithos*-bearing levels, which correspond to the piperock facies. The systematic descriptions of the recorded ichnofossils are presented below in alphabetical order, following the guidelines of Häntzschel (1975).

Ophiomorpha isp. (Fig. 17a). Endichnial, full-relief, vertical to slightly inclined, unbranched, and predominantly straight burrows, oriented perpendicular to the bedding plane. The individual cylindrical tubes measure 35–45 mm in diameter, exhibit oval cross-sections, and reach lengths of approximately 550 mm. Unfilled tubes are common, displaying ring-like structures and the imprint of discoid or ovoid faecal pellets on the external wall of the surrounding sediment.

Palaeophycus isp. (Fig. 17b). The specimen consists of horizontal to slightly inclined, thinly lined, unbranched, straight to slightly curved, cylindrical burrows, oriented parallel or slightly oblique to the bedding plane. The fill is structureless and similar in composition to the host rock. The burrows measure approximately 15 mm in diameter and reach variable lengths of up to 200 mm.

Skolithos annulatus (Howell, 1957) (Fig. 17c). Endichnial, full relief, cylindrical to subcylindrical, vertical to subvertical, straight burrow, highly eroded, with distinct smooth burrow walls exhibiting characteristic ring-like annulations. These annulations are preserved as external imprints on the host sediment due to erosional processes. The burrow depth ranges from 300 to 350 mm, with a diameter of approximately 40 to 45 mm. This specimen is rarely observed in the studied section and is primarily associated with crowded *Skolithos linearis* pipes and, to a lesser extent, *Ophiomorpha*.

Skolithos linearis Haldeman, 1840 (Fig. 17d–e). Endichnial, full-relief, cylindrical to subcylindrical, unbranched, vertical to slightly inclined burrows with distinct or indistinct walls, typically perpendicular to the bedding plane. The burrows are densely spaced or occasionally show gradual spacing variations. Their fill is structureless and consists of the same sediment as the host rock. Diameters range from 25 to 35 mm, and lengths vary from 300 to 400 mm.

Thalassinoides horizontalis Myrow, 1995 (Fig. 17f). Predominantly horizontal, smooth-walled, unlined, straight to slightly inclined, cylindrical, unornamented, Y- to T-shaped, and irregularly branched tunnels with no vertical offshoots. Some false branching in the shape of X is noticed, mostly due to tunnels overlapping. Burrow diameter ranges from 20 to 25 mm, with a maximum observed length of 400 mm. The burrows are parallel to the bedding plane and lack swelling or constrictions at junctions. The infill material is similar to the host rock.

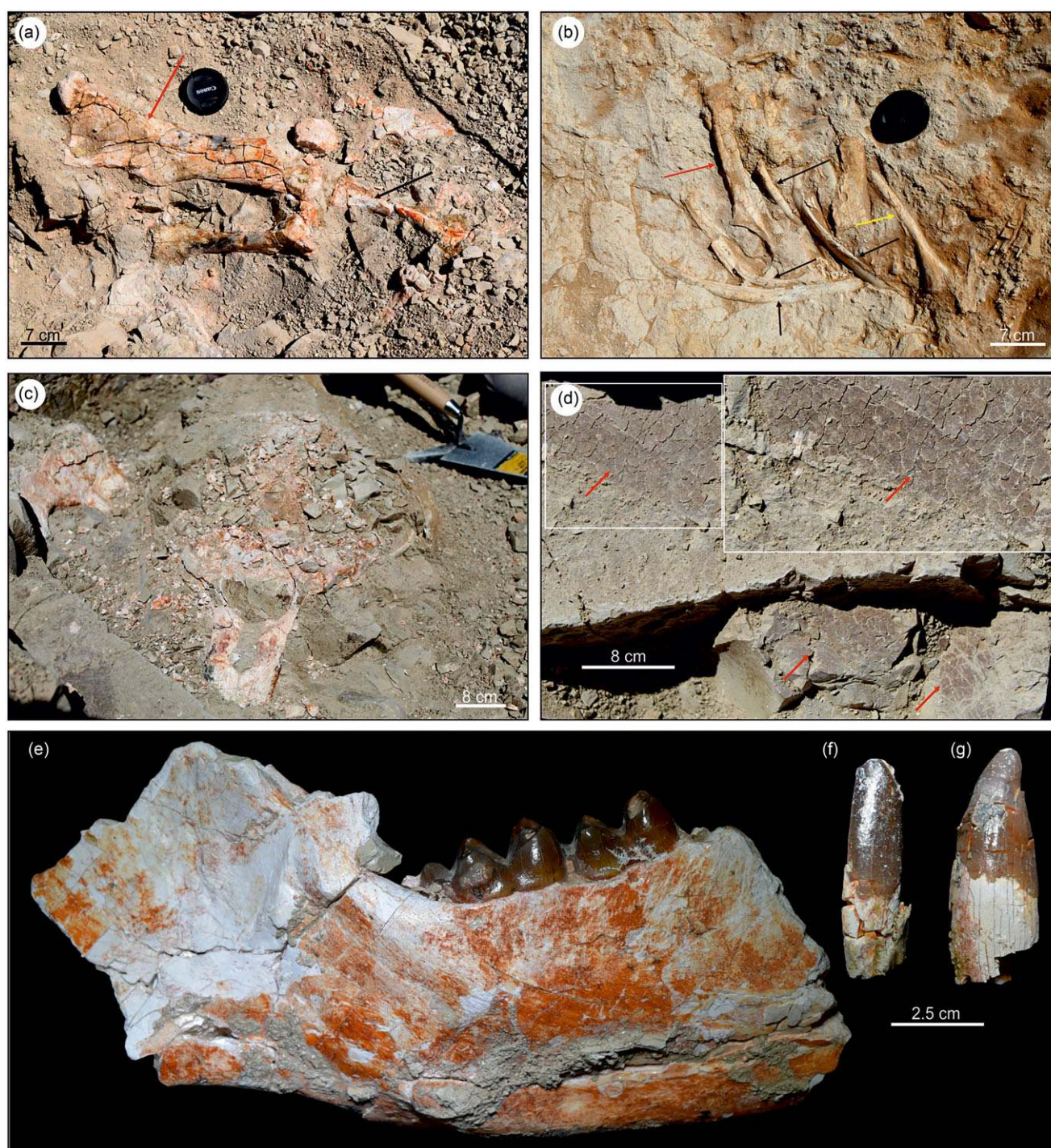


Figure 16. Fossil remains of the proboscidean *Numidotherium koholense* from the Eocene of Djebel El Kohol anticline (Algeria). (a) Left femur (red arrow) associated with two tibiae (black arrows); (b) Multiple anterior skeletal elements including at least four ribs (black arrows), an ulna (red arrow) and a probable radius (yellow arrow); (c) Cranial bones (upper region); (d) Possible fossilized skin impression; (e) Fragments of the left maxilla with M2-/M3/; (f) First upper incisor (I1); (g) Second upper incisor (I2).

5. Discussion

The El Kohol Formation, as examined in this study, is formally subdivided into two lithostratigraphic members: the Marly El Kohol Member and the overlying Siliciclastic Kheneg ed Dis Member. A pronounced lithological transition – marked by a shift from light-coloured, carbonate-rich sediments to darker, clastic-dominated deposits – defines the boundary between these

members. Based on the associated charophyte assemblages, the Marly El Kohol Member is chronostratigraphically assigned to the lower Eocene (Ypresian). This interpretation aligns with the temporal framework established by the magnetostratigraphic study of Costeur *et al.* (2012), which places these deposits within Chron C24n to Chron C22r, corresponding to an estimated age range of approximately 52 to 51 Ma. The overlying Kheneg ed Dis

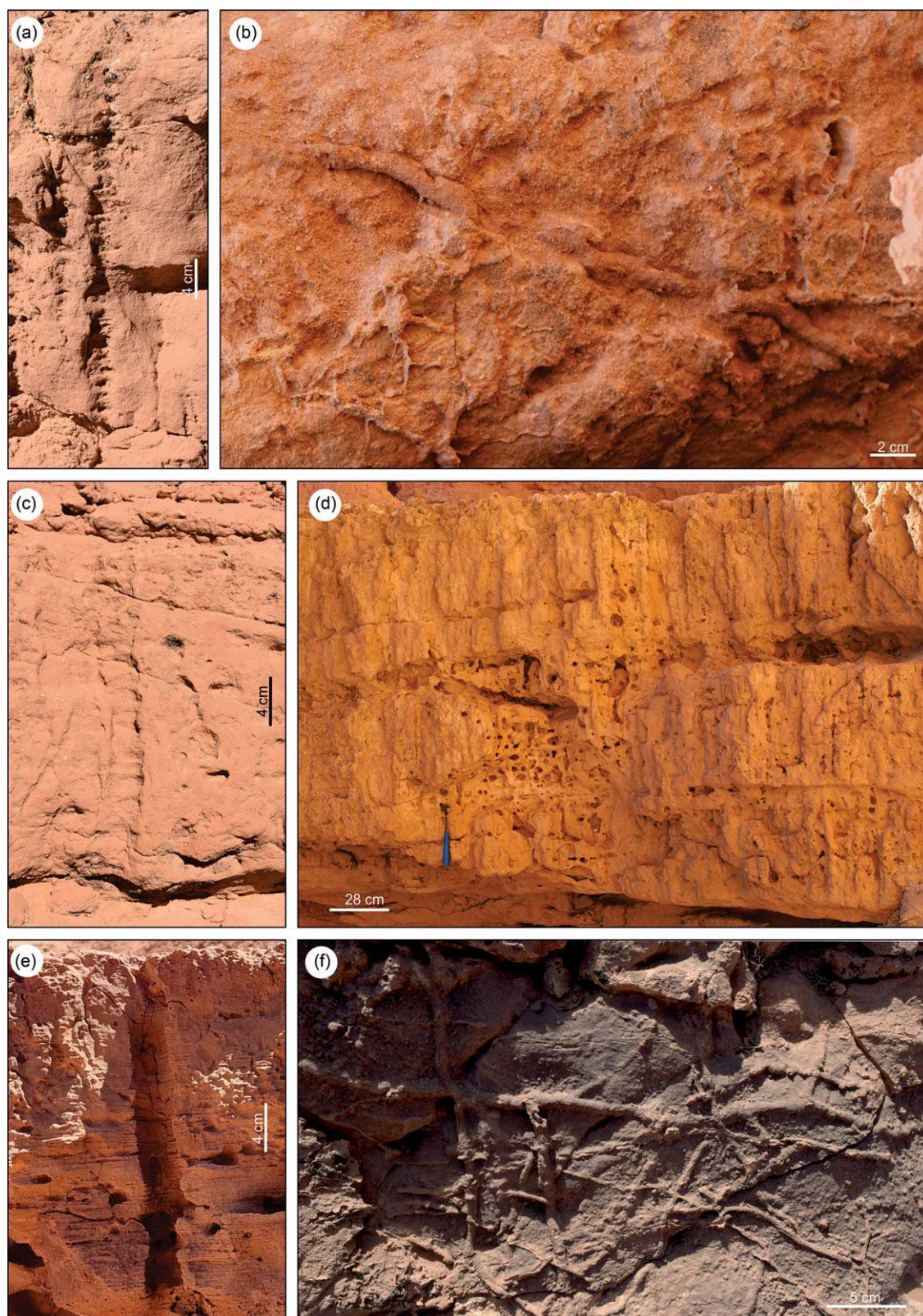


Figure 17. Trace fossils from the Eocene Siliciclastic Kheneg ed Dis Member (Algeria). (a) *Ophiomorpha* isp.; (b) *Palaeophycus* isp.; (c) *Skolithos annulatus*; (d) *Skolithos linearis*-bearing sandstone bed (*Skolithos*-dominated composite pipe rock); (e) Unfilled solitary burrow of *Skolithos linearis*; (f) Simple branched network of *Thalassinoides horizontalis*. (D = hammer for scale, 28 cm long).

Member, positioned stratigraphically above the lower Eocene Marly El Kohol Member, is assigned to the lower-middle Eocene based on its lithological characteristics and its alignment with regional tectonic signals related to the inversion and orogenic development of the Atlas System. According to Rosenbaum *et al.* (2002), the Atlas orogeny reached its peak during the middle Eocene due to Africa-Eurasia convergence. Early evidence for an Eocene tectonic phase – referred to as the ‘Atlas Event’ – was originally proposed by Lafitte (1939) in the Aures Mountains (eastern Algerian Atlas). Subsequent work by Frizon de Lamotte *et al.* (2000) confirmed that this tectonic activity was widespread, extending from Agadir (Morocco) to Tunis (Tunisia).

Field and laboratory investigations resulted in the identification of sixteen sedimentary facies types (Ft1–Ft16), which have been grouped into four principal FAs (FA1–FA4), each representing a distinct depositional setting: (FA1) an open lacustrine system; (FA2) a palustrine environment; and (FA3 and FA4) fluvial environments corresponding to channel-fill deposits and floodplain sediments respectively. These palaeoenvironmental interpretations contribute to a more refined understanding of the evolution of Eocene continental deposits in the Central Saharan Atlas and, more broadly, across North Africa.

Palaeontological findings from the El Kohol Formation provide new insights into the region’s Eocene record. Nine charophyte taxa were identified, including seven species with affinities to European forms and two that appear endemic to Algeria. This assemblage indicates the development of shallow, well-oxygenated lacustrine environments in the Central Saharan Atlas. However, the occurrence of *Lamprothamnium papulosum* in certain intervals suggests episodes of hydrological closure, leading to brackish water conditions typical of playa lakes.

Four ostracod taxa were also recorded, characteristic of transitional environments in both fossil and Recent assemblages. Notably, species of *Neocyprideis* – including *N. meguerchiensis*, identified in both the current samples and adjacent units – are known from lagoonal settings throughout the Eocene Tethyan realm. Members of the Paracyprididae family comprise a significant portion of the assemblage, distinguishing it from other El Kohol Formation sections. This could imply more restricted environmental conditions than previously inferred, although paracypridids are not thought to have specialized for anchialine habitats until later in their evolutionary history. Their peak diversity occurred during the Miocene, when they became prominent components of brackish ostracod faunas, as evidenced by their presence in Mexican amber (Matzke-Karaszt *et al.* 2017). These forms were eventually replaced – at least in lagoonal contexts – by leptocytherid and cytherideine cytherocopines, a transition commonly observed in the Holocene but initiated as early as the late Eocene (Şafak *et al.* 2015). The co-occurrence of cytherideines (*Neocyprideis*) and paracypridids in the Marly El Kohol Member thus represents an important record of this ecological transition in the Eocene of Algeria. Given the sparse fossil record of paracypridids (Martens *et al.* 1998), this finding also contributes valuable data to the Cretaceous–Palaeogene evolutionary history of the group.

The ichthyological assemblage includes fish microremains indicative of a freshwater fauna, comprising taxa such as polypterids and alestids – groups commonly documented from Palaeogene and Neogene vertebrate-bearing localities across Africa. Within the lower Eocene Marly El Kohol Member, the Ko4 level may preserve some of the earliest known representatives of the alestid genus *Hydrocynus* and members of the

distichodontid family (Characiformes). Fragmentary remains of turtle plates were also recovered, although the absence of diagnostic features precludes precise taxonomic assignment. Nevertheless, these specimens can be attributed to freshwater turtles. Additionally, abundant and well-preserved remains of the basal proboscidean *Numidotherium koholense* were identified. This taxon, considered primarily terrestrial, reinforces the interpretation that the vertebrate assemblage reflects a range of continental environments.

Ichnological analysis of the studied succession revealed five ichnotaxa within the Siliciclastic Kheneg ed Dis Member: *Ophiomorpha* isp., *Palaeophycus* isp., *Skolithos annulatus*, *Skolithos linearis*, and *Thalassinoides horizontalis*. This ichnoassociation is composed predominantly of eurybathic forms that are widespread in both marine and continental environments. However, several studies have reported these trace fossils in continental settings, particularly *Ophiomorpha* and *Skolithos* (Merrill, 1984; Netto, 2007). *Skolithos* is the most abundant ichnotaxon and frequently occurs in dense concentrations within specific horizons, forming a distinctive ichnofabric often referred to as ‘pipe rock’ (e.g. Netto, 2007). Its presence is typical of fluvial and other continental deposits (e.g. Netto, 2007; Hasiotis, 2010; Melchor *et al.* 2012). The remaining ichnotaxa are comparatively rare and show limited environmental specificity within the studied context.

6. Conclusions

This study documents the litho- and biostratigraphy, facies evolution, and depositional environments of the Eocene strata exposed in the Djebel El Kohol anticline (Central Saharan Atlas, Algeria), based on comprehensive analysis of lithological features, fossil and ichnofossil assemblages, and microfacies. A revised lithostratigraphic framework is proposed, formally dividing the historically mammal-bearing El Kohol Formation into two members: the Marly El Kohol Member (Lower Eocene) and the overlying Siliciclastic Kheneg ed Dis Member (Lower–Middle Eocene), separated by a prominent erosion surface and a marked lithological transition.

Field investigations and petrographic analyses identified sixteen sedimentary facies types (Ft1–Ft16), which are grouped into four principal FAs (FA1 to FA4) reflecting distinct depositional settings: (FA1) an inland lacustrine system; (FA2) a palustrine environment characterized by freshwater to brackish carbonate deposition, frequent subaerial exposure and paedogenic alteration; and (FA3 and FA4) fluvial environments corresponding to channel-fill deposits and floodplain sediments respectively.

Palaeontological investigations of the Marly El Kohol Member have revealed a diverse assemblage of nine charophyte species, including several endemic forms – *Sphaerochara parvula*, *Nodosochara* (*Turbochara*) sp., *Gyrogona* sp., *Harrisichara* cf. *leptocera*, *Lamprothamnium papulosum*, *Peckichara torulosa* var. *varians*, *Raskyella* cf. *sahariana*, and *Nitellopsis* cf. (*Tectochara*) *dutempleii*. This assemblage supports a Ypresian age and indicates deposition in shallow, oxygenated lacustrine environments, intermittently evolving into brackish, hydrologically closed lakes. The member also yielded four ostracod taxa – *Neocyprideis meguerchiensis*, *Paracypris*? sp. 1, *Paracypris*? sp. 2, and *Thalassocypris*? sp. 1 – suggesting deposition in restricted, transitional settings. Additional fossil material includes fish microremains, notably early alestids and representatives of *Hydrocynus*, along with fragmentary remains of freshwater turtles

and the terrestrial proboscidean *Numidotherium koholense*. Although the Siliciclastic Kheneg ed Dis Member has not yielded any significant fossils, ichnological analysis has revealed the presence of five ichnotaxa: *Ophiomorpha* isp., *Palaeophycus* isp., *Skolithos annulatus*, *Skolithos linearis* and *Thalassinoides horizontalis*. This ichnoassociation includes forms widely known from continental settings and supports deposition under dynamic fluvial conditions.

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