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Fossil Fish Teeth in Phosphatic Series of Jebel Dyr (Algerian-Tunisian Border Area)

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Abstract

The Thanetian phosphatic series of Jebel Dyr syncline, northeastern Algeria, are analyzed for their paleontological content. Materials were concentrated by sample washing and outcrops surface collecting of friable phosphorites facies, yielding a multitude of phosphatised fish teeth rich in species of variable morphology, representing 28 species of Elasmobranchii. The fish fauna indicates tropical to temperate paleo-environmental conditions. Most of the species represent benthic/nektonic forms of coastal areas with neritic and mid-water depths of the continental slope.

Keywords

Thanetian, Phosphatic Series, Algeria, Elasmobranchii, Palaeoenvironment

1. Introduction

The Thanetian phosphatic series of the Algerian-Tunisian border region and their paleontological contents are still insufficiently known, despite the contributions of [1] [2] [3].

The fish fauna characterizing these rocks includes a multitude of species represented by teeth and some isolated vertebrae. We have studied tens of samples collected from phosphatic outcrops of the southeastern flank of Jebel Dyr (**Figure 1**). For the first time, we characterise and establish a general systematic overview of the many fish (elasmobranchs). Furthermore, the assemblages are analysed in order to reconstruct the paleoenvironment during this upper Paleocene period individualized by phosphatogenesis in the area.

Teeth of sharks and rays are characterised by strong heterodontism leading range of morphological disparity [4] [5] [6] [7] described several kinds of heterodonty: monognathic (e.g. in Odontaspididae and Rajidae), dignathic (e.g. in

Carcharhinidae), and ontogenetic (in Hétérodontidiformes). Despite the fact that the heterodontism makes identification of fish species a very difficult task, we were able to identify almost of isolated material at the species level. The characterisation of species was mainly performed based on palaeo-ichthyology literature (e.g.; [8]-[20]). Materials (figured or not) are currently deposited at Tebessa University and referred with collecting number LT.

2. Overviews of Geographic and Geological Settings

The study area Jebel Dyr syncline (**Figure 1(a)** & **Figure 1(b)**) forms part of the Saharan Atlas of eastern Algerian-Tunisian border area, extending to Tunisia. It is situated 20 km Northeast of Tebessa city, the capital province. The main geological Paleocene-Eocene formations of Jebel Dyr encountered at site (**Figure 1(c)**) are more precisely represented by a marly Selandian ("e^{2-3}"), a phosphatic Thanetian ("e^{4}") and Ypresian-Lutetian ("e^{5-6}") of flint limestones [21].

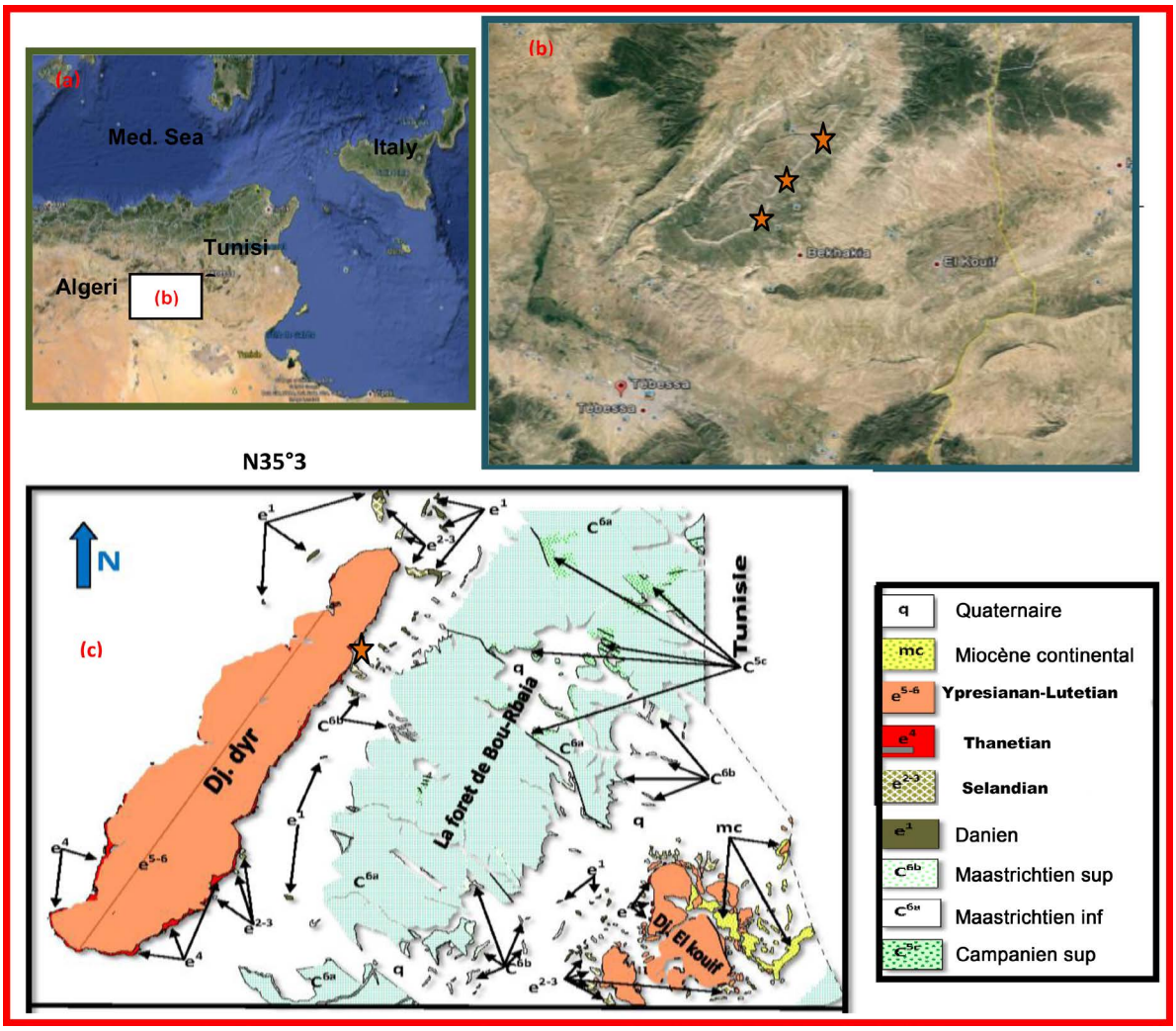

Figure 1. Geographic and geologic position of the study area: (a) Overview; (b) Location of the Jebel Dyr sections in Tebessa region (Google earth, 2015); (c) Simplified geological map of the Tebessa Basin (extract from geological map of Algeria 1/50,000). Red star: The Jebel Dyr sections.

3. Methods and Materials Used

Jebel Dyr sector research was carried out during 2015-2016. The sampling of Thanetian phosphatic layers (total rock) was systematically conducted on outcrops of three sections crossing the southeastern slope of Djebel dyr. The hard layers, with dolomite cement, make the collection of teeth impossible by existing means, therefore, were not sampled. Concurrently, direct investigations for teeth were carried out on the field. However, the most important collecting of teeth materiel was completed after washing the sediment in the Laboratory of Geosciences at the Tebessa University in Algeria. Clean residues were obtained from pre-dried sediment samples washed over a standard set of nested sieves (the last sieve used of a fine mesh is 0.1 mm) after disaggregation in tap water mixed with a wetting agent (detergent). Some samples need subsequent treatment with 5% - 10% hydrogen peroxide (H_2O_2), neutralised with a few drops of ammonia. Fossils were picked from dried residues under a binocular microscope.

Photographs and measurements were taken, where appropriate, to aid in identification. Specimens were subsequently identified to genus level.

Unfortunately many Elasmobranchii teeth are incomplete or broken (existing of just crown or part of the root). These teeth are not resistant to postmortems mechanical damage. So, many of these cannot be identified or determinable to the family level only.

4. Results and Discussion

Fieldwork through three parallel sections (**Figure 1(b)**), carried out on the outcrops of Djebel Dyr formation(**Figure 2(a)**), which shows sub-tabular layers, as well as the laboratory tasks, allowed us to combine and finalize a stratigraphic log for this site(**Figure 2(b)**). This lithostratigraphic column established shows a formation revealing 08 layers of phosphates of Thanetian age, relatively friable of decimetric order, alternating with layers of limestone and marl-limestone and two layers of hard phosphates supported in Ypresian flint limestone to at the top.

The Thanetian fish assemblages of sampled phosphate of Jebel Dyr formation include many remains cartilaginous fish. Twenty-eight species (Elasmobranchii) are identified (**Table 1**), (**Figures 3-6**), twenty-three of which are sharks (Euselachii), however only five are rays (Batoidea). All together, they represent eighteen families of eight orders (**Table 1**). Systematic specification of these fossil groups has not been published previously for the Paleogene basin of the Algerian-Tunisian border area.

The Lamniformes with 9 species and ~25% of the total number of collected specimens are the most diverse order. Among the frequented occurring, Odontaspididaes (*Brachycarcharias* and *Carcharias*) are the most abundant, flowed by Mitsukurinidaes and Otodontidaes. Next in abundance are the Carcharhiniformes with 6 species and ~23% of the total number of specimens. The Myliobatiformes are represented by 4 species and close to 14%. Among them, the rare presence of

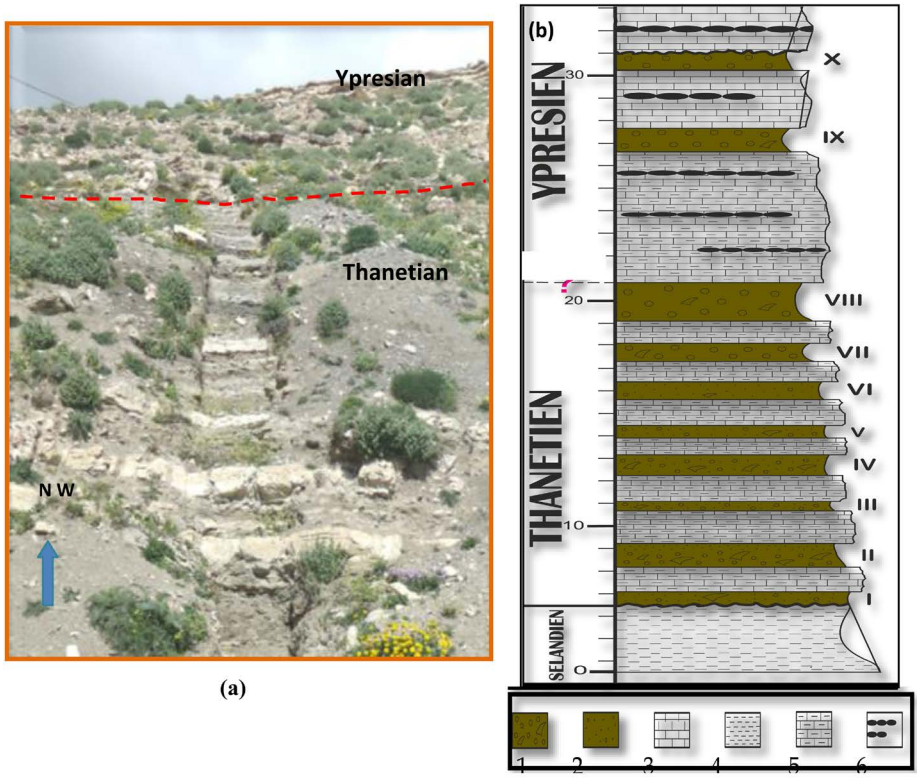

Figure 2. (a) Field photograph of a view (section) represents the profile of the southeastern side towards the North showing Outcrops the Ypresian-Thanetian formation of Djebel Dyr; (b) Lithostratigraphy of the: the studied Djebel Dyr sections with phosphorites layers 1 to 10 indicated; 1 = coarse-grained phosphorites; 2 = fine-grained phosphorites; 3 = limestone; 4 = marl; 5 = marly limestone; 6 = chert.

Table 1. Systematic overview of fish species identified from Thanetian phosphatic series of Jebel Dyr.

Order	Family	Species
Lamniformes Berg, 1958	Odontaspididae Müller & Henle, 1839	*Brachycarcharias lerichei* (CASIER, 1946)
		Carcharias hopei (Agassiz, 1843)
		Odonstaspis winkleri Leriche, 1905
	Mitsukurinidae Jordan, 1898	*Striatolamia striata* (Winkler, 1874)
		Anomotodon novus (Agassiz, 1843)
	Otodontidae Glückman 1964	*Otodus obliquus* Agassiz, 1843
		Cretalamna appendiculata (Agassiz 1843)
	Lamnidae J. P. Müller and Henle, 1838	*Isurolamna affinis* (Casier, 1946)
	Jaekelotodontidae Gluckman 1964	*Mennerotodus* sp.
Charcharniformes Compagno, 1973	Carcharhinidae Jordan & Evermann, 1896	*Abdounia beaugei* (Arambourg, 1935).
		Physogaleus secundus (Winkler, 1874)
	Triakidae Gray, 1851	*Galeorhinus mesetaensis* (Noubhani & Cappetta, 1997)
		Palaoegaleus vincenti (Daimeries, 1888)
		Mustelus biddlei Baut & Genault, 1995
	Scyliorhinidae Gill, 1862	"*Scyliorhinus*" *gilberti* Casier, 1946
Squatiniformes Debuen, 1926	Squatinidae Bonaparte, 1838	*Squatina prima* (Winkler, 1874)

Continued

Heterodontiformes Berg, 1937	Heterodontidae Gray 1851	*Heterodontus sp*
Orectolobiformes Applegate, 1972	Ginglymostomatidae T.N. Gill, 1862	*Nebrius bequaerti* (Leriche, 1920)
		Delpitoscyllium africanum (Leriche, 1927)
		Ginglymostoma subafricanum Arambourg 1952
	Hemiscylliidae T.N. Gill, 1862	*Hemiscyllium daimeriesi* (Herman, 1972)
	Orectolobidaes Jordan & Fowler, 1903	*Squatiscyllium nigeriensis* (WHITE, 1934)
Pristiformes Nelson 1994	Pristidae Bonaparte, 1838	*Pristis sp*
Myliobatiformes Compagno, 1973	Myliobatidae Bonaparte, 1838	"*Myliobatis" sulcidens* Dartevelle & Casier, 1943
	Dasyatidae Jordan, 1888	*Dasyatis hexagonalis* Arambourg 1952
	Mobulidae GILL 1893	*Archaeomanta priemi* Herman 1979
		Burnhamia daviesi (Woodward, 1889)
Rajiformes Berg, 1940	Rajidae Bonaparte, 1831	*Raja sp*

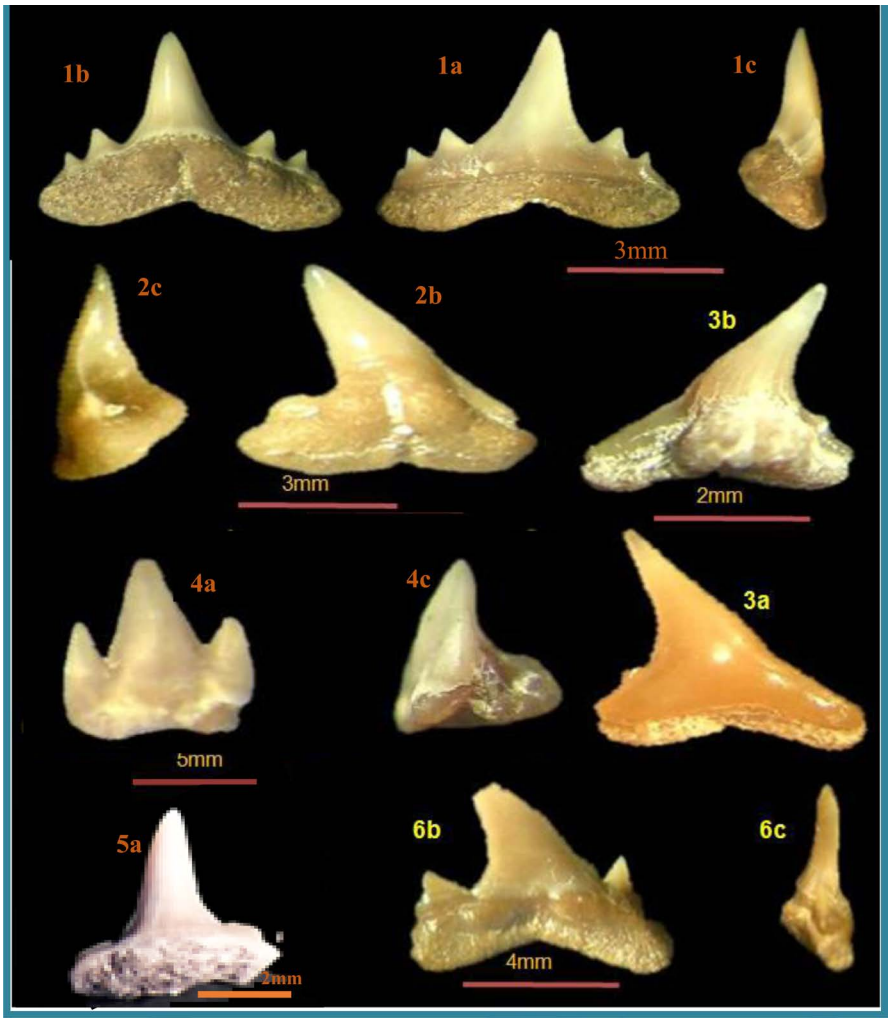

Figure 3. Elasmobranchs teeth from the Thanetian phosphatic serie of Jebel Dyr (Algerian-Tunisian border area); 1. *Abdounia beaugei*; 2. *Palaoegaleus vincenti*; 3. *Galeorhinus mesetaensis*; 4. *Delpitoscyllium africanum*; 5. *Squatina prima*; 6. *Brachycarcharias lerichei.* a: labial; b: lingual; c: lateral; d: occlusal views.

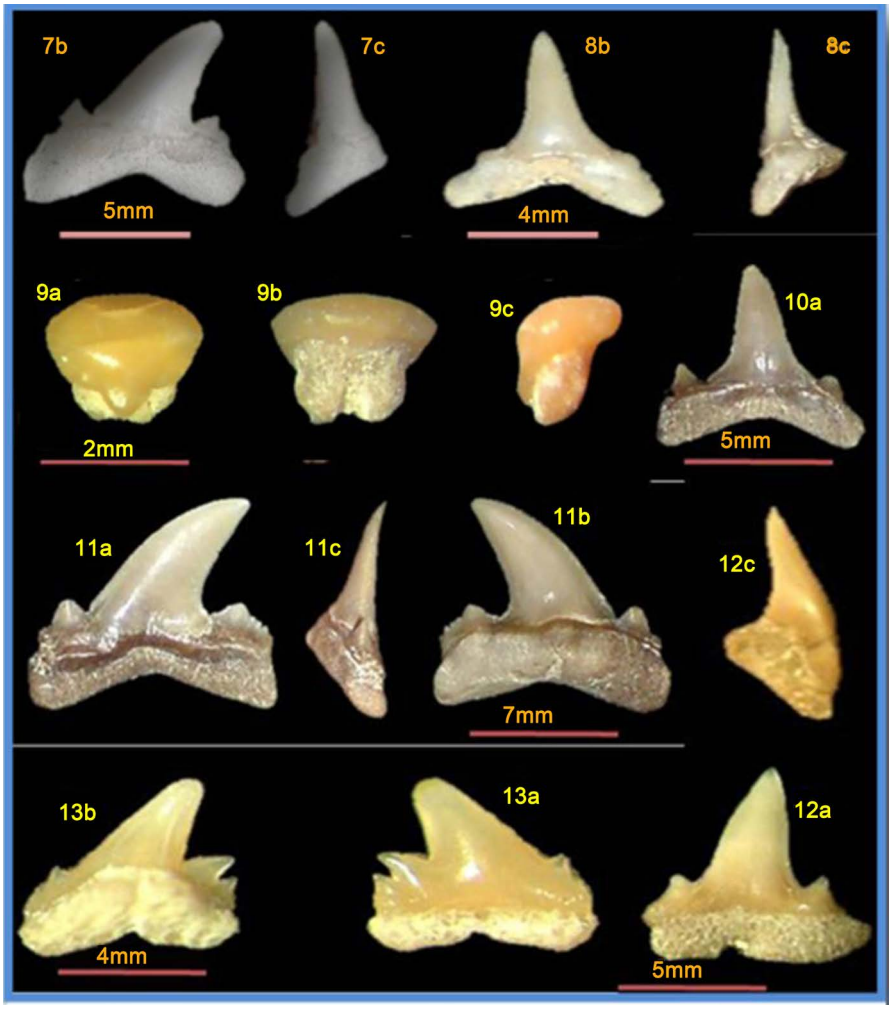

Figure 4. Elasmobranchs teeth from the Thanetian phosphatic serie of Jebel Dyr (Algerian-Tunisian border area); 7. *Brachycarcharias lerichei*; 8. *Anomotodon novus*; 9. *Mustelus biddlei* 10. *Brachycarcharias lerichei*; 11. *Mennerotodus sp*; 12. *Abdounia beaugei*; 13. *Galeorhinus mesetaensis.* a: labial; b: lingual; c: lateral views.

Myliobatidae (mollusc predators, common in high energetic shallow environments) is surprising. Orectolobiformes represented by four species are also, frequent with 14%. The families of the Squatinidae, the Heterodontidae, Rajidae and Pristidae each represented by a single species, are less frequent and together represent nearly 24% of the total number of specimens.

Table 2 summarizes dentition types based on [6] [12] [22] and main features of the teeth collected at the Jebel Dyr Thanetian phosphorites, demonstrating that, in spite the spectacular diversity of the assemblage, teeth of sharks represent similar trophic adaptations [22] [23]:

- Tearing type in Odontaspididae, Mitsukurinidae and Jaekelotodontidae. The teeth of this type generally have well developed sharp edges and often one or more pairs of sharp lateral denticles, whereas the email of the lingual surface of the crown can be smooth. The fish of this type prefer near the coastal environments or leave near the bottom in deep water.

- Cutting Type in Otodontidae and Lamnidae. The teeth in this group are wide, have a high crown, erect and fairly flat (*Otodus*). The functional row of teeth forms a sharp, more or less continuous blade; where the teeth are separated from each other. Forms of this type are nekto-pelagic.
- Cutting-Clutching type in Carcharhinidae. Teeth flattened with a large crown and high root. They are interlocked making an integral thread. The cusps allow to retain the prey, while the flattened teeth of the other jaw act in the manner of a guillotine.
- Clutching type in Ginglymostomatidae, Hemiscylliidae and Orectolobidaes. The teeth are poorly differentiated generally provided with lateral denticles for prey holding. The fish of this type prefer benthic habits, living close to the bottom.
- Crushing type in Myliobatidaes, Squatinidae and Rajidae. These teeth have a morphological diversity from forms with totally, smooth teeth (*Raja*). The crowns have bumpy surfaces. The teeth are staggered and closely intertwined. Fish with this dentition prefer a benthic lifestyle.

Figure 5. Elasmobranchs teeth from the Thanetian phosphatic serie of Jebel Dyr (Algerian-Tunisian border area); 14. *Nebrius bequaerti*; 15. *Archaeomanta priemi*; 16. *Burnhamia daviesi*; 17. *Ginglymostoma subafricanum*; 18. *Myliobatis sulcidens*; 21. *Hemiscyllium daimeriesi*; 23. *Squatiscyllium nigeriensis.* a: labial; b: lingual; c: lateral; d: occlusal; e: oral; f: basilar views.

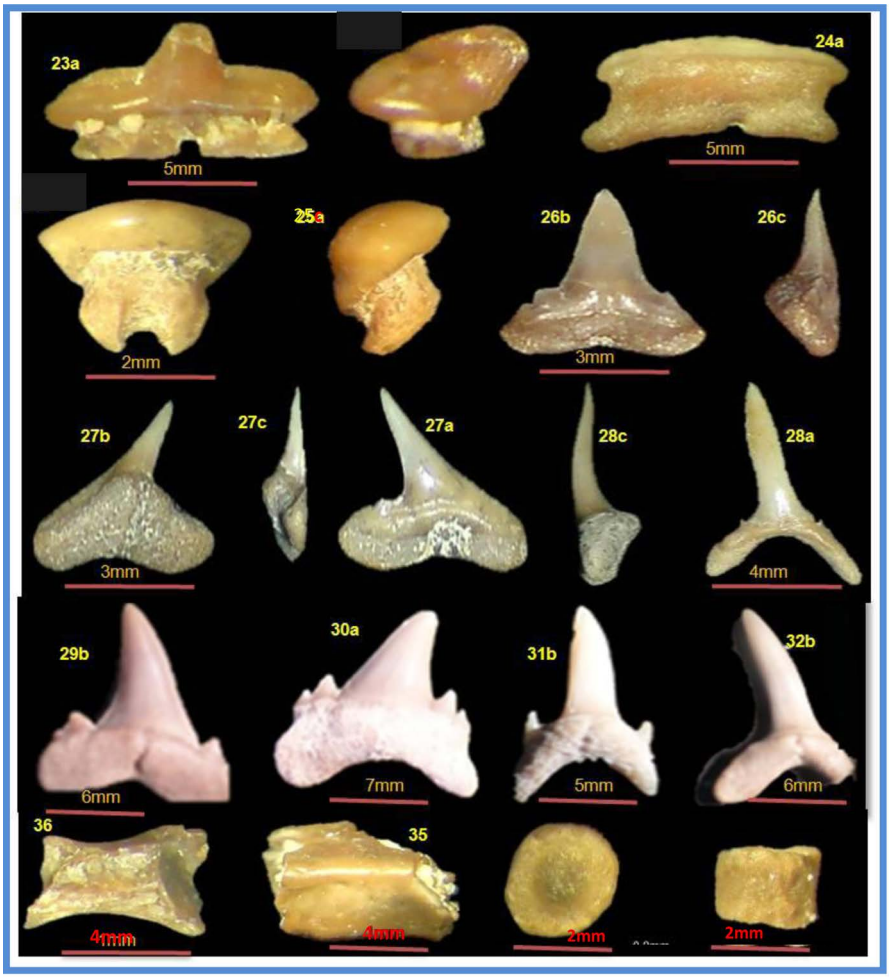

Figure 6. Elasmobranchs teeth and vertebrae from the Thanetian phosphatic serie of Jebel Dyr (Algerian-Tunisian border area); 23. *Raja sp.*; 24. *Heterodontus sp.*; 25. *Dasyatis hexagonalis*; 26. *Abdounia beaugei*; 27. *Physogaleus secundus*; 28. *Carcharias hopei*; 29-30. *Cretalamna appendiculata*; 31. *Brachycarcharias lerichei*; 32. *Isurolamna affinis*; 33-36. Sectioned fossil vertebral centrum of sharks. a: labial; b: lingual; c: lateral; d: occlusal; e: oral views.

- Grinding type in Dasyatdae. Teeth are high crowned and of polygonal shape, closely intertwined and forming a real dental plaque with an almost flat surface. This type is found in fishes preferring benthic habits where they can feed on prey with hard resistant envelopes.
- Clutching-Grinding type of Heterodontidae. Anterior teeth cusps generally provided with lateral denticles are of clutching type, while the lateral teeth, with massive spreading crown more or less cambered are of grinding type. The genera with dentition type prefer benthic habits and live mainly on hard bottoms.

In summary, a relationship between dentition type and living environment, can observed as following:

- The Tearing type is specifically confined to the Lamniformes, confined to coastal and epi-bathyal areas.

Table 2. Dentition type and occurrence of fish teeth from the Thanetian phosphatic series of Jebel Dyr (Algerian-Tunisian border area).

Family	Dentition types and main features of collected specimens	Occurence
ODONTASPIDIDAE (Sand sharks)	Tearing type; large dagger-shaped teeth, long and tapering, often with two small, sharp denticles next to the main crown; small and strong tapering in *Odontaspis*. The crown is smooth, the root is short with spaced lobes in *Brachycarcharias*, or long and close together to *Carcharias*.	Frequent
MITSUKURINIDAE (Goblin sharks)	Tearing type; small unsymmetrical teeth, thrown towards the commissure with a blunted apex; wide and low denticles; root large and relatively flat with a deep groove (*Striatolamia*).	Uncommon
OTODONTIDAE (Megatoothed sharks)	Cutting type; Teeth large robust with unsserrated triangular crown, smooth cutting edges and roughly triangular side cusps (*Otodus*). *Cretolamna* teeth have a compressed root which has a rectangular looking shape. The main cusp is broad and there are two stocky triangular shaped cusplets.	Rare
LAMNIDAE (Mackerel sharks)	Cutting type; Teeth slack cusplets and have thick, but mesio-distally compressed, roots with nearly vertical lateral margins and a straight cusp. The lingual protuberance bears an elliptical foramen (*Isurolamna*).	Uncommon
CARCHARHINIDAE (Requim sharks)	Cutting-Clutching type; teeth are generally small, inclined to a sharp notch between the posterior dentil and the rest of the crown (*Adounia*). In general, the crown is blade-like and distally directed. The mesial cutting-edge continues on to the shoulder and bears weak serrations and can be strongly serrate with up to four cusplet-like serrations (*Physogaleus*).	Frequent
JAEKELOTODONTIDAE	Tearing type, *Mennerotodus* teeth have a fine and high main cusp and lateral cuspids that are not well developed. They are distinguished by the presence of fine crenulations between the crown and the lateral denticles.	Rare
TRIAKIDAE (hound sharks)	Clutching-crushing type: Small ring of teeth flat main cusp highly developed and curved. The denticles decreasing from top to bottom edge (*Galeorhinus*). The *Mustelus* teeth are characterised by a crushing type dentition. They are slightly asymmetrical and transversely elongated, with a reduced, distally directed cusp. The crown is as high as the root.	Common
SCYLIORHINIDAE (Cat sharks)	Type Clutching/Tearing; Teeth laterally spread; the outer face is slightly convex. Pairs of lateral denticles (Scyliorhinus) flank the wide cusp, sharp and angled towards the corner.	Rare
SQUATINIDAE (Shark Angels)	Crushing type; small triangular tooth, its root behind rejects the crown angles. The base of the root has a rhombic shape (*Squatina*).	Rare
HETERODONTIDAE (bullhead sharks)	Clutching-grinding type: flat teeth and stretched, without sharp cusps. The labial face of the crown extends over the splayed root lobes and the apron may bear ornamentation (*Heterodontus*).	Uncommon
GINGLYMOSTOMAT1DAE (Nurse sharks)	Clutching type: teeth generally small, the number of denticles can multiply gradually and laterally. (*Nebrius*). *Delpitoscyllium* Teeth are longer than broad with a triangular cusp and a pair of divergent lateral cusplets. The cusplets develop low on the crown face but project relatively high. Occlusally, the *Burnhamia* teeth are hexagonal in shape and are arranged in a pavement-like fashion.	Frequent
HEMISCYLLIIDAE (Bamboo sharks)	Clutching type; The teeth have a main tip cusp narrowly triangular and two small lateral tips similar in each side and have broad-based (*Hemiscyllium*).	Uncommon
ORECTOLOBIDAE (Wobbegong sharks)	Clutching type, Teeth fairly compressed laterally to high cusp, pointed, inclined inwards. The outer face of the crown is quite convex. The inner medial protuberance is well developed, long and rather slender at its end. The root is tall, squat, flat basal face in profile, but concave anteriorly in labial view (*Squtiscyllium*).	Uncommon
MYLIOBATIDAE (Eagle rays)	Crushing type; Online teeth, dentition plates or real millstones. Palace mills high crown of polygonal contour. The indented portion is the root of the tooth, the thin crown, is a smooth portion and hard (*Myliobatis*).	Rare
DASYATIDAE (Whiptail stingrays)	Grinder type: tiny teeth about 2 mm, ornate. The forms found are loops. The root is higher in profile (*Dasyatis*).	Uncommon
MOBULIDAE (Mantarays, Devilrays)	Cutting-Clutching type; Teeth *Archaeomanta* are easily recognized by their peg-like design and bulbous root. Unlike the living manta ray, the crown rises directly from the root, bears a median ridge and is fully covered with enameloid.	Rare
RAJEDAE (skates fish)	Crushing type, teeth usually small shaped like inverted trumpets. The anterior and lateral have a cusp more or less elongated (*Raja*).	Rare
PRISTIDAE (Sawfish)	Rostral "teeth" (referred herein as spines). *The* tooth is longer than broad, the crown is globular & rounded, has a transverse crest. In general, elongated rostral spines with sharp or smoothly rounded posterior edges tend to be channeled ones (*Pristis*).	Rare

- Cutting type dentition is found in fishes living near the bottom or in open water neritic habitats.
- Subtype cutting/grinding characterises both coastal and bathyal forms.
- The crushing, grinding, grinding/clutching and clutching types are essentially restricted to benthic and nektic forms of the neritic zone.

Table 3 specifies climatic, environmental and bathymetric preference of the species represented in the phosphate series of Jebel Dyr, allow deductions and

Table 3. Environmental preferences of the thanetian ichthyological assemblage recovered from Jebel Dyr phosphatic layers (Algerian-Tunisian border area).

Taxa	Climate			Environment			Bathymetry	
	Tropical/ Subtropical	Temperate	Cold	Litoral/Neritic	Semipelagic/ Pelagic	Bathyal	Nektic	Benthic
Brachycarcharias lerichei	✪	☆		✪				
Odonstaspis winkleri	✪	☆		✪				
Striatolamia striata	✪	☆			✪	☆		✪
Carcharias hopei	✪	☆		✪				✪
Anomotodon novus	✪	☆				☆		✪
Otodus obliquus	✪			✪			☆	✪
Cretalamna appendiculata	✪			✪	☆		☆	✪
Abdounia beaugei		✪		✪	☆		✪	☆
Galeorhinus mesetaensis	☆	✪		✪				✪
"Scyliorhinus" gilberti	✪	✪		✪			☆	✪
Squatina prima		✪			✪	☆		✪
Heterodontus sp		✪		☆				✪
Isurolamna affinis		✪		✪			✪	
Archaeomanta priemi		✪		✪			✪	☆
Nebrius bequaerti	✪			✪				✪
Delpitoscyllium africanum	✪	☆		✪	☆			✪
Hemiscyllium daimeriesi	✪			✪	☆			✪
Squatiscyllium nigeriensis	✪			✪				✪
Myliobatis sulcidens	✪	☆						✪
Physogaleus secundus		✪		✪			✪	☆
Mennerotodus sp.	☆	✪		✪			✪	
Palaoegaleus vincenti		✪		✪				✪
Mustelus biddlei		✪		✪				✪
Raja sp	✪	☆			☆	✪	✪	
Ginglymostoma subafricanum	✪	☆		✪	☆			✪
Burnhamia daviesi	✪	☆		✪	☆			✪
Pristis sp	☆	✪		☆	✪		✪	
Dasyatis hexagonalis	✪			✪	☆		☆	✪

☆ Less characteristic; ✪ Characteristic.

insights which to be drawn from these data:

1) A direct relationship between fish and their distributions on the one hand and the ambient temperature and ocean currents on the other hand.

2) The predominance of forms of warm water at tropical and subtropical distribution such as *Brachycarcharias, Carcharias, Odontaspis, Striatolamia, Anomotodon.* However, stenothermic forms downright tropical as *Otodus* are present but in a rare way.

3) Another group of Species preferring temperate or moderately warm water is present: as *Abdounia beaugei, Physogaleus secundus*, *Isurolamna affinis and Archaeomanta priemi.*

4) Forms that inhabit temperate or relatively cold waters, as *Raja* might indicate deeper water environment with lower temperature. Likely, currents can carry sharks from water more or less hot to achieve higher latitude.

5) The majority of the represented fishes inhabit the neritic littoral zone, although some genera, such as *Striatolamia striata and Anomotodon novus* inhabit the pelagic zone. Others groups such as R*aja*, which are extremely rare, even live in bathyal zones. Currents allow forms of cold water who live in deep water to appear near shallower water. This may explain the co-occurrence of temperate and warm indicators.

6) Among the recognized Species 07 are nektonic and benthic at a time. With respect to the remaining groups only 04 have a nektic lifestyle otherwise 17 forms are benthic.

In summary, the fish assemblage indicates a relatively warm sea, but not strictly tropical. Thus, most of the forms demonstrate a shallow marine, coastal environment, with occasionally rocky bottoms, suitable for molluscs and shellfish predators, as well as sandy bottoms frequented by small sharks such as *Odontaspis* the so-called "sand sharks" [24] [25] [26] [27] [28].

Many fish groups encountered in this phosphatic serie still live in the Mediterranean and in the Atlantic Ocean: *Carcharias, Galeorhinus, Physogaleus, Mustelus a*nd *Raja.*

There is a strong resemblance between ichthyologic fauna composition of the Algerian-Tunisian border area (South Tethys) with that of the Anglo-Franco-Belgian basin during the Paleogene [29] [30] [31] [32]. This wide geographical distribution of sharks and rays demonstrates shows their biostratigraphic potential.

Finally, given the geological data and the absence of the purely pelagic and bathyal forms, it can be assumed that this Thanetian assemblage occupied a relatively narrow gulf. The last was between mainland and open sea, agreeing with the paleogeographical interpretation of [33]. It indicating that Tebessa (Dyr) area was immersed between the Algerian promontory and the island of Kasserine (**Figure 7**).

5. Conclusions

1) The Jebel Dyr phosphatic serie yielded a wealth of fish remains with many

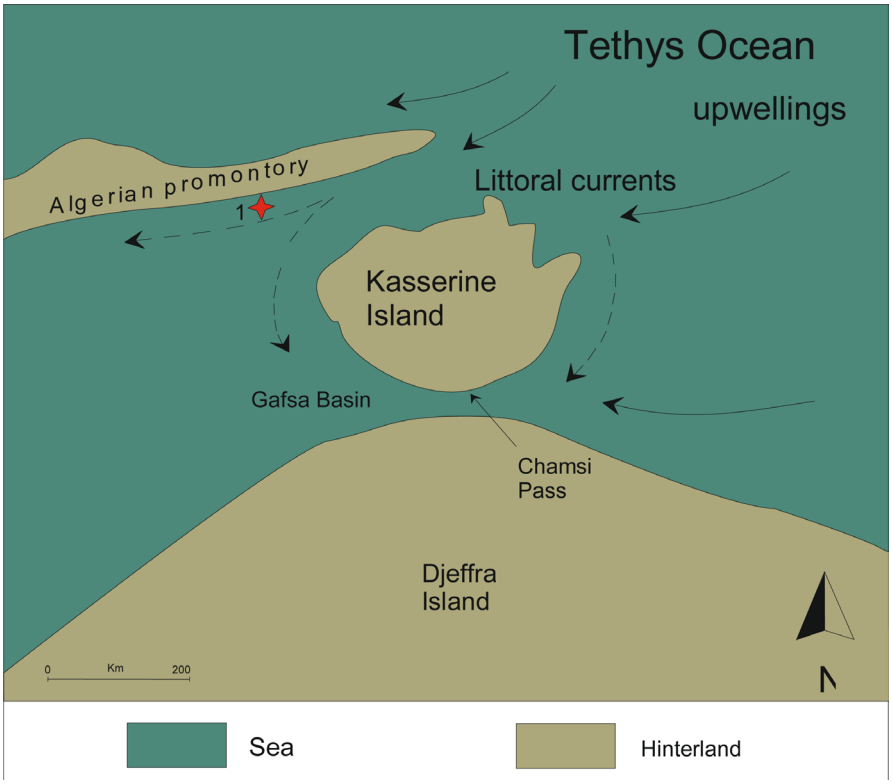

Figure 7. Supposed Paleocene-Eocene paleogeography in Algerian-Tunisian border area ([33], modified). Red star indicates position of sample locality (Jebel Dyr).

predators, represented by 28 species of Elasmobranchii (Euselachii and Batoidea).

2) The fossil forms of the Elasmobranchii recognized in these phosphate layers confirm the Thanetian age for this formation of Jebel Dyr.

3) Dentition types mainly characterize benthic and nectic forms of the neritic littoral.

4) The fish fauna indicates a marine, coastal, shallow water environment with both rocky and sandy bottom, and temperature to subtropical climatic conditions.

5) The appropriate paleobiogeographic indication is almost similar with the most contemporary of the Mediterranean fish.

6) Apparently, the Jebel Dyr assemblage of fish occupied during Thanetian a relatively narrow golf separated from open sea.

We conclude that Jebel Dyr fish fauna preferred inhabit the neritic zonal environments, which gave the highly opportunistic predator ability to prey on various animal groups, such as molluscs (bivalves, gastropods and cephalopods), crustaceans, echinoderms, annelids, sipunculids and fish. The wealth of biota on the continental shelf and upper slope contrasts strongly to the pelagic or bathyal zones, where potential food is less abundantly available, more dispersed and less varied.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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