

The marine vertebrate faunas from the Late Cretaceous phosphates of Syria

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Abstract – Marine vertebrate faunas from the latest Cretaceous phosphates of the Palmyrides Chain of Syria are described for the first time. Recent fieldwork in the phosphatic deposits of the Palmyra area (mines of Charquieh and Khneifiss, outcrops of Bardeh, Soukkari and Soukhneh) have yielded a rich and diversified assemblage of marine vertebrates, including more than 50 species of chondrichthyes, osteichthyes, squamates, chelonians, plesiosaurians and crocodylians. Selachians are the most abundant and diverse component of the faunas and are represented by at least 34 species of both sharks and rays. Actinopterygians include representatives of six families, the most common being the enchodontids. Squamates are known by six mosasaurid species and an indeterminate varanoid. Chelonians are represented by at least two bothremydids and two chelonoids. Finally, elasmosaurid plesiosaurs and indeterminate crocodylians are also present in the fossil assemblages. The difference in faunal composition observed between the sites is interpreted as being due to palaeoecological preferences related to the Hamad Uplift palaeostructure. The marine vertebrate faunas of Syria show close affinities with those of the latest Cretaceous phosphatic deposits of North Africa and the Middle East and are typical of the southern Tethyan realm. From a biostratigraphical point of view, the selachians are the only suitable material to provide elements of an answer to the long debated question of the age of the Syrian Senonian phosphates. They suggest an Early Maastrichtian age for most of the phosphates of the Palmyrides Chain.

1. Introduction

During the end of the Cretaceous and part of the Tertiary period, the platforms bordering the southern Tethys were characterized by a highly phosphatic terrigenous and carbonated sedimentation in shallow marine environments. Since the first discoveries in Palestine (Lartet, 1869) and Algeria (Thomas, 1873 *in* Arambourg, 1952), phosphatic deposits have been known over wide areas of a southern Mediterranean belt cropping out from North Africa to the Middle East (Lucas & Prévôt-Lucas, 1996).

The economic exploitation of phosphatic deposits has yielded a great number of vertebrate fossils. Marine vertebrate remains are quite abundant, mainly selachian teeth and, to a lesser degree, osteichthyan and reptile bones and teeth (Arambourg, 1952). Continental vertebrates have also been recovered, such as mammals in Morocco (Gheerbrant, Sudre & Cappetta, 1996), as well as pterosaurs and dinosaurs

in Jordan and Negev (Arambourg *et al.* 1959; Lewy, Milner & Patterson, 1992; Frey & Martill, 1996; Martill, Frey & Sadaqah, 1996), but they remain very scarce.

Although the bulk of marine vertebrates from the latest Cretaceous phosphatic deposits are known from Morocco (Arambourg, 1952; Rage & Wouters, 1979; Cappetta, 1987; Gmira, 1995; Noubhani & Cappetta, 1997), remains have been unearthed from most of the southern Mediterranean margin regions, namely in Egypt (Zdansky, 1935; Cappetta, 1991; Werner & Bardet, 1996; Lapparent de Broin & Werner, 1998), Palestine and Negev (Raab, 1963; Lewy & Cappetta, 1989; Cappetta, 1990; Chalifa & Lewy, 1991; Chalifa, 1996), Jordan (Avnimelech, 1949; Arambourg *et al.* 1959) and Iraq (Arambourg *et al.* 1959).

In Syria, records of Late Cretaceous vertebrates were, until recently, very scarce. Only an isolated dinosaur bone, found in indeterminate Cenomanian to Senonian deposits of the Damascus Basin, has been described (Hooijer, 1968). Fish remains have also been recorded from the Senonian phosphates of the

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Palmyrides Chain (Arambourg *et al.* 1959; Atfeh & Faradjev, 1963; Dubertret, 1963, 1966; Ponikarov *et al.* 1967; M. Mouty & A. K. Al Maleh, unpub. report, Ministry of Petroleum and Mineral Resources of Syria, 1983; Atfeh, 1989; Al Maleh & Mouty, 1994), but have never been described.

Recent fieldwork in the latest Cretaceous phosphates of the Palmyra area has yielded a significant and diverse assemblage of marine vertebrates, including chondrichthyans (sharks and rays), osteichthyans (actinopterygians), squamates (mainly mosasaurids), plesiosaurians, chelonians and crocodylians. Description of the first latest Cretaceous marine vertebrate faunas of Syria is the aim of the present paper. A discussion of the biostratigraphical position of the Syrian phosphatic deposits, as compared to other southern Mediterranean phosphate sites, is given.

2. Geographical, stratigraphical and petrographical settings

The first mention of phosphatic deposits in Syria was made by Dubertret, Keller & Vautrin (1932). Phosphate deposits are relatively widespread in Syria, ranging from Santonian to Late Eocene and cropping out mainly in the Kurg Dagh, the Coastal Chain and the Palmyrides Chain (Atfeh & Faradjev, 1963; Al Maleh, 1974).

Late Cretaceous sediments of the Palmyrides Chain contain the bulk of the phosphate rock resources of Syria (Atfeh, 1989). The Palmyrides Chain forms a 350 km long system of narrow ridges that extends from the Anti-Liban to the West of the Euphrate Graben in a global southwest–northeast direction (Ponikarov *et al.* 1967) (Fig. 1). The chain is divided into southern and northern ranges by the Neogene–Quaternary Dawwa depression located around Palmyra. Most of the phosphates are concentrated in the southern range of the Palmyrides Chain where they have been mined for years in the Khneifiss and Charquieh (Sawwaneh al Hamra) mines, located about 50 km southwest of the oasis of Palmyra and 150 km northeast of Damascus (Al Maleh & Mouty, 1994) (Fig. 1). In addition to Khneifiss (southern mine) and Charquieh (mines A and B), three other localities of non-economic phosphates have been studied in the Palmyra area: Bardeh (Kharbaqah barrage), Soukkari (eastern Jebel Abtar on Palmyra road) and Soukhneh, about 60 km northeast of Palmyra (Fig. 1).

In Syria, the Cretaceous is classically divided into six lithostratigraphical units or formations ranging from Barremian–Aptian (K1) to Campanian (K6) and an overlying Maastrichtian–Palaeocene unit called the Bardeh Formation (Mouty & Al Maleh, unpub. report, Ministry of Petroleum and Mineral Resources of Syria, 1983). Senonian deposits represent the main part of the Cretaceous series in the Palmyrides Chain.

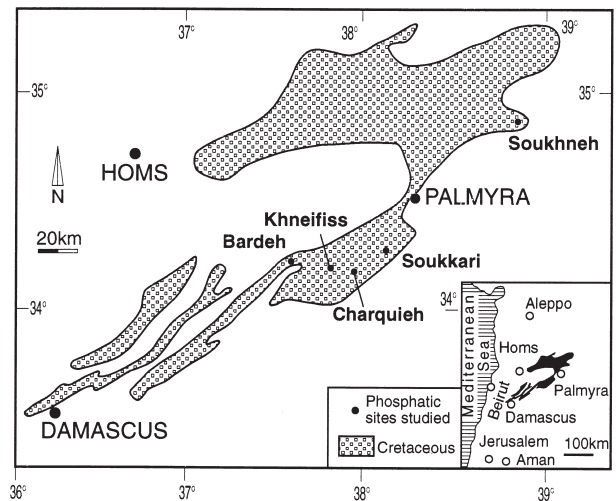


Figure 1. Geographical location of the studied phosphatic sites and of the Cretaceous exposures in Syria.

The K5 and K6 units or Soukhneh Group (Henson, unpub. S. P. C. report, 1939 in Dubertret, 1963) includes most of the Senonian sediments and is divided into the Rmah (K5) and Sawwaneh (K6) formations. The Rmah Formation includes mainly marls and limestones and ends up with flint bars intercalated with shelly or marly limestones. The Sawwaneh Formation is mainly composed of a basal phosphatic member overlain by reddish-yellow marls with calcareous nodular levels (Erek Marls) and a carbonate series of marly limestones and phosphatic glauconious marls which are replaced locally by a siliceous horizon (Tantour Member). The thickness of the Sawwaneh Formation ranges from 17 m to 317 m, increasing generally northwards without significant facies changes, which suggests subsidence and deepening of the basin towards the north.

The basal phosphatic deposits of the Sawwaneh Formation represent the main phase of the phosphatogenesis in Syria and are those which are economically exploited. They vary in thickness, reaching a maximum of 10–12 m in the central southern range of the Palmyrides Chain (Mouty & Al Maleh, unpub. report, Ministry of Petroleum and Mineral Resources of Syria, 1983). They become thinner westwards and disappear totally below the Erek Marl and Tantour Member of the westernmost extremities of the Palmyrides Chain. They are generally represented by either soft or hard, granulated, decimetre- to metre-size banks with local carbonated or conglomeratic levels (Henson, unpub. S. P. C. report, 1939 in Dubertret, 1963).

Simplified stratigraphical columns have been produced for all the studied sites (Fig. 2) and are briefly described below. Stratigraphical correlations between the different sites are difficult because of significant lateral facies variations and the lack of key levels.

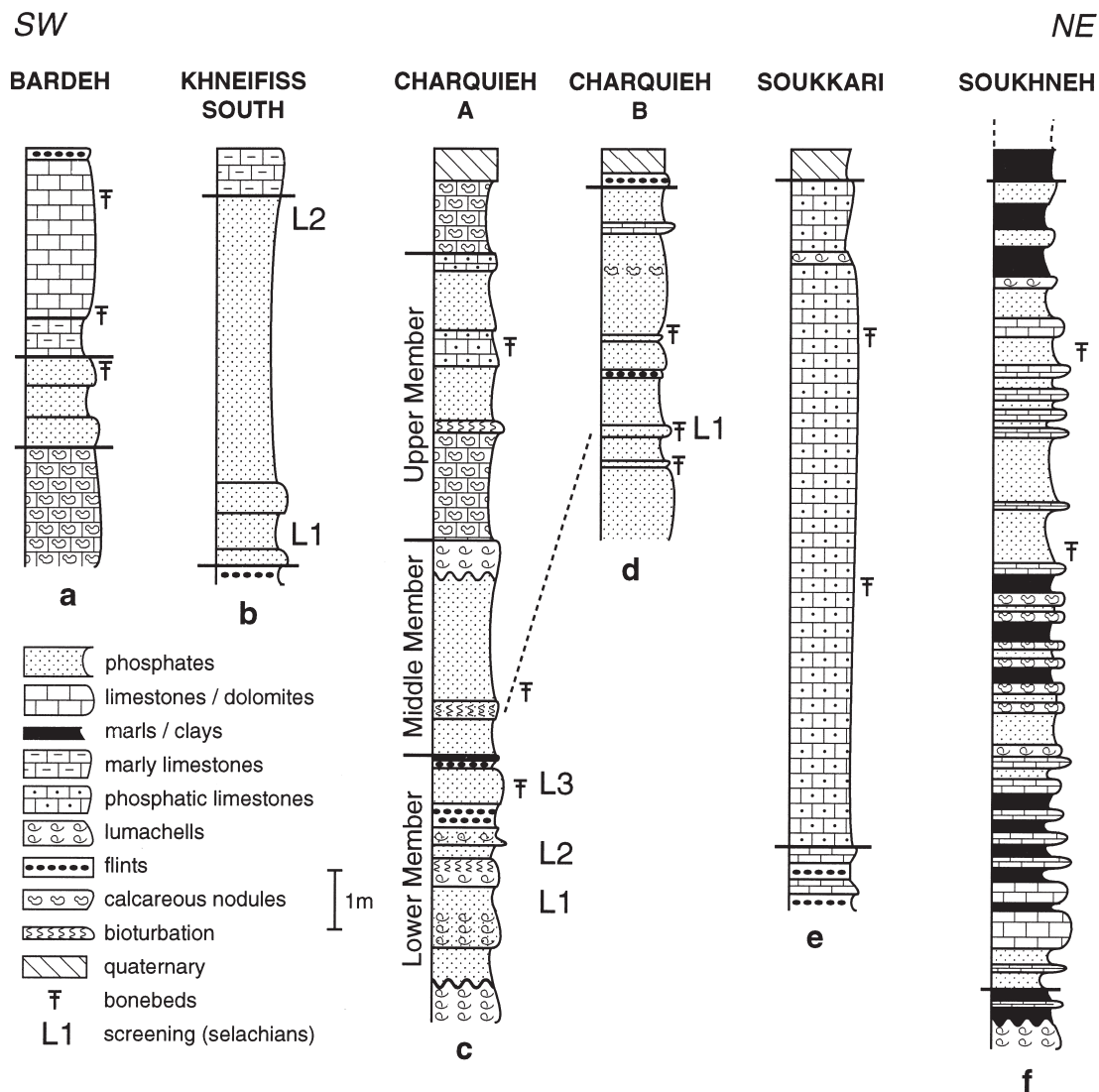


Figure 2. Stratigraphical columns of the studied phosphatic sites.

However, the selachian faunal assemblages suggest some differences, as discussed below (see Section 4).

Bardeh – The stratigraphical succession in Bardeh includes thick basal limestones with large disc-shaped structures, about 1.5 m thick hard compact phosphates and upper, pale marls and limestones rich in fish remains (Fig. 2a). The phosphatogenesis ends at the top of the limestones with a flint level.

Khneifiss – The Khneifiss phosphates are mainly calcareous, with abundant organic remains, and they are of the highest grades in Syria (Atfeh, 1989). The main phosphatic zone overlies dark massive cherts and underlies pale marls with important syndimentary folds. Two phosphatic levels, separated by marly limestones and cherts are present. The lower phosphatic level is about 9 m thick and the upper about 4 m thick. Both levels are either hard or friable. In the northern mine, the lower level is hard and the upper one is lacking. In the studied southern mine (Fig. 2b), the lower

phosphatic level and part of the marly limestones are not known and the upper phosphatic level lies directly on cherts. This phosphatic level is mostly friable, yellow to reddish in colour and very rich in vertebrate remains.

Charquieh – Two mines (A and B) are exploited here. Generally, the phosphates are intercalated within a lower lumachellic limestone mainly composed of the oyster *Ambigostrea villei* (Coquand, 1862) (determination A. V. Dhondt) and an upper alternation of marls, dolomites and limestones, covered or not by Quaternary sediments. The phosphates are yellow to grey, mainly soft, and increase in thickness towards the south and southeast. In mine A, where the phosphatic level is about 13 m thick and divided by the mine workers into lower (soft phosphates ending with yellow clay and chert key-beds), middle (sandy phosphates) and upper (hard phosphates with limestones and dolomites) members (Fig. 2c), several bone-

chert-, bioturbated- and pebble-beds occur. In mine B, the series is incomplete and the phosphates, about 9 m thick, include only the middle member and a small part of the upper member (Fig. 2d). The top of the series is a massive chert level, not observed in mine A, covered by Quaternary sediments. It should be noted that the ammonite *Libycoceras ismaeli* (Zittel, 1895) (determination H. Gauthier) has been found within the phosphatic series of Charquieh, but its precise stratigraphical occurrence remains unknown.

Soukkari – The phosphates crop out along the road to Palmyra in an anticlinal structure. The series is composed of basal limestone and chert levels underlying yellow, marly limestones. A pebble-bed marks the beginning of the phosphatic deposits which are hard, about 10 m thick and end with a mud ball level (Fig. 2e). At least two turtle plate bone-beds occur within the phosphatic series. At the top of the series, about 10 m above the phosphatic levels, is a conglomerate which marks the end of the phosphatogenesis. It can be roughly correlated to the flint level previously mentioned in the description of Bardeh.

Soukhneh – The classical stratigraphical series is exposed in an anticlinal structure near the town of Soukhneh (see Dubertret, 1966, p. 322). It is composed successively of basal massive cherts, silicified reddish lumachells including thin phosphatic levels, alternation of marly limestones rich in bivalves and soft phosphate levels and finally, greenish marls ending with a phosphatic bed overlain by pale marly limestones and marls (Fig. 2f). Soukhneh represents the northeasternmost outcrop of the phosphatic series in the Palmyrides.

The facies of the Soukhneh Group show significant vertical and lateral variations (Al Maleh & Mouty, 1994). In the phosphate rocks and phosphatic limestones, a wide spectrum of facies is encountered. The facies vary from biomicrite–microsparite with a small content of phosphatic grains to friable phosphatic arenite. The phosphatic components are generally granular with grain sizes of 0.05 to 0.5 mm; occasionally, the phosphate grains are millimetric and rarely centimetric to decimetric in size (vertebrate remains), and represent 10–80% of the rock. Some phosphatic rocks contain conglomerate-like chert pebbles and large shell horizons. The petrography of the phosphatic components reveals different kinds of phosphatic grains; among these are phosphatic pellets, coated phosphatic grains composed of two or three aggregated grains, grains with non-phosphatic nuclei, irregular grains, coprolite grains resulting from the epigenesis of organic matter, grains with inclusions of non-organic, organic and mineral substances, fish scales, teeth and vertebrae, irregularly shaped and reworked grains. Phosphate beds may contain some limy and cherty clasts along with phosphatic grains which in turn contain organic matter in variable amounts.

3. Palaeontology

The marine vertebrate faunas of Syria are composed of several groups of fishes (selachians and actinopterygians) and reptiles (squamates, plesiosaurians, chelonians and crocodylians). Vertebrate remains are abundant in all the studied sites except Soukkari and Soukhneh and are mainly represented by randomly distributed isolated bones and teeth. Articulated specimens (portions of vertebral column and chelonian shell) are scarce and have been found only in Charquieh A and Khneifiss, but as isolated remains, they are found without particular concentration or orientation. Bone-bed levels, composed almost exclusively of chelonian shell fragments, occur randomly several times in the series. The material is kept in the collections of the Muséum National d'Histoire Naturelle of Paris, France (MNHN–Collection Syrie), the Université des Sciences et Techniques du Languedoc of Montpellier, France (UM–Collection Syrie), and the General Company for Phosphate and Mines of Homs, Syria (GCPM).

3.a. Selachians

Both sharks and rays are represented in the latest Cretaceous phosphatic deposits of Syria (Figs 3, 4, Table 1). Selachians are the main component of the marine vertebrate faunas and are known in all sites by numerous isolated teeth. Sharks include Hexanchiformes, Lamniformes, Orectolobiformes and Carcharhiniformes and at least 17 species are recorded. Batoids are represented by at least 17 species of both Rajiformes and Myliobatiformes, known mainly from Charquieh and Khneifiss.

Hexanchiformes are only represented by *Hexanchus* sp. in Bardeh and Khneifiss. *Hexanchus Rafinesque*, 1810 is of poor biostratigraphical value as it has been found in Jurassic to Recent strata almost worldwide (Cappetta, 1987).

The Lamniformes include at least 11 species, namely *Scapanorhynchus rapax* Quaas, 1902; *Anomotodon* aff. *A. plicatus* Arambourg, 1952; *Anomotodon* sp., *Squalicorax bassanii* Gemmellaro, 1920; *S. pristodontus* Agassiz, 1843; *S. kaupii* Agassiz, 1843; *S. africanus* Cappetta, 1991; *Squalicorax* cf. *S. yangaensis* Darteville & Casier, 1943; *Squalicorax* sp., *Cretolamna biauriculata* Wanner, 1902; *Cretolamna* cf. *C. maroccana* Arambourg, 1935; *Cretolamna* cf. *C. appendiculata* Agassiz, 1843; and *Carcharias* sp. *Scapanorhynchus rapax* occurs in Charquieh A, Khneifiss and Soukkari. It is a rather common mitsukurinid in the Lower Maastrichtian phosphatic deposits of Morocco (Arambourg, 1952; H. Cappetta, pers. obs.). It also occurs in the Maastrichtian phosphates of northern Brazil (Rebouças & Silva Santos, 1956) and Jordan (Cappetta, Pfeil & Schmidt-Kittler, in press). Teeth of the widespread mitsukurinid *Anomotodon* aff. *A. plicatus* occur in Khneifiss and Bardeh; in the latter locality, another indeterminate

Table 1. Selachian faunal list with geographical and stratigraphical occurrences

	Charquieh								
	Bardeh	Mine A			Mine B	Khneifiss		Soukkari	Soukhneh
		L1	L2	L3		L1	L2		
Hexanchiformes									
<i>Hexanchus</i> sp.	X					X	X		
Lamniformes									
<i>Scapanorhynchus rapax</i>		X	X	X		X		X	
<i>Squalicorax bassanii</i>		X	X		X	X			X
<i>Squalicorax pristodontus</i>	X	X	X	X	X	X	X	X	
<i>Squalicorax kaupi</i>			X	X	X		X	X	
<i>Squalicorax africanus</i>				X		X			
<i>Squalicorax</i> cf. <i>S. yangaensis</i>	X					X			
<i>Squalicorax</i> sp.	X	X	X	X	X	X			
<i>Cretolamna biauriculata</i>	X		X	X	X	X			
<i>Cretolamna</i> cf. <i>C. maroccana</i>		X	X	X	X	X			
<i>Cretolamna</i> cf. <i>C. appendiculata</i>					X	X			
<i>Carcharias</i> sp.		X	X	X	X	X	X		
<i>Anomotodon</i> aff. <i>A. plicatus</i>	X					X	X		
<i>Anomotodon</i> sp.	X								
Orectolobiformes									
<i>Chiloscyllium</i> sp. 1					X				
<i>Chiloscyllium</i> sp. 2				X					
<i>Plicatoscyllium</i> sp.		X	X	X	X	X	X		
Carcharhiniformes									
<i>Squatigaleus</i> sp.			X		X				
<i>Pteroscylidium</i> sp.						X	X		
Rajiformes									
<i>Ctenopristis</i> sp.		X	X	X	X	X	X		
<i>Dalpiazia stromeri</i>		X	X		X				
<i>Ganopristis</i> sp.						X	X		
<i>Plicatopristis strougoi</i>		X	X						
<i>Schizorhiza stromeri</i>		X	X		X				X
<i>Parapalaebates atlanticus</i>		X	X	X	X			X	
<i>Hypsobatis</i> sp.		X	X	X	X	X	X		
<i>Youssoubatis</i> sp.		X	X	X	X	X	X		
<i>Hamrabatis</i> sp.		X	X						
<i>Rhinobatos</i> sp.1		X	X	X		X	X		
<i>Rhinobatos</i> sp.2		X					X		
<i>Ataktobatis</i> sp.					X				
<i>Erguita</i> sp.		X	X	X	X				
Myliobatiformes									
<i>Coupatezia</i> sp.1		X	X		X				
<i>Coupatezia</i> sp.2			X						
<i>Rhombodus</i> aff. <i>R. meridionalis</i>		X		X	X	X	X		
<i>Rhombodus</i> sp.			X		X			X	
Myliobatiformes incert. fam.		X	X	X	X	X			

species of *Anomotodon* Arambourg, 1952 is characterized by its large size. The anacoracids are represented by several species of *Squalicorax* Whitley, 1939, well documented in Charquieh, Khneifiss and Bardeh, yet the most diversified assemblage occurs in Khneifiss. *S. bassanii* is represented in the Campanian and Maastrichtian of Morocco, Egypt and Negev (Cappetta, 1987). *S. pristodontus* occurs in Campanian and Maastrichtian deposits worldwide (Cappetta, 1987). *S. kaupi* is mainly common in Campanian deposits, but also occurs in Lower Maastrichtian localities (Cappetta & Case, 1975). *S. africanus* has been found in the Lower Maastrichtian rocks of Egypt (Cappetta, 1991), Morocco (Noubhani & Cappetta, 1997) and Jordan (Cappetta, Pfeil & Schmidt-Kittler, in press). *S. yangaensis* is a quite rare

species only found to date in Lower Maastrichtian localities of Morocco (Arambourg, 1952; Noubhani & Cappetta, 1997). In Syria, a very similar species, referred to as *Squalicorax* cf. *S. yangaensis* is mainly abundant in Khneifiss; Bardeh has also yielded teeth referable to this species. The cretoxyrhinids are represented by three species of *Cretolamna* Glickman, 1958. *C. biauriculata* occurs only in Lower Maastrichtian strata of Morocco (Oued Erguita), where it is rather common. In Syria, it occurs in Bardeh, Charquieh and Khneifiss. *Cretolamna* cf. *C. maroccana* is also present in Charquieh and Khneifiss and its teeth are not as large as those collected in the Maastrichtian of Morocco; this species occurs from the Upper Campanian in the Negev phosphate deposits (Lewy & Cappetta, 1989). The stratigraphical

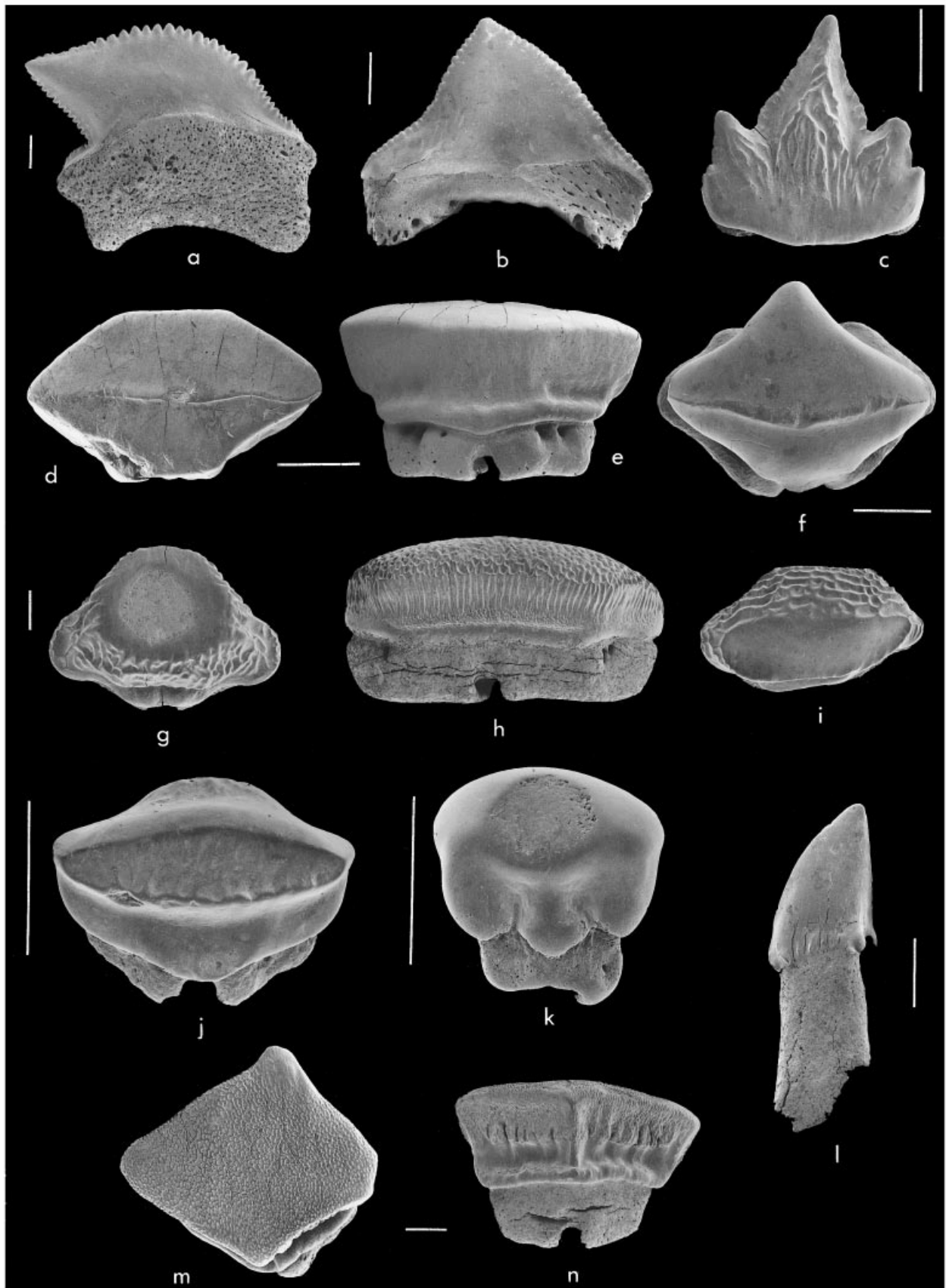


Figure 3. Selachians. (a) *Squalicorax bassanii* (UM-CHB1), lateral tooth of a young individual, lingual view; (b) *Squalicorax africanus* (UM-CHA1-1), anterior tooth, labial view; (c) *Plicatoscyllium* sp. (UM-CHA1-2), latero-anterior tooth, labial view; (d) *Youssoubatis* sp. (UM-CHA1-3), lateral tooth, occlusal view; (e) same tooth, lingual view; (f) *Erguitaia* sp. (UM-CHB2), latero-anterior tooth, occlusal view. (g–i) *Parapalaeobates* sp.; (g) (UM-CHB3), anterior tooth, occlusal view; (h) (UM-CHB4),

interest of *Cretolamna* cf. *C. appendiculata*, found at Charquieh B and Khneifiss, is limited because its stratigraphical range is wide (from Albian to Upper Ypresian) (Cappetta, 1987). Abundant teeth of a small odontaspimid found at Charquieh and Khneifiss are here referred to as an indeterminate species of *Carcharias* Rafinesque, 1810.

Orectolobiformes include two indeterminate species of the hemiscyllid *Chiloscyllium* Müller & Henle, 1837 and one of *Plicatoscyllium* Case & Cappetta, 1997. In Syria, *Chiloscyllium* is known in Charquieh, whereas *Plicatoscyllium* occurs in Charquieh and Khneifiss. The former ranges from Campanian to Recent (Cappetta, 1987). The latter occurs in the Campanian and Maastrichtian deposits of Morocco (Noubhani & Cappetta, 1997) and in the Maastrichtian localities of Texas (Case & Cappetta, 1997).

Carcharhiniformes are represented by *Squatigaleus* sp. in Charquieh and *Pteroscylidium* sp. in Khneifiss. The triakid *Squatigaleus* Cappetta, 1989 is known in the Campanian and Maastrichtian deposits of Morocco (Cappetta, 1989; Noubhani & Cappetta, 1997), and in the Maastrichtian localities of Egypt (Cappetta, 1991) and Texas (Case & Cappetta, 1997). The scyliorhinid *Pteroscylidium* Cappetta, 1980 has been recorded from the Late Cretaceous of the Middle East, North and West Africa and Europe (Cappetta, 1987; Noubhani & Cappetta, 1997); it occurs also in the Maastrichtian of Texas (H. Cappetta, unpub. data).

The Rajiformes include *Dalpiazia stromeri* Checchia Rispoli, 1933; *Plicatopristsis strougoi* Cappetta, 1991; *Schizorhiza stromeri* Weiler, 1930; *Parapalaeobates atlanticus* Arambourg, 1952; and indeterminate species of *Ctenopristsis* Arambourg, 1940; *Ganopristsis* Arambourg, 1935; *Hypsobatis* Cappetta, 1992; *Youssoubatis* Cappetta, 1992; *Hamrabatis* Cappetta, 1991; *Rhinobatos* Linck, 1790; *Ataktobatis* Cappetta & Corral, 1999; and *Erguitaia* Cappetta, 1989. The sclerorhynchids consist of *Dalpiazia stromeri*, *Schizorhiza stromeri*, *Plicatopristsis strougoi*, *Ctenopristsis* sp. and *Ganopristsis* sp. *Dalpiazia stromeri* occurs through all the Maastrichtian localities of Africa but seems more abundant at the base of the stage (Cappetta, 1987). In Syria, it has only been found in Charquieh, and is mainly abundant in the middle part of the phosphate series (middle member). *Schizorhiza stromeri* is known in Charquieh and Soukhneh. This species is interesting because of its narrow stratigraphical and wide geographical distribution, being known only in the Maastrichtian of North and West Africa, the Middle

East, and North and South America (Cappetta, 1987). *Plicatopristsis strougoi* is known only in Charquieh A. This species occurs in the Lower Maastrichtian of Egypt (Cappetta, 1991). *Ctenopristsis* is present in Charquieh and Khneifiss but is not very common. It is known elsewhere in the Campanian of Negev (Lewy & Cappetta, 1989) and in the Maastrichtian rocks of North and West Africa and the Middle East (Cappetta, 1987). *Ganopristsis*, found only in Khneifiss, occurs mainly in the Maastrichtian of Europe, North Africa and the Middle East (Cappetta, 1987) but appears as early as the Santonian in Negev. The rhinobatoid *Parapalaeobates atlanticus* has been found in Charquieh and Soukkari. It is a common genus of the Campanian and Maastrichtian of North and West Africa and the Middle East (Cappetta, 1987). In Morocco, it is frequent in the Campanian (Imin Tanout) and in the lowermost Maastrichtian (phosphatic deposits). Another rhinobatoid, *Ataktobatis*, found in Charquieh B only, has been recently described from the Maastrichtian of the Basque Country (Cappetta & Corral, 1999); this genus occurs also in the Maastrichtian of Morocco (Noubhani & Cappetta, 1997, as *Rhinobatos*) and Egypt (Cappetta, 1991, also as *Rhinobatos*). The rhinobatids are represented in Syria by two indeterminate species of *Rhinobatos* found in Charquieh A and Khneifiss. This genus has a wide stratigraphical and geographical distribution, being known from Cretaceous to Recent deposits (Cappetta, 1987). The hypsobatids are known by *Hypsobatis* and *Youssoubatis*. *Hypsobatis* is mainly abundant in the Lower Maastrichtian of Morocco and Egypt, the first representatives being collected in the Upper Campanian of Negev (Lewy & Cappetta, 1989). In Syria, it has been found in Charquieh and Khneifiss. *Youssoubatis*, found in Charquieh and Khneifiss, is common in the Upper Maastrichtian deposits of Morocco; it appears as soon as the Upper Campanian in the Oron syncline of Negev (Lewy & Cappetta, 1989). *Hamrabatis*, present in Charquieh A only, was first described in the Lower Maastrichtian of Egypt (Cappetta, 1991) and was then collected in the Upper Maastrichtian of Texas (Case & Cappetta, 1997). Finally, *Erguitaia* (Rajiformes *incertae sedis*) has been recovered from Charquieh. It is known in the Lower Maastrichtian deposits of Morocco and Egypt (Cappetta, 1989, 1991); in Morocco, it never occurs in the upper levels of the Maastrichtian.

Myliobatiformes are known in Syria by the genera *Coupagezia* Cappetta, 1982 and *Rhombodus* Dames, 1881. The dasyatoid *Coupagezia* occurs only in

lateral tooth, lingual view; (i) (UM-CHB5), more lateral tooth, occlusal view; (j) *Hamrabatis* sp. (UM-CHA1-4), latero-anterior tooth, occlusal view; (k) *Ataktobatis* sp. (UM-CHB6), anterior tooth, occlusal view; (l) *Plicatopristsis strougoi* (UM-CHA1-5), rostral tooth, upper (or lower) view. (m, n) *Rhombodus* sp.; (m) (UM-CHB7), lateral tooth, occlusal view; (n) (UM-CHB8), anterior tooth, lingual view. The figured specimens are housed in the collections of the Laboratoire de Paléontologie, Université de Montpellier II (UM-Collection Syrie; CHA1 = Charquieh A, screening level L1; CHB = Charquieh B; KHN = Khneifiss). Scale bar represents 1 mm.

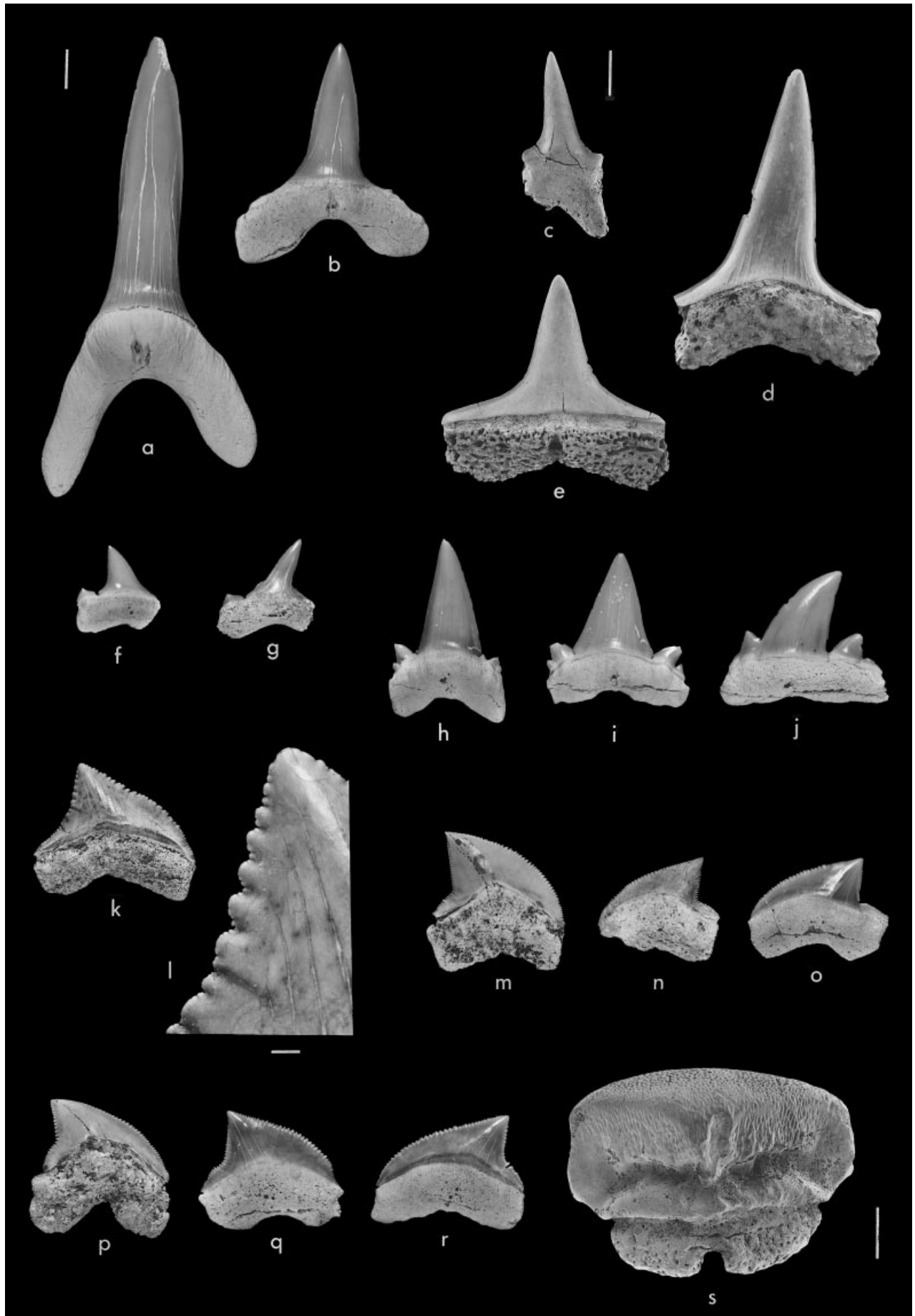


Figure 4. For legend see facing page.

Charquieh and is represented by two indeterminate species; this genus ranges from the Campanian (Imin Tanout, Morocco) to the Middle Eocene of North and West Africa and Europe (Cappetta, 1987). The rhombodontid *Rhombodus* is particularly interesting because of its narrow stratigraphical range and wide geographical occurrence. In Morocco, it is absent from the lowermost Maastrichtian but is very abundant in the upper part of the stage. Until now, this genus has been unknown worldwide in deposits older than Maastrichtian (Cappetta, 1987; Lewy & Cappetta, 1989; Welton & Farish, 1993). In Syria, it has been identified in Charquieh, Khneifiss and Soukkari. *Rhombodus* aff. *R. meridionalis* Arambourg, 1952, a frequent species in the Lower Maastrichtian rocks of Morocco and Egypt, occurs in both Charquieh and Khneifiss. An indeterminate myliobatiforme occurs frequently in Charquieh and Khneifiss and is also known in the Lower Maastrichtian deposits of Egypt and Morocco.

3.b. Actinopterygians

Actinopterygians (Fig. 5, Table 2) are represented by isolated remains, mainly teeth, jaw elements and vertebrae found in all localities. They are an abundant and diversified component of the fossil assemblages. The Syrian material is here assigned to six families of Neopterygii, including the Lepisosteidae and Pycnodontidae, and among teleosts the Enchodontidae, Dercetidae, Eotrigonodontidae and Phyllodontidae.

The enchodontid *Enchodus elegans* Darteville & Casier, 1949 is the main component of the teleost fauna and consists of hyopalatine bones, teeth and vertebral centra, found in all sites except Soukkari. It is very abundant in Khneifiss. The palatine bears a single terminal tooth, set at right angle to the bone. The tooth is long and straight, with a strongly asymmetrical cross-section and two cutting edges, located mesiolabially and distolabially. The labial face is almost flat and smooth. The lingual face is strongly convex, striated, and bears a shallow groove just behind the distal edge (see Arambourg, 1952). Amphicoelous, constricted centra with acute articular surface borders, lateral excavations divided by a longitudinal ridge, anteriorly located parapophyses, and fused neural

arches may also belong to *Enchodus* Agassiz, 1843 (see Arambourg, 1952). *Enchodus* was a large Late Cretaceous open-sea predator (Goody, 1976). *E. elegans* is known from the Maastrichtian deposits of West and North Africa (Darteville & Casier, 1949; Arambourg, 1952), the Middle East (Arambourg *et al.* 1959; Raab, 1967) and South America (Rebouças & Silva Santos, 1956).

The dercetid *Stratodus apicalis* Cope, 1872 is known by elongated jaw fragments and vertebrae recovered from Khneifiss and Charquieh B. The dentary and palatines bear several occlusal rows of dental alveoli of various sizes. The vertebral centra are large, amphicoelous, constricted, with rounded articular surface borders, two lateral ridges that may be coalescent and a fused neural arch (see Arambourg, 1952). *S. apicalis* is a large open-sea predatory teleost known from the Campanian–Maastrichtian deposits of North America (Cope, 1872; Applegate, 1970; Case, 1979), West and North Africa (Arambourg, 1952; Darteville & Casier, 1959) and the Middle East (Avnimelech, 1957; Arambourg *et al.* 1959; Raab, 1963; Chalifa & Lewy, 1991).

The eotrigonodontid *Stephanodus libycus* (Dames, 1883) is represented by typical hook-shaped pharyngeal teeth and shovel-shaped oral teeth with crenulated dorsal border, found in Khneifiss and Charquieh. This species is common in the latest Cretaceous deposits of North and West Africa (Gemmellaro, 1920; Weiler, 1930; White, 1934; Darteville & Casier, 1949; Maccagno, 1950; Arambourg, 1952; Churcher, 1988) and the Middle East (Arambourg *et al.* 1959; Raab, 1963).

Phyllodontid crushing teeth have been found only in Charquieh A. They are circular in outline and less than 5 mm in diameter. Their occlusal surface is either covered with enamel bearing radial striations (unworn functional teeth) or exhibits a ring of enamel surrounding the centrally exposed dentine (highly worn functional teeth). Their basilar surface bears a foramen with striated edges, typical for the Paralbulinae (Estes, 1969). These teeth look like those of *Pseudoegertonia* Darteville & Casier, 1949 from the Maastrichtian of Morocco and Jordan (Arambourg, 1952; Arambourg *et al.* 1959) and the Palaeocene of Congo (Darteville & Casier, 1949). Phyllodontids

Figure 4. Selachians. (a, b) *Scapanorhynchus rapax*; (a) (UM-CHA1-6), anterior tooth, lingual view; (b) (UM-CHA1-7), lateral tooth, lingual view. (c–e) *Anomotodon* aff. *A. plicatus*; (c) (UM-KHN1), parasymphyseal tooth, labial view; (d) (UM-KHN2), latero-anterior tooth, lingual view; (e) (UM-KHN3), lateral tooth, lingual view. (f, g) *Cretolamna* cf. *C. appendiculata*; (f) (UM-CHB9), latero-anterior tooth, lingual view; (g) (UM-KHN4), lateral tooth, lingual view. (h–j) *Cretolamna* cf. *C. maroccana*; (h) (UM-CHB10), anterior tooth, lingual view; (i) (UM-CHB11), lower lateral tooth, lingual view; (j) (UM-CHB12), upper lateral tooth, lingual view. (k–l) *Squalicorax* cf. *S. yangaensis* (UM-KHN5), lateral tooth, lingual view and detail of the cutting edge of the same specimen. (m–o) *Squalicorax kaupi*, (m) (UM-KHN6), anterior tooth, lingual view; (n) (UM-KHN7), lateral tooth, lingual view; (o) (UM-KHN8), lateral tooth, lingual view. (p–r) *Squalicorax pristodontus*; (p) (UM-KHN9), anterior tooth, lingual view; (q) (UM-KHN10), latero-anterior tooth, lingual view; (r) (UM-KHN11), lateral tooth, lingual view. (s) *Rhombodus* aff. *R. meridionalis* (UM-CHB13), lateral tooth, lingual view. Abbreviations as in Figure 3. Scale bars represent 5 mm for (a, b), (f–k) and (m–r); 1 mm for (c–e), (l) and (s).

Table 2. Actinopterygian, squamate, chelonian, plesiosaurian and crocodylian faunal list with geographical and stratigraphical occurrences

	Charquieh			Khneifiss	Soukkari	Soukhneh
	Bardeh	Mine A	Mine B			
Actinopterygii						
<i>Enchodus elegans</i>	X	X	X	X		X
<i>Stratodus apicalis</i>				X		
<i>Stephanodus libycus</i>		X	X	X		
Phyllodontidae indet.		X				
Lepisosteidae indet.			X			
Pycnodontidae indet.		X	X		X	
Teleostei indet.	X	X	X	X		
Squamata						
<i>Prognathodon giganteus</i>	X			X		
<i>Platecarpus ptychodon</i>			X	X		
<i>Leiodon anceps</i>	X	X	X	X		
<i>Mosasaurus lemonnieri</i>	X	X		X		
<i>Globidens</i> sp.		X		X		
Plioplatecarpini indet.	X	X	X	X		
Plioplatecarpinae indet.	X					
Mososaurinae indet.				X		
Mososauridae indet.	X	X	X			X
Varanoidea indet.		X			X	
Chelonii						
<i>Taphrosphys sulcatus</i>		X	X			
<i>Nigeremys</i> group	X	X		X		
Cheloniiidae indet.				X		
Chelonioidea indet.	X	X	X	X		
Chelonii indet.					X	X
Plesiosauria						
Elasmosauridae indet.	X	X	X	X		X
Crocodylomorpha						
Crocodylomorpha indet.	X	X		X		

were widespread in Late Cretaceous and Early Cenozoic fresh water, estuarine and marine deposits of North America, Europe and Africa (Estes, 1969).

The Lepisosteidae are represented in Charquieh B by a large diagnostically opisthocoelous vertebra (Patterson, 1973) with lateral surfaces excavated by deep grooves. Lepisosteidae are known from Early Cretaceous time to the Present in Africa, North and South America, Europe and Asia (see Wenz & Brito, 1992).

Pycnodontid remains consist of isolated teeth and fragments of jaw bearing parallel rows of ovoid teeth. The teeth are typically of crushing type with a finely punctuated occlusal face. They are only known in Charquieh and Soukkari. Pycnodonts were durophagous fishes, mainly inhabitants of shallow marginal and reefal zones of the Tethys and developing Atlantic oceans from Late Triassic to Eocene times (Nursall, 1996).

Bony fragments characterized by an external surface ornamented by tubercles have been found in Khneifiss. Tuberculated remains from the Maastrichtian phosphates of Morocco and Negev have been attributed respectively to the varanoid *Pachyvaranus crassispondylus* Arambourg, 1952 (Arambourg, 1952, pl. 41, figs 2, 3) and the dercetid *Stratodus apicalis* (Chalifa & Lewy, 1991, pl. 2, figs 4–7). The Syrian specimens differ from those of Morocco and Negev in having

more spaced and non-aligned tubercles. A preliminary histological study of the fragments from Syria and Morocco reveals that they belong to derived teleost fishes and not to reptiles; moreover, they belong to different taxa (F. Meunier, pers. comm.). Pending a detailed study of the material, it is referred here as Teleostei gen. and sp. indet.

Finally, numerous short amphicoelous vertebral centra, common in all outcrops except Soukkari and Soukhneh, are here referred to as Teleostei gen. and sp. indet.

3.c. Squamates

After selachians, mosasaurid remains are the most abundant (Fig. 6a–g, Table 2); they are represented by numerous teeth and vertebrae, disarticulated skull, girdle and limb bones, most of them found in Bardeh and Khneifiss. Some articulated remains are known in Khneifiss. Six mosasaurid species, including plioplatecarpines and mososaurines, as well as an indeterminate varanoid, have been recognized. The Plioplatecarpinae include *Prognathodon giganteus* Dollo, 1904; *Platecarpus ptychodon* Arambourg, 1952; and an indeterminate Plioplatecarpini. The Mososaurinae are represented by *Leiodon anceps* Owen, 1840; *Mosasaurus lemonnieri* Dollo, 1904; and an indeterminate species of *Globidens* Gilmore, 1912.

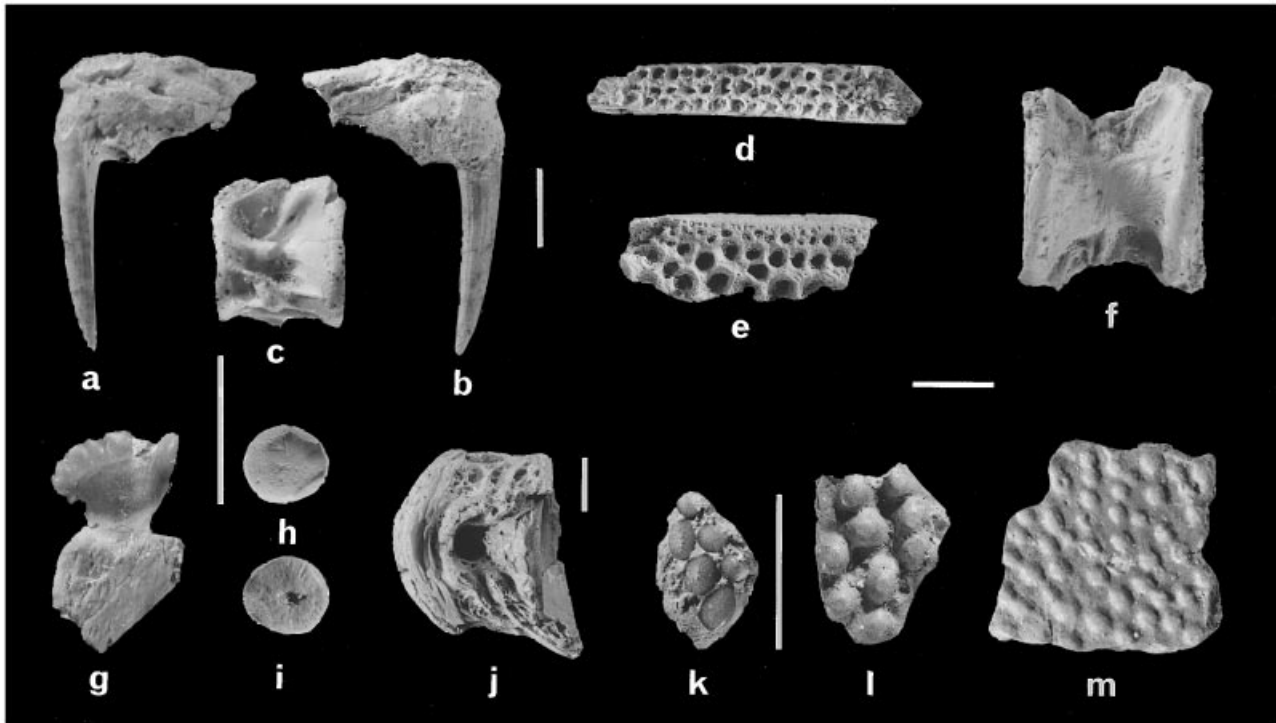


Figure 5. Actinopterygians. (a–c) *Enchodus elegans*; (a) (MNHN-KHN1), palatine tooth, labial view; (b) (the same), lingual view; (c) (MNHN-CHA1), precaudal vertebra, left lateral view. (d–f) *Stratodus apicalis*, (d) (MNHN-KHN2), dentary, occlusal view; (e) (MNHN-CHB1), palatine, occlusal view; (f) (MNHN-KHN3), vertebra, lateral view; (g) *Stephanodus libycus* (MNHN-KHN4), oral tooth, lingual view. (h, i) Phyllodontidae gen. and sp. indet. (MNHN-CHA2), tooth; (h), dorsal view; (i), basilar view. (j) Lepisosteidae gen. and sp. indet. (MNHN-CHB2), vertebra, ventral view. (k) Pycnodontiform gen. and sp. indet. (MNHN-CHB3), jaw fragment, occlusal view. (l, m) Teleostei gen. and sp. indet.; (l) (MNHN-KHN5); (m) (MNHN-KHN6), tuberculated bony elements, external view. The figured specimens are housed in the collections of the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris (MNHN-Collection Syrie; BAR = Bardeh; CHA = Charquieh A; CHB = Charquieh B; KHN = Khneifiss). Scale bar represents 1 cm.

Prognathodon giganteus is the most common mosasaurid species and is known at Bardeh and Khneifiss. Its teeth are characterized by large and robust crowns (height 3–3.5 cm; basal mesiodistal length 2–2.7 cm) with subcircular basal cross-section, subequal convex labial and lingual faces, two carinae, and vermiculated enamel especially marked on the blunt apical region (Lingham-Soliar & Nolf, 1989; Bardet *et al.* 1997). *P. giganteus* is known from the Campanian of France (Bardet *et al.* 1997), the Maastrichtian of Belgium (Dollo, 1904; Lingham-Soliar & Nolf, 1989) and possibly of Congo (Lingham-Soliar, 1994a). This species also occurs in the uppermost Cretaceous of Egypt ('mosasaur gen. et sp. indet.' of Zdansky, 1935, pl. 1), Negev and Jordan (N. Bardet, pers. obs.) and tentatively Angola ('Mosasauridae indet.' of Telles Antunes, 1964, pl. 26, fig. 4).

A few teeth found at Khneifiss and Charquieh B look much like those of *Platecarpus ptychodon* from the Maastrichtian of Morocco (Arambourg, 1952), Jordan (Arambourg *et al.* 1959), Negev (Raab, 1963) and Angola ('Platecarpinae indet.' of Telles Antunes, 1964, pl. 26, fig. 11). They are small (crown height 1.5 cm; basal mesiodistal length 0.9 cm) and very compressed with two carinae, subequal lingual and labial

surfaces bearing vertical striations that are more numerous on the lingual face and developed only on two-thirds of the crown height. Despite the fact that *P. ptychodon* is exclusively based on isolated teeth, this taxon is here provisionally regarded as valid because its teeth are quite different from those of other mosasaurids.

Khneifiss, Charquieh and Bardeh have yielded some remains, including partially articulated delicate jaw bones with associated teeth, here referred to as *Plioplatecarpini* gen. and sp. indet. The dentary fragment is characterized by its slenderness and a dorsolateral wall much higher than the dorsomedial one, unlike *Platecarpus* Cope, 1869a, *Plioplatecarpus* Dollo, 1882 and *Yaguarasaurus* Páramo, 1994 (Russell, 1967; Lingham-Soliar, 1994b; Páramo, 1994). Unfortunately this bone is unknown in *Selmasaurus* Wright & Shannon, 1988 and *Halisaurus* Marsh, 1869 and remains poorly described in *Ectenosaurus* Russell, 1967. The teeth are small, slender (crown height 1.3–1.5 cm; basal mesiodistal length 0.9 cm), abruptly posteriorly recurved from about the midpoint of the crown, with circular basal cross-section, very sharp apex, two carinae, and finely striated, subequal lingual and labial surfaces. They resemble those of

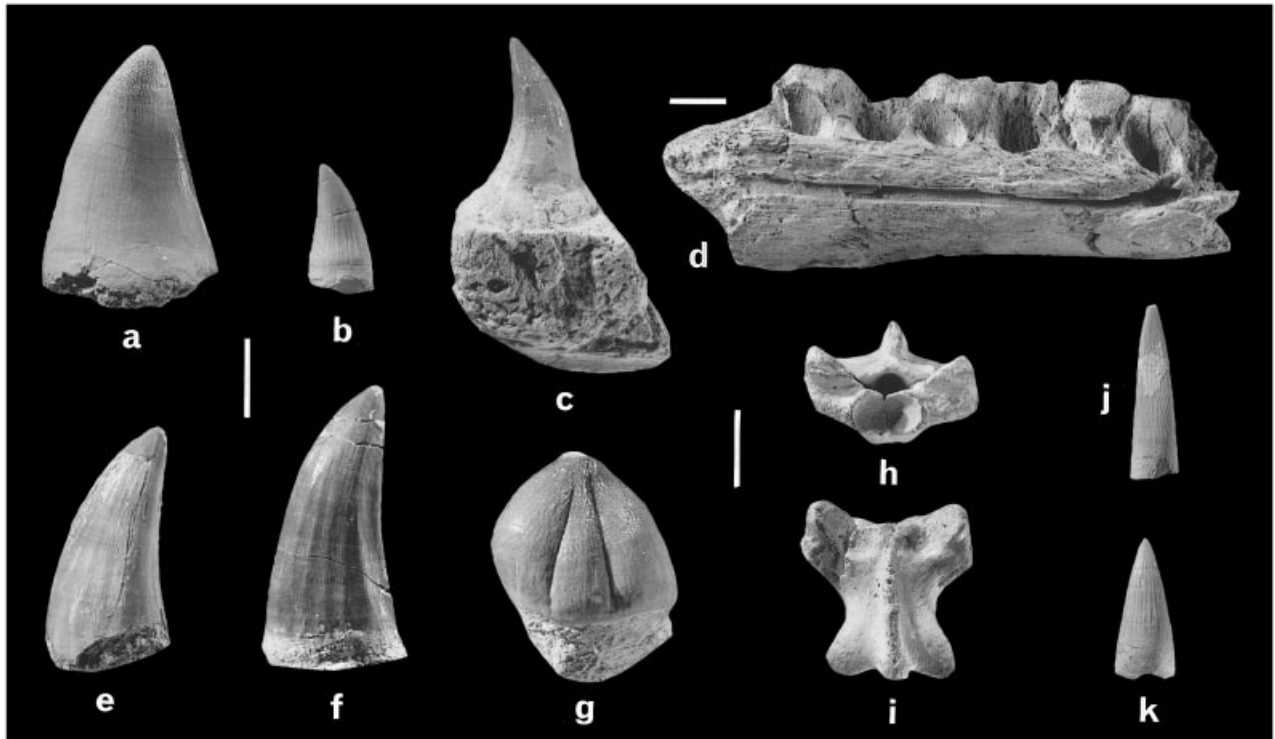


Figure 6. Squamates, plesiosaurians and crocodilians. (a) *Prognathodon giganteus* (MNHN-KHN7), marginal tooth, labial view. (b) *Platecarpus ptychodon* (MNHN-CHB4), marginal tooth, labial view. (c, d) Plioplatecarpini gen. and sp. indet. (MNHN-KHN8a-b); (c), marginal tooth, labial view; (d), dentary, lingual view. (e) *Leiodon anceps* (MNHN-KHN9), marginal tooth, labial view. (f) *Mosasaurus lemonnieri* (MNHN-BAR1), marginal tooth, labial view. (g) *Globidens* sp. (MNHN-KHN10), marginal tooth, labial view. (h, i) Varanoidea gen. and sp. indet. (MNHN-CHA3), dorsal vertebra; (h), anterior view; (i), dorsal view. (j) Elasmosauridae gen. and sp. indet. (MNHN-CHA4), tooth, labial view. (k) Crocodylomorpha gen. and sp. indet. (MNHN-CHA5), tooth, labial view. Abbreviations as in Figure 5. Scale bar represents 1 cm.

Plioplatecarpus but are shorter and slender. They differ clearly from those of *Platecarpus* and *Yaguarasaurus*. Jaw and teeth remains of the same unnamed taxon have been found recently in the Maastrichtian phosphates of Morocco (Bardet, Pereda Suberbiola & Iarochène, unpub. data).

Leiodon anceps occurs in all outcrops except Soukkari and Soukhneh. It is characterized by large laterally compressed teeth (crown height 3–3.4 cm; basal mesiodistal length 1.5–1.8 cm) with elliptical basal cross-section, sharp apex, subequal convex labial and lingual faces, two pronounced carinae, lateral profile with convex mesial face and concave distal face, and smooth highly polished enamel (Lingham-Soliar, 1993). *L. anceps* is commonly found in the Campanian–Maastrichtian deposits of Europe and Brazil (Lingham-Soliar, 1993). It is also frequent in the phosphates of North Africa (Arambourg, 1952) and the Middle East (Arambourg *et al.* 1959; Raab, 1963) and probably occurs also in the Maastrichtian of Angola ('Mosasauridae indet.' of Telles Antunes, 1964, pl. 26, figs 1–3).

Mosasaurus lemonnieri is known at Bardeh, Khneifiss and Charquieh A. The crowns of the teeth are large and robust (height 3.2–4 cm; basal mesiodis-

tal length 0.8–2.2 cm), with elliptical basal cross-section, lingual face more convex than the labial one, acute apex, and two well developed carinae (Russell, 1967). The labial face bears seven facets and the lingual face about twelve, as in *M. lemonnieri* (Lingham-Soliar, 1994a). This species has been found in the Campanian deposits of the Basque Country (Bardet, Corral & Pereda Suberbiola, 1997) and in the Maastrichtian of Belgium (Dollo, 1889) and Congo (Lingham-Soliar, 1994a).

A few *Globidens* teeth have been found in Khneifiss and Charquieh A. The crowns are typically bulbous, irregularly subspherical and low (height 1.5–2.5 cm, approximately the basal mesiodistal length) with a constriction at the base of the crown, an apical nubbin and two shallow vertical grooves. They are similar to the 'type 2' of Russell (1975), which is known from Campanian–Maastrichtian localities of Jordan (Avnimelech, 1949; Arambourg *et al.* 1959), Negev (Raab, 1963), Egypt (Leonardi & Malaroda, 1946), Angola (Telles Antunes, 1964) and Brazil (Price, 1957).

Indeterminate plioplatecarpine caudal vertebrae with free chevrons are known in Bardeh and articulated mosasaurine caudal vertebrae with fused chevrons in

Khneifiss. Indeterminate mosasaurid elements (squamosal, scapula, etc.) have been unearthed from Bardeh, Charquieh and Soukhneh.

Finally, small vertebrae conforming with those of *Pachyvaranus crassispondylus* from the Maastrichtian of Morocco (Arambourg, 1952) are known in Charquieh A and Soukkari (Fig. 6h, i). They are low and wide (total height 1.5 cm, length and proximal width 2–2.3 cm), with elliptic cotyle visible in ventral view, low neural arches and robust, almost horizontally oriented zygapophyses. These vertebrae are typical for aquatic varanoids and are here referred to as Varanoidea gen. and sp. indet.

3.d. Chelonians

Chelonian remains (Fig. 7, Table 2) include mainly shell plates; a lower jaw, vertebrae, girdle elements and limb bones are also known. Both marine-littoral pleurodirans (Bothremydidae) and marine cryptodirans (Chelonioidea) are represented.

The Bothremydidae (Fig. 7a–c, f, g) are known in Charquieh and to a lesser extent in Bardeh and Khneifiss by at least two taxa, that is, *Taphrosphys sulcatus* (Leidy, 1856) and a probable member of the *Nigeremys* group (*sensu* Antunes & Broin, 1988). *T. sulcatus*, known only in Charquieh, is represented by numerous shell elements characterized by a marked ornamentation of dichotomized *sulci* more or less united in salient polygons, granulations and rounded crests (Antunes & Broin, 1988; Lapparent de Broin & Werner, 1998). A xiphiplastron bearing viscerally a long and narrow pubic scar, and a round ischiac scar located near the posteromedial edge of the bone, is diagnostic for this species (Gaffney, 1975). The shell elements are either thin, moderately ornamented, and with acute borders or thick, with marked dichotomized *sulci*, and obtuse borders. These differences, which could be related to growth, sexual or individual variations, have already been mentioned by Gaffney (1975) for the New Jersey (USA) population of *T. sulcatus*. *Taphrosphys* Cope, 1869b was a marine-littoral turtle known from the Maastrichtian to the Eocene of North and South America, Africa and southern Europe (Gaffney, 1975; Antunes & Broin, 1988; Lapparent de Broin & Werner, 1998). *T. sulcatus* has been recorded only in the Maastrichtian of New Jersey and Egypt (Gaffney, 1975; Lapparent de Broin & Werner, 1998). In addition to this species, another large, indeterminate bothremydid is present in Bardeh, Charquieh A and Khneifiss. The morphology of large femora (length estimated between 16 and 25 cm) with sigmoid diaphysis, tibial and fibular processes separated by a wide intertrochanteric fossa and distal extremity bearing separated condyles, is intermediate between that of fresh water and marine turtles (see Zangerl, 1953a). It differs from *Taphrosphys* and could represent a member of the

Nigeremys group (see Walker, 1979), which includes the largest known bothremydids (Lapparent de Broin & Werner, 1998). It also applies to a very large and thick incomplete pleural (preserved length 13 cm, width 11 cm, thickness 2 cm) from Charquieh A, ornamented by slightly dichotomized *sulci* (as in *Arenila* Lapparent de Broin & Werner, 1998, but different from *Taphrosphys*) and to a large, narrow, triangular suprapygal (length 11 cm, maximal width 9.8 cm, thickness 1.5 cm) from Khneifiss, exhibiting a large iliac sutural area, extending along most of the lateral borders of the bone (unlike *Bothremys* Leidy, 1865, *Taphrosphys* and *Arenila*; see Lapparent de Broin & Werner, 1998). Unfortunately, *Nigeremys* Broin, 1977 and *Sokotochelys* Halstead, 1979 remain poorly known, making comparisons impossible. Bothremydids of the *Nigeremys* group were hitherto known only from Maastrichtian deposits of Nigeria and Egypt (Lapparent de Broin & Werner, 1998).

The Chelonioidea material (Fig. 7d, e, h–j) found in Khneifiss and Bardeh is indeterminate at the family level except for two cervical (height about 6 cm, length and width about 8 cm) and one caudal (height and length 2.5 cm, width 3 cm) vertebrae from Khneifiss which are low and wide, as in Cheloniidae and unlike the Dermochelyidae and Protostegidae (Zangerl, 1953b; Hirayama & Chitoku, 1996). The centra bear reniform to elliptic articular surfaces. The cervical centrum is procoelous while the caudal seems to be amphicoelous. Similar cervical vertebrae are known in the Rusaifa quarry, Jordan (N. Bardet, pers. obs.). A large mandible (preserved length 10.5 cm, maximal width 16 cm) from Charquieh B preserves the dentary and coronoids. It is mainly characterized by its width (angle between the dentary branches about 90°), a very narrow triturating surface, a high symphyseal beak, a lingual ridge slightly higher than the labial one, a reduced spur marking the posterior end of the horny beak and the occurrence of numerous and well-marked nutrient foramina located mainly on the area covered by the horny beak (lateral and dorsal surfaces of the dentary). Though this last character is common in highly aquatic and marine turtles because of the occurrence of a thick horny beak (F. de Lapparent, pers. comm.), this mandible is different from all Chelonioidea in which this element (or the skull) is known. The only taxon to which it could be compared is *Toxochelys* Cope, 1873, which also bears a primary type mandible with very narrow triturating surface (see Zangerl, 1953a). However, the angle between the dentary branches of *Toxochelys* (between 60° and 80°) never reaches the value of the Syrian mandible. *Toxochelys* differs mainly by its low symphyseal region without a marked beak, a symphyseal median crest separating the two branches of the dentary, a concave triturating surface and a lingual ridge lower than the labial one (Zangerl, 1953a). A large humerus from Bardeh (length about 27 cm) is mainly characterized by a dorsoven-



Figure 7. For legend see facing page.

trally flattened diaphysis, an ectepicondylar foramen developed into a shallow groove and an expanded distal extremity, as in marine turtles (Zangerl, 1980). Moreover, it has a nearly straight and slender shaft, a single and large radial tuberosity located at some distance of the humeral head, an ulnar tuberosity forming an acute angle with the diaphysis, and two individualized distal condyles. On the basis of these features, this humerus looks like those of primitive chelonoids such as *Toxochelys* and *Osteopygis* Cope, 1868 (Zangerl, 1953a; Hirayama, 1992). A fragmentary scapula from Charquieh A has flattened branches forming a relatively wide angle of about 105° to 110°, as is common in the Chelonioidea (Gaffney & Meylan, 1988). This angle is roughly comparable to that of *Toxochelys* (95° to 110°). Finally, peripheral and costal plates without ornamentation and punctured by coarse nutrient foramina and sinuous grooves, like those of typical marine turtles, are rather common in Khneifiss, Bardeh and Charquieh A. In summary, at least two chelonoid turtles occur in the Syrian phosphates: an indeterminate Cheloniidae and a primitive *Toxochelys*-like indeterminate Chelonioidea. Chelonioidea representatives occurred worldwide during Late Cretaceous times (see Zangerl, 1953a,b, 1980).

Finally, indeterminate Chelonii remains, namely eroded shell fragments, have been observed in Soukkari and Soukhneh.

3.e. Plesiosaurians

The plesiosaurian remains (Fig. 6j, Table 2), found in all sites but Soukkari, are much less abundant than those of selachians and mosasaurids. The site where they are more abundant is Charquieh A. Isolated teeth and cervical vertebrae have been found and are referred here to Elasmosauridae gen. and sp. indet. The teeth are long, slender (height 2–3 cm; basal diameter 0.6–0.9 cm), slightly recurved, and have finely ridged enamel crowns. Cervical vertebrae have typical centra with dumbbell-shaped, platycoelous articular surfaces and lateral surfaces with longitudinal keels, which are elasmosaurid synapomorphies (Bardet, Godefroit & Sciau, 1999). Elasmosaurids achieved a worldwide distribution during Late Cretaceous times (Welles, 1962; Brown, 1981).

3.f. Crocodilians

Crocodilian remains (Fig. 6k, Table 2) are very scarce and consist of isolated dermal scutes and teeth from Bardeh, Charquieh A and Khneifiss. The scutes are deeply and irregularly pitted. The teeth are laterally compressed, medially recurved and bear two unserrated carinae and numerous longitudinal ridges on both faces of the crown. The material is non-diagnostic and is referred to as *Crocodylomorpha* gen. and sp. indet.

4. Biostratigraphical correlations

It should be noted that the selachian faunas collected in different levels of the phosphatic series at Charquieh are not identical and show significant variations between the different layers of the same member (mainly the lower member) and between the members themselves. In Charquieh A, three members can be distinguished (see Fig. 2c) with different faunal contents. Phosphates that are soft enough for screening occur mainly in the lower member where three different horizons were sampled (called L1, L2, L3; see Fig. 2c and Table 1). This lower member is characterized by the relative abundance of Lamniformes: *Scapanorhynchus rapax*, many *Cretolamna* cf. *C. maroccana*, a rather diversified association of *Squalicorax* (*S. africanus*, *S. kaupi*, *S. bassanii*, *Squalicorax* sp.), a few *Parapalaeobates atlanticus* and scarce rostral and oral teeth of *Dalpiazia stromeri*. The batoids are abundant and diversified, with many teeth of *Hypsobatis* sp., whereas *Plicatopristsis strougoi* and *Hamrabatis* sp. are located in L1 and L2 levels. The middle member consists of pinky to rusty phosphates, that are too hard for screening, yet a level occurs at the lower third of the member which is very rich in turtle plates and where teeth of *Squalicorax bassanii*, *Dalpiazia stromeri* and *Parapalaeobates atlanticus* are common (see Fig. 2c). In the upper member, only thin levels of rather hard phosphate occur, and the collected teeth are generally worn and small. The most abundant elements are *Hypsobatis* sp. and *Rhombodus* sp. Despite the short distance separating the two Charquieh mines, the mine B series is very different from that of mine A. The most striking difference is the complete lack of conglomeratic, gravel and oyster levels. Some levels consisting of soft phosphate are particularly rich in turtle remains and

Figure 7. Chelonians. (a–c) *Taphrosphys sulcatus*; (a) (MNHN-CHB5), left xiphiplastron, dorsal (visceral) view; (b) (MNHN-CHA6), fourth right pleural plate, dorsal view; (c) (MNHN-CHA7), second right peripheral plate. (d, e) Chelonioidea gen. and sp. indet. (MNHN-CHB6), mandible, (d), dorsal view; (e), left lateral view. (f) Bothremyidae gen. and sp. indet., *Nigeremys* group (MNHN-BAR2), right femur, posterior view. (g) Bothremyidae gen. and sp. indet., *Nigeremys* group (MNHN-KHN11), suprapygial plate, ventral view. (h) Cheloniidae gen. and sp. indet. (MNHN-KHN12), cervical vertebra, anterior view. (i) Chelonioidea gen. and sp. indet. (GCPM-CHA1), left scapula, posterior view. (j) Chelonioidea gen. and sp. indet. (MNHN-BAR3), right humerus in two fragments, dorsal view. Abbreviations as in Figure 5 plus GCPM = General Company for Phosphates and Mines (Homs, Syria). Scale bar represents 2 cm.

selachian teeth (see Fig. 2d). The selachian assemblage is characterized by the abundance of *Parapalaeobates atlanticus*, many rostral teeth of *Dalpiazia stromeri* and *Squalicorax bassanii*; *Rhombodus* sp. teeth are also rather common.

The lithological differences between the two Charquieh mines render correlations difficult between the phosphatic levels, yet if the faunal content is considered, it appears that the vertebrate association (turtles and selachians) is very similar between the middle member of mine A and the so-called 'turtle level' of mine B. Considering this faunal similarity, the middle member of mine A could be correlated with the incomplete mine B series including turtle and selachian remains (see Fig. 2c,d). The marine vertebrate data are in agreement with the geological data of the mine workers (see description of Charquieh stratigraphy in Section 2). Nevertheless, correlations between the other sites have turned out to be very difficult.

5. Palaeoecology and palaeobiogeography

On a regional scale, the relative abundance and distribution of marine vertebrates in the Late Cretaceous phosphates of Syria could be correlated to the evolution of the Hamad Uplift structure, which controlled the phosphatic sedimentation in the Palmyridean Basin (Al Maleh & Mouty, 1994).

During Senonian times, the Hamad Uplift, emerged since the beginning of the Mesozoic, was submerged by marine transgressive waters and separated two basins which started differentiating at this time: the Palmyridean Basin to the north and the Rutbah Basin (Iraq) to the south. During the deposition of the Sawwaneh Formation, the north-central region of the northern rim of the Hamad Uplift was submitted to particular sedimentation conditions linked to palaeogeographical differences. In this area, the Hamad Uplift forms submarine highs especially suitable for phosphate concentration (Al Maleh & Mouty, 1994). Associated factors such as the warming of the platform and nutrient enrichment of the waters by upwelling currents coming from the northern edge of the Arabian Platform caused planktonic proliferation, the main source of phosphate accumulation and base of a prolific food chain completed by vertebrates. The phosphate-rich zone is extended from Bardeh to Soukhneh, but the main concentration occurs in the mine region of Charquieh and Khneifiss. On the other hand, to the north, the Palmyridean Basin experienced steady subsidence and deepening, characterized by pelagic calcareous sedimentation almost devoid of phosphate (Al Maleh & Mouty, 1994). As a result of these palaeogeographical differences, marine vertebrates were particularly abundant in the waters rich in food resources of the central region of the Palmyridean Basin, while they were scarce in the pelagic realm of the northern region of the same

basin. This is probably the reason why vertebrate remains are commonly found in the present mine region, whereas they are very scarce in the northern range of the Palmyrides Chain.

At the local scale of the southern range of the Palmyrides Chain, the marine vertebrate faunas of each fossiliferous site are in agreement with palaeogeographical conditions linked to the distance relative to the Hamad Uplift. In Charquieh, which represents very shallow environments with submarine highs located very close to the Hamad Uplift (Al Maleh & Mouty, 1994), the faunas are dominated by littoral groups such as bothremydid turtles, rays and, to a lesser extent, pycnodontid and phyllodontid fishes. At Bardeh and Khneifiss, which are interpreted as open-sea environments located farther from the Hamad Uplift, the faunas are dominated by nectonic groups such as lamniforme sharks, enchodontid and dercetid fishes, mosasaurid lizards and chelonoid turtles.

On a global scale, the marine vertebrate faunas of Syria are typical of the southern Tethyan realm and show close affinities with those of the Late Cretaceous phosphatic deposits of North Africa and the Middle East. The selachian faunas exhibit strong similarities to those of the Maastrichtian of the Benguerir area (Ganntour Basin) and Oued Erguita (Souss Basin) of Morocco and of Egypt (Cappetta, 1987, 1991; Noubhani & Cappetta, 1997). These faunas are mainly characterized by *Scapanorhynchus rapax*, *Squalicorax bassanii*, *Parapalaeobates atlanticus* and species of *Hypsobatis* and *Hamrabatis*. The actinopterygian faunas are dominated by enchodontids, namely *Enchodus elegans*. The association of this taxon with *Stratodus apicalis* and *Stephanodus libycus* is typical of North West Africa and the Middle East. It should be noted that, whereas *Enchodus elegans* and *Stephanodus libycus* are restricted to low palaeolatitudes (below 20° N and 20° S; see Camoin *et al.* 1993), *Stratodus apicalis* has also been reported from higher palaeolatitudes (above 30–40° N) in North America (Cope, 1872; Applegate, 1970; Case, 1979). The Syrian mosasaurid assemblage differs significantly from the boreal one from the northern Tethyan margin (see Bardet & Pereda Suberbiola, 1996) and shows similarities to the Middle East and North Africa faunas. The assemblage is dominated by *Prognathodon giganteus* and, to a lesser extent, *Leiodon anceps*. As for the selachian and mosasaurid associations, bothremydid turtles of the *Nigeremys* and *Taphrosphys* groups are mainly common in the low latitudes of the southern Tethyan realm, although the New Jersey occurrence of *Taphrosphys* is located above 20° N. The palaeobiogeographical affinities of invertebrates found in the Syrian phosphates are coherent with those of the marine vertebrates. The oyster *Ambigostrea villei* (found in Charquieh A) is characteristic of the Mediterranean Tethyan province, having been found in North Africa, the Middle East and southern Europe, while it is absent

from northern Europe (Dhondt *et al.* 1999). Similarly, the ammonite *Libycoceras ismaeli*, also recovered from Charquieh, is exclusively known at the low latitudes of the southern Tethyan margin (see Zaborski & Morris, 1999). The faunal differences between the southern and northern margins of the Mediterranean Tethys could be related to palaeolatitudinal gradients (Bardet & Pereda Suberbiola, 1996). The marine vertebrate assemblages from the Middle East and North Africa, as well as those from West Africa and eastern South America, show close similarities and are all included in a palaeolatitudinal belt located between 20° N and 20° S.

6. Age of the Syrian phosphatic deposits

Because biostratigraphical evidence (invertebrates, microfossils) is most often absent in phosphatic deposits due to carbonate dissolution, the precise age of the Syrian phosphates has been debated for a long time and is still subject to controversy. It is considered to be either restricted to the Late Campanian (Cayeux, 1935; Dubertret, 1963, 1966; Mouty & Al Maleh, unpub. report, Ministry of Petroleum and Mineral Resources of Syria, 1983; Al Maleh & Mouty, 1994) or to span the Late Campanian and Early Maastrichtian (Atfeh & Faradjev, 1963; Ponikarov *et al.* 1967; Atfeh, 1989).

The question of the age of the Syrian phosphates is not an isolated problem but concerns all phosphatic deposits of the Arabic Platform and is, moreover, related to the definition of the Campanian–Maastrichtian boundary, a problem currently debated worldwide (see Odin, 1996; Ward & Orr, 1997).

In Jordan, the Campanian–Maastrichtian interval

includes parts of the Belqa Group, namely the Wadisir Formation (cherts and limestones), the Amman Formation (including the Sultana and Qatrane phosphates separated by the Bahiya Coquina oyster bioherm) and the Muwagger Formation (marls, chalks and cherts) (Jallad, Abu Murrey & Sadaqah, 1989; Powell, 1989; Fig. 8). The Campanian–Maastrichtian boundary is located either at the base of the Wadisir Formation (Jallad, Abu Murrey & Sadaqah, 1989) or at its top (Powell, 1989); in any case, the Jordan phosphates are included within the Maastrichtian, an age supported by the selachian assemblages (Cappetta, Pfeil & Schmidt-Kittler, in press).

In Negev, the Campanian–Maastrichtian succession includes the Mishash Formation, which consists of a lower Chert Member and an upper Phosphatic Series Member (with lower and upper phosphates separated by porcelanites), and the Ghareb Formation (Nathan & Shiloni, 1989; Fig. 8). The Campanian–Maastrichtian boundary is located somewhere between the upper phosphates of the Mishash Formation and the basal part of the Ghareb Formation. According to the selachian faunas, the Main Phosphorite of the Phosphatic Series are Early Maastrichtian in age, whereas the Phosphatic Carbonates are Late Campanian (Lewy & Cappetta, 1989).

In Egypt, phosphate-bearing beds are known as the Duwi Phosphate Formation which is located between the underlying Nubian Formation (sandstones and shales) and the overlying Dakhla Formation (shales) (Issawi, 1989; Fig. 8). The phosphates have been classically considered as Late Campanian to Early Maastrichtian in age. In the Red Sea region, where the series is the most complete, there are at least four phosphatic sequences, the most important being located in

SYRIA			JORDAN		NEGEV			EGYPT	
BARDEH GROUP	Marls & Chalks		MUWAGGER Formation	Marls & Chalks	GHAREB Formation	Marls & Chalks		DAKHLA Formation	Shales
	SAWWANEH Formation	Tantour Member	BELQA GROUP	AMMAN (=AL HISA PHOSPHORITE) Formation		MISHASH Formation	PHOSPHATIC SERIES Member	DUWI PHOSPHATE Formation	Phosphates
		Erek Marls							Qatrana (= Ruseifa) Phosphates
Phosphates	Bahiya Coquina	Phosphates			Phosphates				Shales & Marls
RMAH Formation	Cherts & Limestones	WADISIR (=AMMAN SILICIFIED LIMESTONE) Formation	Cherts & Limestones	CHERT Member	NUBIAN Formation	Variegated (=Quseir) Shales			

Figure 8. Comparative simplified stratigraphy of Late Cretaceous phosphates from the Middle East and North Africa. References used are Al Maleh & Mouty (1994) for Syria; Jallad, Abu Murrey & Sadaqah (1989) and Powell (1989) for Jordan; Nathan & Shiloni (1989) for Negev; and Issawi (1989) for Egypt.

the middle and upper part of the Duwi Formation and being separated by an important sequence of oyster limestones (Issawi, 1989). On the basis of the selachian assemblages (Cappetta, 1991), this series is considered as Early Maastrichtian, an age confirmed by calcareous nannofossils (Schränk & Perch-Nielsen, 1985).

Finally, in Iraq, phosphatic deposits occur in the lower part of the Digma Formation (Upper Campanian) and within the overlying Maastrichtian Tayarat Formation (Al Bassam, Al Dahan & Jamil, 1983).

As previously mentioned, the latest Cretaceous phosphatic beds of Syria occur mainly at the base (phosphates) and scarcely at the top (Tantour Member) of the Sawwaneh Formation, in the upper part of the Soukhneh Group (Henson, unpub. S. P. C. report, 1939 in Dubertret, 1963; Fig. 8). The underlying Rmah Formation has been considered as Coniacian–Lower Campanian, according to the ammonite fauna (*Barroisicerias onilahyense* Basse, 1947; *Reesideoceras gallicum* Basse, 1947; *Scaphites* Parkinson, 1811 sp. indet.; *Pseudoschloenbachia* Spath, 1921 sp. indet.; etc.) and the pelagic microfauna (*Dicarinella concavata* (Brotzen, 1934); *Marginotruncana coronata* (Bolli, 1945); *Contusotruncana fornicata* (Plummer, 1931)) (Dubertret, 1966; Ponikarov *et al.* 1967; Mouty & Al Maleh, unpub. report, Ministry of Petroleum and Mineral Resources of Syria, 1983; Al Maleh & Mouty, 1994). Based on the occurrence of the microscopic pelagic fossil *C. fornicata*, the Sawwaneh Formation has been assigned to the Campanian (Henson, unpub. S. P. C. report, 1939 in Dubertret, 1963). Moreover, its stratigraphical position below the Maastrichtian marl with the microfossil *Gansserina gansseri* (Bolli, 1951) suggests a Late Campanian age (Al Maleh & Mouty, 1994). Nevertheless, this biostratigraphical evidence is not direct (no microfossil has hitherto been found within the phosphatic series) but has been deduced from regional scale correlations.

The vertebrate evidence, especially the selachians, indicates a different dating. It suggests an Early Maastrichtian age for at least the sites of Khneifiss, Charquieh and Soukkari. In these sites, the occurrence of *Rhombodus* is particularly interesting as, until now, this ubiquitous genus has been exclusively collected from Maastrichtian deposits (see Cappetta, 1987, 1991; Lewy & Cappetta, 1989). The presence of *Squalicorax africanus* is also significant because it has hitherto been found in the Lower Maastrichtian of Egypt (Cappetta, 1991), Morocco and Jordan (Cappetta, Pfeil & Schmidt-Kittler, in press). The selachian teeth are very scarce in Soukhneh, but the occurrence of *Schizorhiza stromeri*, a worldwide distributed species until now only found in Maastrichtian deposits (Cappetta, 1987), supports provisionally a Maastrichtian age for this outcrop. At Bardeh, the selachian fauna is too poor to give a precise dating but, as no Maastrichtian markers have been recovered,

a Late Campanian age cannot be definitively excluded.

Most other marine vertebrates do not yield precise biostratigraphical evidence as they occur in the Campanian–Maastrichtian interval. Among the turtles, the bothremydids *Taphrosphys sulcatus* and all *Nigeremys* group taxa are until now known only in Maastrichtian formations (Gaffney, 1975; Lapparent de Broin & Werner, 1998). The invertebrate data are also inconclusive for dating. The oyster *Ambigostrea villei* is known from both Campanian and Maastrichtian (Dhondt *et al.* 1999). The use of the ammonite *Libycoceras ismaeli* as a Maastrichtian index fossil has long been subject to confusion because this species has also been found in association with typical Campanian biostratigraphical markers (see Reiss, 1962). Thus, *L. ismaeli* seems also to range from the Campanian to Maastrichtian (see Zaborski & Morris, 1999).

As previously pointed out by Dubertret (1963) and Nathan & Shiloni (1989), the phosphates of the Soukhneh Group (Syria), Belqa Group (Jordan), Mishash Formation (Negev) and Duwi Formation (Egypt) are probably lithostratigraphically equivalent, forming a major phosphatic belt extending from Iraq to Egypt, but not necessarily contemporaneous. Based on what has been discussed above, most phosphatic deposits of these regions are regarded as spanning the Upper Campanian–Lower Maastrichtian interval.

In summary, most of the Syrian phosphates studied here could be regarded as Early Maastrichtian in age on the basis of the selachian data. The occurrence of Late Campanian phosphates, though it cannot be excluded, remains to be attested firmly by biostratigraphical evidence which is currently lacking.

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