The Central Mediterranean Naturalist	3(3): 131 - 146	Malta, December 2001

ADDITIONS TO, AND A REVIEW OF, THE MIOCENE SHARK AND RAY FAUNA OF MALTA

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ABSTRACT

Bulk sampling sediments and surface picking have increased the number of fossil sharks and rays from the Miocene of the Maltese Islands by 10 species and confirmed another. These are: *Sphyrna arambourgi, Rhizoprionodon taxandriae, Scyliorhinus* sp, *Chaenogaleus affinis, Galeorhinus goncalvesi, Triakis angustidens, Squatina* sp., *Rhynchobatus pristinus, Raja gentili* and *Gymnura sp. Hexanchus griseus* was confirmed. The species "*Galeocerdo*" *aduncus* is synonymised with "*G*" *contortus*, and referred to the genus *Physogaleus*. These new records, and a taxonomic revision of the species described previously, increased the Maltese fauna to 24 species, comparable with the Miocene of France and Portugal. This paper is not meant to be an exhaustive review of the fossil selachian and batid fauna of the Maltese Islands but rather for the present we have confined ourselves to revising Menesini (1974).

INTRODUCTION

This paper is the result of a pilot study to investigate the possibilities of extracting a microvertebrate fauna from the Maltese Islands. The results were surprisingly good, and are listed below in the Systematic section. The original fauna of 14 species, after a conservative revision was reduced to 13, to which this study added an additional 11, making 24 species in total.

The fossil sharks' teeth of Malta have been known to the outside world for more than five hundred years (Pogatcher, 1898). They were believed to be a protection against poisoning, and thus were exported from Malta in large numbers during Medieval and Hospitaller times (Zammit Maempel 1989). Originally known as *Glossoptera* ("stone tongues"), *Linguae Melitensis* (Maltese tongues) or *Linguae St Pauli* (St. Paul's tongues), also adder's tongues and serpent tongues (Zammit Maempel, 1975), it was the Danish geologist and anatomist, Niels Steensen, in 1669, who recognised them as sharks' teeth. Sharks' teeth and other Maltese fossils were first illustrated by Scilla (1670) who recognised the relationship between Recent and fossil specimens.

Despite the exposure that Maltese sharks have enjoyed down the centuries, it is remarkable that when they were monographed in the 1970's, only fourteen species were described (Menesini, 1974 – see Table 1)). This contrasts with about fifty species from the Miocene of southern France (Cappetta, 1970), twenty eight from the Miocene of Portugal (Antunes & Jonet, 1970), or thirty species from the Belgian Miocene (Leriche, 1926).

A closer look at the published Maltese fauna shows that it comprises only large species, principally pelagic lamniforms and large carcharhinids. This is typical of many of the older museum collections, where most of the sharks' teeth they contain were collected by eye from the surface of the outcrop. Indeed, no small teeth at all, i.e. under 5mm, were figured by Menesini (1974).

In this brief report, which reviews the Maltese shark fauna, it is impractical to reproduce the text and figures of Menesini. Thus, the larger, previously described, teeth in the fauna are not figured and the reader must refer to Menesini (1974) in order to fully understand some of the systematic points made below.

The new material (figured in Plates 1 and 2) is deposited at the National Museum of Natural History, Mdina, Malta.

STRATIGRAPHY

The stratigraphic framework used in Fig. 1 is based on that of Pedley (1978) and Rehfeld & Janssen (1995). Seven horizons were sampled (see map at Fig. 2).

1 The Lower Main Phosphorite Conglomerate – C1
(L.M.C.B. Pedley & Bennett 1985); C1 (Rehfeld & Janssen 1995) of Rdum il-Vigarju near Bahrija.

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Table 1. The fauna described by Menesini (1974) with its current names.

Name used in Menesini (1974)	Current name	Vernacular name
Odontaspis acutissima Agassiz 1843	*Carcharias taurus* Rafinesque 1810	Sand tiger shark
Isurus hastalis (Agassiz 1843)	*Cosmopolitodus hastalis* (Agassiz 1843)	Spear-toothed shark
Isurus desori (Agassiz 1843)	*Isurus oxyrhinchus* Rafinesque 1810	Shortfin mako shark
Isurus retroflexus(Agassiz 1843)	*Isurus retroflexus* (Agassiz 1843)	Mako shark
Isurus benedini (Le Hon 1871)	*Parotodus benedini* (Le Hon 1871)	none
Lamna cattica (Philippi 1846)	*Carcharoides catticus* (Philippi 1846)	none
Procarcharodon megalodon (Agassiz 1843)	*Carcharocles megalodon* (Agassiz 1843)	Mega-toothed shark
Alopias latidens (Leriche 1908)	*Alopias latidens* (Leriche 1908)	Thresher shark
Alopias exigua (Probst 1879)	*Alopias vulpinus* (Bonnaterre 1780) *Alopias superciliosus* (Lowe 1840)	Thresher sharks
Galeocerdo aduncus Agassiz 1843	*Physogaleus aduncus* (Agassiz 1843)	Tiger shark
Carcharhinus egertoni (Agassiz 1843)	In part: *C. falciformis* (Bibron 1849) and *N. eurybathrodon* (Blake 1862)	Requiem shark Lemon shark
Hypopriodon acanthodon (Le Hon 1871)	*Negaprion* sp. ? *N. eurybathrodon* (Blake 1862)	Lemon shark
Hemipristis serra Agassiz 1843	*Hemipristis serra* Agassiz 1843	Snaggletooth shark
Sphyrna prisca Agassiz 1843	*N. eurybathrodon* (Blake 1862)	Lemon shark

The two *Hexanchus* teeth come from a thin horizon of sub-cm phosporite intraclasts scattered through the first 10-15 cms of the overlying Middle Globigerina Limestone resting uncomformably on the planed-off surface of the actual Lower Main Phosphorite Conglomerate (C1). Its age has been assigned approximately to the base of the Burdigalian (Mazzei 1985) and it lies on strata of Aquitanian age. The phosphorite conglomerates have been associated with a low-stand in sea-level with strong bottom currents (Carbone *et al.* 1987) but see Rehfeld & Janssen (1995). Their precise age needs further study (Rehfeld & Janssen 1995) as they indicate a still-stand in deposition of an unknown duration. The teeth were collected by scanning the surface outcrop.

2 **The glauconitic level in the Blue Clay at Ras il-Pellegrin** [referred to as "livello glauconitico a Pettinidi" by Menesini (1974)]. This horizon is only a few metres thick and occurs some 3.5-5.5 metres below the top of the Blue Clay Formation (Pedley 1978). Again there is disagreement as to age: Serravallian-Tortonian (Pedley, 1987), Langhian-Serravallian (Pedley *et al* 1976) but Serravallian by Kienel *et al* (1995) and by Janssen (1999). Di Geronimo *et al* (1981) suggested a circalittoral environment. This horizon has never been formally described. Sample size: 4 kg

3. **One of the minor phosphorite conglomerate beds** that are found locally at Bahrija. The specimens were found by scanning the weathered surface, not by sieving.

4 **The Greensand at Ta' Gordan - Gozo.** There is some disagreement on the date of this formation, being assigned to the later Tortonian by e.g. Pedley (1987), to the Serravalian-Tortonian (see table in Pedley *et al* 1976) and more recently to the Messinian (Kienel *et al* 1995). Pedley *et al* (1976) suggest that it was deposited in a shallow water environment with strong currents. Teeth were collected by surface scanning.

5. **The glauconitic level in the Blue Clay at Ras il-Karraba – Malta** [see (2) above]. Sample size: 3 kg

6. **The Upper Main Phosphorite Conglomerate – Gozo** L.M.P.C. "B" of. Pedley & Bennett(1985), C2 of Rehfeld & Janssen (1995) of Ras ir-Reqqa (Gozo). This bed separates the late Burdigalian strata of the Middle Globigerina Limestone from the Langhian beds of the Upper Globigerina Limestone (Carbone *et al* 1987) which is also in agreement with the approximate dating of Mazzei (1985). Sample size: 2 kg

7. **The glauconitic level in the Blue Clay at In-Nuffara – Gozo** [see (2) above]. Sample size: 1kg

METHODS

Excluding the minor phosphorites at Bahrija and the Greensand at Ta' Gordan, bulk samples of sediments were collected, disaggregated and wet sieved to 500 microns. The resulting concentrate was examined with a x10 hand-lens. The localities visited and horizons sampled are given in Table 2. In general, the preservation was better and the yield of determinate teeth more in "Glauconites" (glauconitic silty

Table 2. Sample horizons and localities with significant records.

Sample	Horizon	Locality	Fauna
1	C1 phosphorite	Rdum il-Vigarju between one or two km south of Bahrija, Malta 35°54'30"N:14°20'10"E	*Hexanchus*
2	Glauconite level in the Blue Clay	Ras il-Pellegrin, Malta 35°55'00" N:14°20'10" E	*Carcharhinus, Squatina, Scoliodon Hexanchus Galeorhinus*
3	Minor phosphorites in the Middle Globigerina Lmst.	Bahrija about one and a half km south of locality 2, Malta 35°54'00" N:14°20'00" E	*Hexanchus Scyliorhinus Carcharhinus*
4	Greensand	Ta' Gordàn, Gozo 36° 4' 20" N: 14° 14' 10" E.	*Carcharhinus* spp
5	Glauconite level in the Blue Clay	Ras il-Karraba about 1.5km north of Ras il-Pellegrin, Malta 35°55'40" N:14°20'25" E	*Carcharhinus, Rhizoprionodon*
6	C2 phosphorite	Ras ir-Reqqa, Gozo 36°4'50"N: 14°14'10"E.	*Carcharhinus, Rhizoprionodon Sphyrna Triakis Rhynchobatis*
7	Glauconite level in the Blue Clay	In-Nuffara, 2.8km E of Rabat, Gozo. 36°2'30"N:14°13'10"E.	Female & male *Raja, Carcharhinus Galeorhinus Scyliorhinus Gymnura*

clays) than in the phosphoritic horizons, where the teeth were somewhat abraded.

SYSTEMATIC PALAEONTOLOGY

Being only a pilot study, we are keeping the systematics to a minimum. It is not our intention to modify the taxonomy, nor materially add to the written descriptions of the studied taxa; we do not have sufficient material to accomplish this. However, it is not our intention to perpetuate obvious errors in inconsistencies in the literature so some taxonomic changes are introduced. The synonymies are restricted to immediately relevant texts.

The species listed below are placed in their traditional systematic hierarchy, solely to avoid taxonomic confusion.

Genus *Hexanchus* Rafinesque 1810

Hexanchus griseus (Bonnaterre 1788)
Six-gill shark
Plate 1, fig b.

Material: 3 upper teeth.

Provenance: C1 Conglomerate; Rhum il-Vigarju; Blue Clay, Ras il-Pellegrin.

Remarks: For Neogene species of *Hexanchus*, the species *H. gigas* (Sismonda 1857) is usually employed. However, we have been unable to identify any convincing characters, other than size to separate Recent and Miocene specimens. Upper teeth of *Notorynchus primigeneus* Agassiz 1843, tend to be more robust and have less sigmoid crowns than those of *Hexanchus*. It is curious that the, considerably larger, lower anterolateral teeth of *Hexanchus* have not yet been recorded from Malta though a probable specimen has been observed in a private collection. These records confirm the presence of this species in the Miocene of the Islands; it was recorded from the Globigerina Limestone by Adams (1870) solely on the basis of his identification of a tooth figured by Scilla (1670).

Genus *Carcharias* Rafinesque 1810

Carcharias taurus (Bonnaterre 1778)
Sandtiger shark

Synonymy: see also Cappetta, 1970.
1970 *Odontaspis acutissima* Agassiz: Cappetta p. 29, Pl. 1, figs 1-22, Pl. 2, figs 1-16
1974 *Odontaspis (Synodontaspis) acutissima* Agassiz: Menesini, p. 127, Pl. 1, figs 1-9.

Material & Provenance: see Menesini (1974)

Remarks: In the 1970's (Menesini, 1974), the genus *Odontaspis* was considered a senior synonym of *Carcharias*. Now they are considered distinct and separate genera (ICZN, 1987 Opinion 1485). We cannot find any characters to separate Miocene examples of *Carcharias acutissima* Agassiz 1844 from the Recent *C. taurus* Rafinesque 1810, and

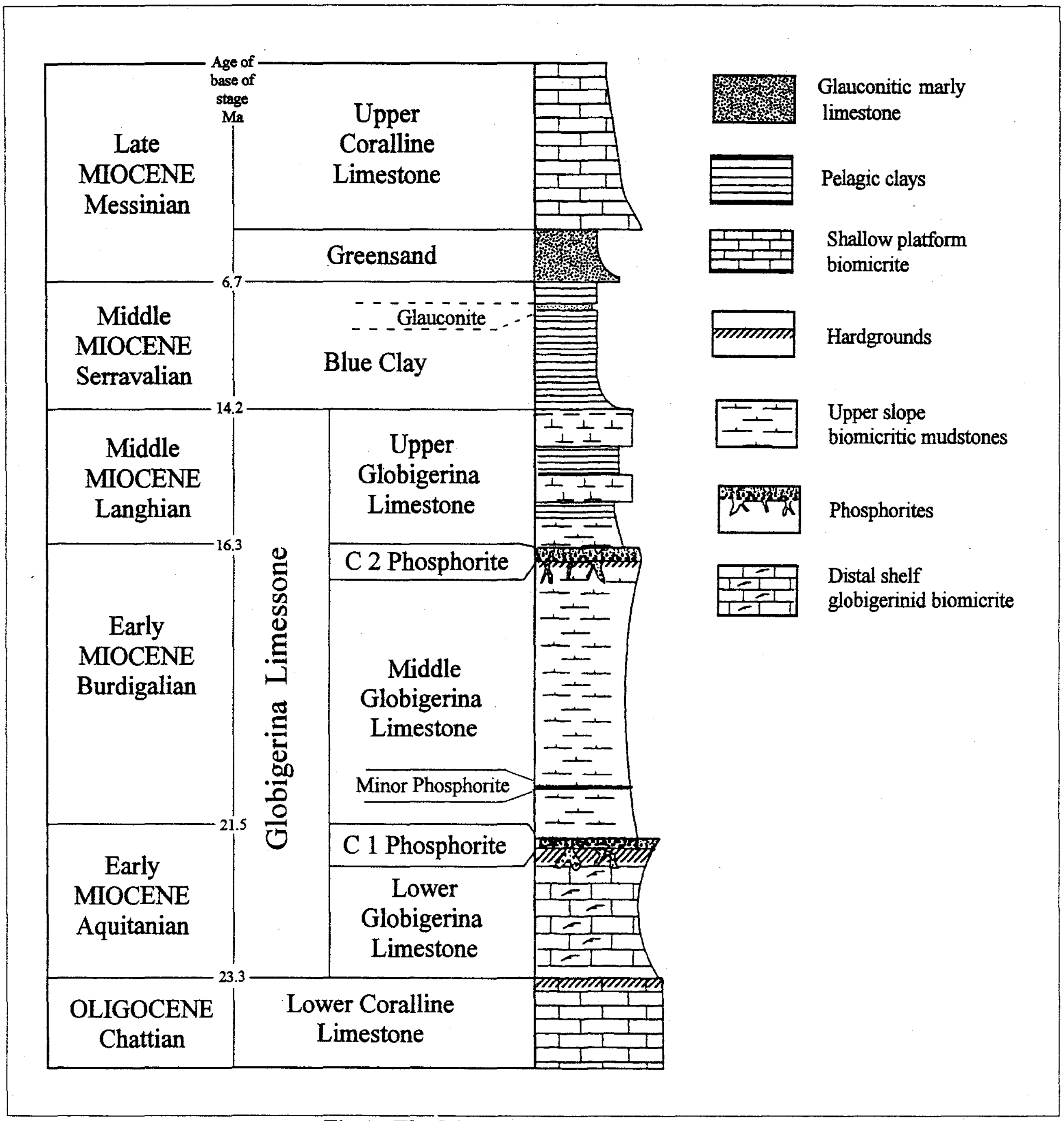

Fig 1. The Maltese stratigraphic column.

so we follow Kemp (1991) and refer to the Miocene examples of the lineage as *C. taurus*. Purdy *et al.* 2001 refer the species *acutissima* to *Odontaspis*, presumably in error. Teeth of *Odontaspis* have unstriated lingual crowns and multiple lateral cusplets, are stout and strongly lingually recurved.

Genus *Cosmopolitodus* Glyckman 1964

Cosmopolitodus hastalis (Agassiz 1843)
Spear-toothed shark

Synonymy: see also Cappetta, 1970.

1970 *Isurus hastalis* Agassiz: Cappetta p. 18, Pl. 5, figs 1-13.1974 *Isurus hastalis* Agassiz: Menesini, p. 129, Pl. 2, figs 1-13.

2001 *Isurus xiphodon* Agassiz: Purdy *et al*, p. 119, fig 29.

Material & Provenance: see Menesini (1974)

Remarks: "*Isurus*" *hastalis* Agassiz 1843 is considered to be more closely related to the Recent Great white shark *Carcharodon* than the Mako sharks. Thus the use of the genus "*Isurus*" is inappropriate. Here we follow Glyckman (1964, 1980) and Siverson (1999) and use *Cosmopolitodus* for members of the *Carcharodon* lineage with unserrated teeth.

Purdy *et al* used the name "*Isurus xiphodon*" Agassiz 1843 for teeth traditionally referred to as *hastalis*. Leriche (1926: 399) includes *xiphodon* in his synonomy of *hastalis* and (1926: 407) points out the uncertainty of the origin of the types, now lost, of *xiphodon*. Agassiz (1843) in his plate explanation, states that they are from the "Gypse of the Paris region," – a terrestrial/fluviatile, ? Eocene deposit, that certainly yields no sharks. In view of this degree of uncertainty, the nominal species *xiphodon* can only be regarded as a *nomen dubium*.

Genus *Isurus* Rafinesque 1810

Isurus oxyrinchus Rafinesque 1810
Shortfin mako shark

Synonymy: 1974 *Isurus desori* Agassiz: Menesini, p. 131, Pl. 3, figs 1-8.

Material & Provenance: see Menesini (1974)

Remarks: In the teeth of Miocene sharks, there is often little or no morphological difference between the fossil and Recent counterparts. In many cases a fossil name was used because the dentition of the Recent representative of the lineage was poorly known. Both Cappetta (1970, and Menesini (1974) used *Isurus desori* Agassiz 1843. Unfortunately the name *I. desori* has been used both for Oligocene representatives of the *Carcharodon* lineage and for anterior teeth of *Isurolamna gracilis* (Le Hon 1871) [= *Lamna rupeliensis* (Le Hon 1871)] (Leriche, 1910). Thus, we feel that is preferable to use the senior synonym, which is *Isurus oxyrinchus*, the Recent Shortfin mako shark.

Isurus retroflexus (Agassiz 1843)
Longfin mako shark

Synonymy, Material & Provenance: see Menesini (1974, p. 132-134)

Remarks: The Maltese teeth figured by Menesini (1974, pl. 4, 1-6) are extremely poorly preserved, but two (Pl. 3, figs 7 & 8) are sufficiently intact to be confidently referred to this species.

Genus *Parotodus* Cappetta 1980

Parotodus benedini (Le Hon 1871)
No vernacular name
Synonymy: 1974: *Isurus benedini* Le Hon: Menesini, p. 134, pl. 1, figs 10-17, *non* figs 14 & 17.

Material & Provenance: see Menesini (1974).

Remarks: Superficially the teeth of this rare pelagic shark resemble those of *Isurus retroflexus*, but the dentition lacks the elongate anterior teeth of *Isurus*, and possesses a much more robust "*Otodus*-like" root. Oligocene specimens of *Parotodus* were figured by Leriche (1910, plate 16, figs 1-15). Two of these, figs 5 and 6, were referred by Purdy *et al*

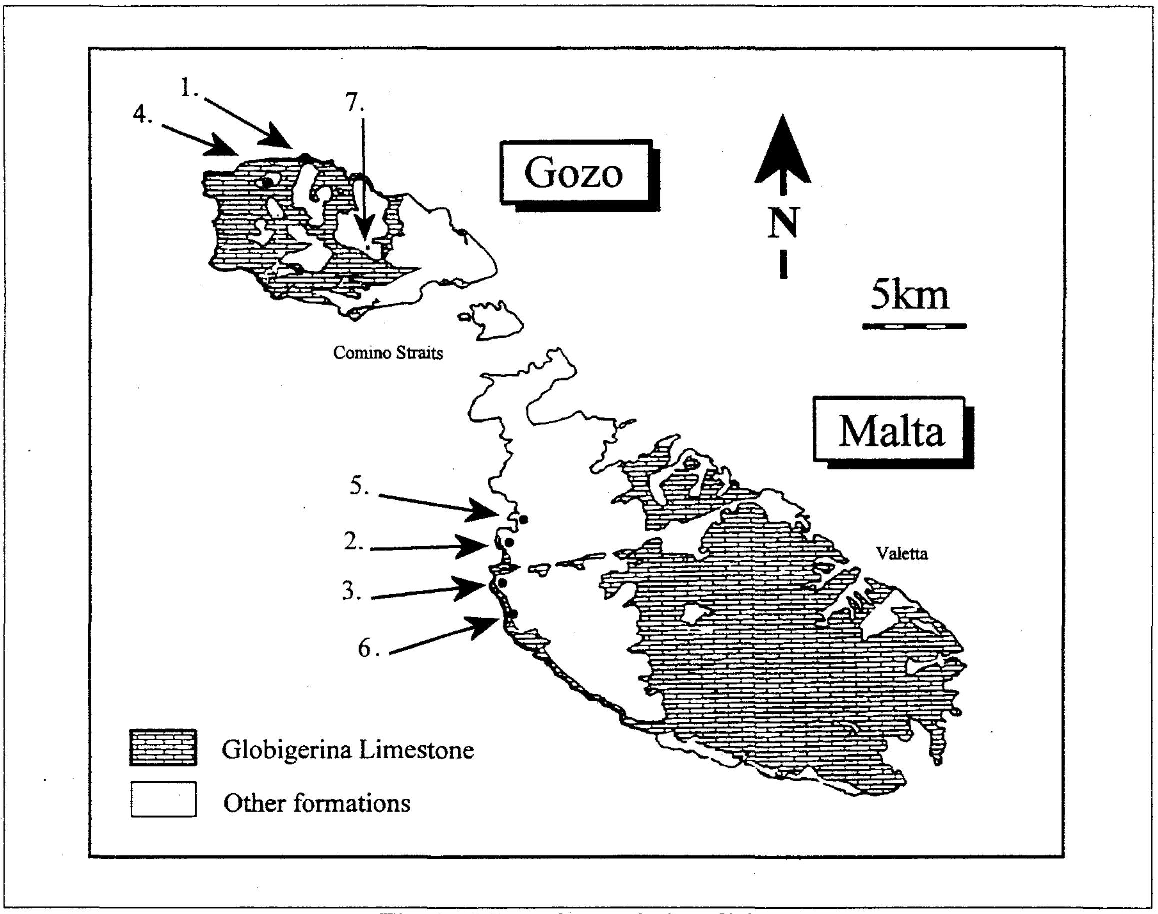

Fig. 2. Map of sample localities

2001 to "*Lamna*" *rupeliensis* [= *Isurolamna gracilis* (Le Hon 1871)]. This is certainly incorrect. The roots of these teeth are quite dissimilar to those of *Isurolamna*, they have no lingual groove, and are quite "*Otodus*-like". They are however, very similar to the late Eocene species *Parotodus mangyshlakensis* Kozlov *in* Zhelezko & Kozlov, 1999, which, although it shares many features with *Parotodus benedini*, may prove to be of a separate, and not necessarily closely related, lineage (Siverson pers. com.).

Both Purdy *et al.* and Kent & Powell (1999) reconstruct the dentition of *Parotodus benedini* in the manner of a lamnid; that is with an intermediate tooth. We find this relationship difficult to accept, preferring Otodontidae Glyckman 1964, as suggested by Zhelezko & Kozlov, 1999. The tooth they cite as an "intermediate tooth" closely resembles those found in an upper parasymphysial position in *Cretoxyrhina*, *Otodus* and *Carcharocles* (Shimada 1997, and pers. obs.). The one illustrated by Purdy *et al.* (fig. 23) is relatively much bigger than symphysials of *Cretoxyrhina*. See Siverson (1999) for his comments on "intermediate" and parasymphysial teeth.

One tooth from Malta, figured by Menesini (1974, Plate 1, fig. 17) could be an upper lateral of *Isurus retroflexus*. Another, an incomplete tooth, (Menesini 1974, Plate 1, fig. 14) bears a close resemblance to *Alopias grandis* Leriche 1942. Should this be the case, it would be the first record of this rare species outside the New World. Both these teeth would merit closer examination.

Genus *Carcharoides* Ameghino 1901

Carcharoides catticus (Philippi 1846)
No vernacular name

Synonymy: 1974 *Lamna cattica* (Phillippi 1846) Menesini, p. 135, pl. 1, figs 18-20.
2001 *Triaenodon obesus* (Rüppell 1835) Purdy *et al.*, p. 156, fig. 57, k-n.

Material & Provenance: C1 and the minor phosphorite conglomerates in the lower Middle Globigerina where it is not uncommon; it is extremely rare in C2.

Remarks: *Carcharoides* is a poorly-known, uncommon genus, present in the Neogene of both the Old and New World. The anterior teeth have a sand shark tiger-like appearance, whilst the lateral teeth more closely resemble those of *Lamna*. The crown histology is osteodont, in common with all lamniform sharks. It is very much larger, and only superficially similar to the teeth of *Triaenodon*, to which Purdy *et al.* (2001) refer it. *Triaenodon* is a carcharhinid shark with small teeth with a simple gradient monognathic heterodonty, and an orthodont histology. Teeth of *Carcharoides* are larger, of different proportions and histology, and can be separated into anterior and lateral teeth, while those of *Triaenodon* cannot. The lower lateral teeth of *Triaenodon* often exhibit double mesial lateral cusplets, a feature never recorded in *Carcharoides*. For these reasons we reject the suggestion that *Carcharoides catticus* is a junior synonym of *Triaenodon obesus* and concur with Cappetta (1987) that it is a lamniform.

Genus *Carcharocles* Jordan & Hannibal 1923

Carcharocles megalodon (Agassiz 1843)
Mega-toothed shark

Synonymy: 1974 *Procarcharodon megalodon* (Agassiz 1843), Menesini, p. 137, pl. 5, figs 1-10, pl. 6, figs 1-9.
2001 *Carcharodon megalodon* Agassiz 1835, Purdy *et al.*, p. 156, fig. 57, k-n.

Material & Provenance: see Menesini (1974).

Remarks: Much has been written and much more needs writing about this most well-known and misunderstood species.

By referring the giant toothed species *megalodon* to the extinct genus *Procarcharodon* the junior synonym of *Carcharocles* Jordan & Hannibal, 1923, Menesini was implying that *megalodon* was not closely related to the Recent Great white shark, *Carcharodon*. This was not the opinion of Purdy *et al.* (2001), who synonymised *Carcharocles* and *Palaeocarcharodon* under *Carcharodon*. This is a relationship we reject, however, a lengthy discussion of this is outside the scope of this paper, so we will restrict our comments to absolute basics.

Much of the confusion surrounding *megalodon* nomenclature involves the difference between a biological and a purely morphological species. In the case of fossil sharks' teeth, often the morphology is all one has, thus separate species have occasionally been described for anterior and lateral teeth. Such was the situation with "*Lamna*" *verticalis* and "*Odontaspis*" *hopei* (see Ward, 1989). Once an artificial tooth set is constructed, or an associated dentition is discovered, these mistakes become apparent. Like many sharks, the dentition of *Carcharocles* changes with the age. In the Miocene, teeth of young individuals of *C. megalodon* have lateral cusps, which are progressively lost with age. These changes, in the lifetime of an individual shark, closely mimic the changes that take place in the *megalodon* lineage. Thus, an adult shark in the late Oligocene will possess similar teeth to a young or adolescent shark in the Late Miocene. This leads to a conflict in nomenclature.

In the Middle Miocene the juvenile dentition of an individual shark may be referred to as *C. angustidens* (Agassiz 1843) or *C. turgidus* (Agassiz 1843) while the teeth retain their lateral cusps. They may be called *C. chubutensis* (Ameghino 1906) *C. polygyrus* (Agassiz 1843) or *C. subauriculatus* (Agassiz 1843), whilst the teeth are losing their denticles, and become *C. megalodon* once the denticles are fully lost. Thus, using purely tooth morphology, a shark may produce teeth of several different "species" during its lifetime. This is a nonsensical situation, but can be remedied by applying a name only to the adult morphology in any one formation; albeit difficult if the material is scarce. This was the

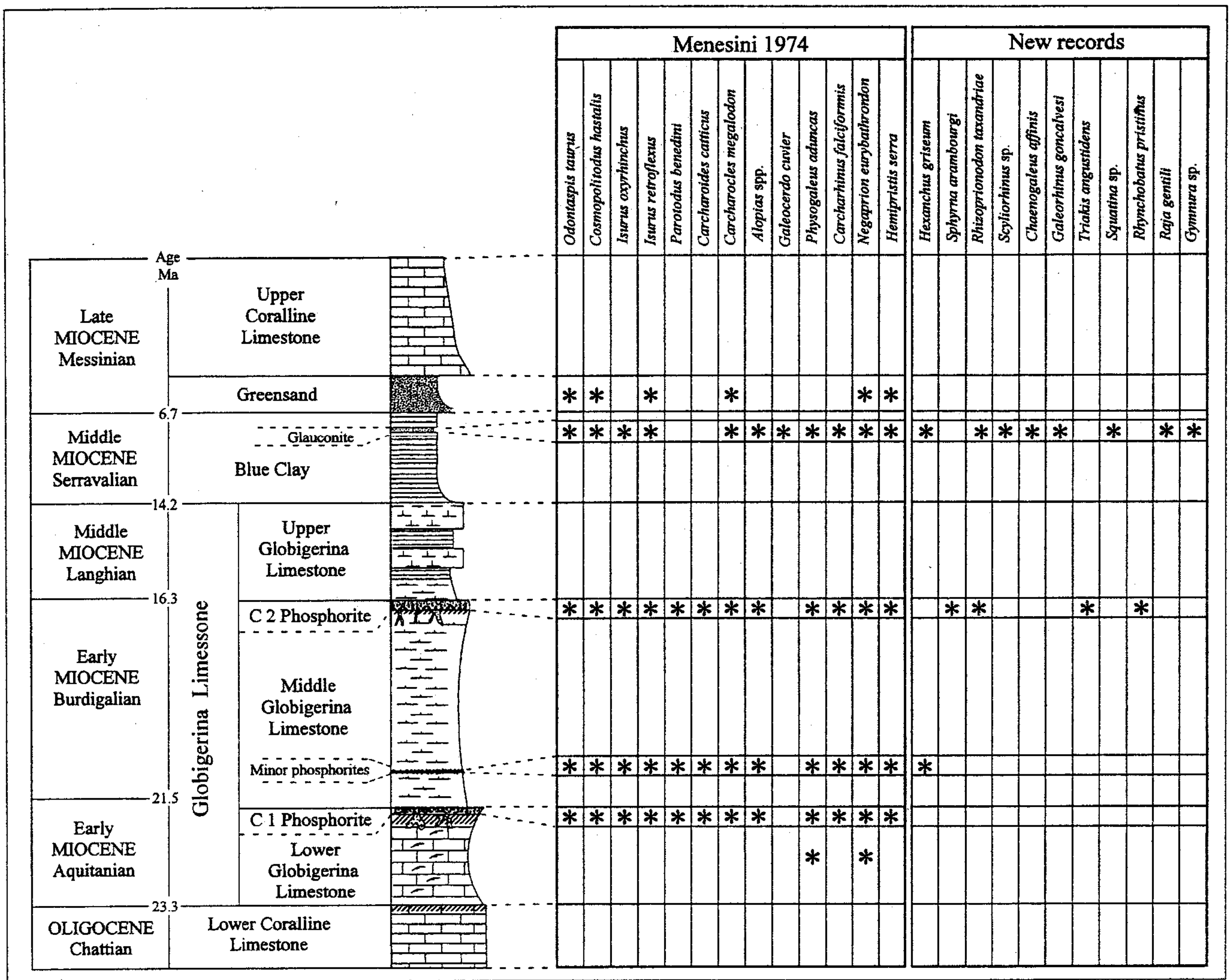

Fig. 3. Provisional distribution of sharks and rays in the Maltese stratigraphical column

enlightened approach taken by Menesini (1974: 137), one of the first palaeoichthyologists to recognise the importance of ontogeny in *megalodon* tooth morphology. She rejected Leriche's assertion, that *megalodon* could only be characterised by the absence of lateral cusps (Leriche, 1926: 418; Menesini, 1974: 138).

When one removes the confusion caused by the plethora of nominal morphospecies, it appears unlikely that there was ever more than one species of *Carcharocles* at any time, worldwide. It is difficult to conceive more than one giant shark in any habitat, and the fossil evidence does not contradict this. Thus, from the development of serrated teeth in the mid-late Ypresian, Early Eocene, to its eventual extinction in the early Pliocene, the *Carcharocles* lineage could be regarded as a single species, or any number of chrono species. Which approach one takes, makes very little difference to our overall concept of *Carcharocles*.

Genus *Alopias* Rafinesque 1810

Alopias sp.
Thresher shark

Material & Provenance: see Menesini (1974).

Remarks: The teeth figured by Menesini (plate 4, 7-14) are fragmentary, and difficult to interpret. The stouter specimens figured as *Alopias latidens* (Leriche 1908) (plate 4, figs 7-11) could represent *Alopias vulpinus*. The more gracile fragments listed as *A. exigua* (Probst 1879) (plate 4, figs 12-14) are most probably those of *Alopias superciliosus*.

A. latidens appears to be a member of an extinct lineage with extremely wide teeth, whereas "*Alopias exigua*" of authors usually appears to be a mixture of *Alopias vulpinus* and *Alopias superciliosus*. It is certainly likely that two, perhaps three, species of *Alopias* were present in the Miocene of Malta. More complete material is needed to confirm this.

Genus *Galeocerdo* Müller & Henle 1837

Galeocerdo cuvier **Peron & LeSueur 1822**
Tiger shark

Synonymy: 1974 *Galeocerdo aduncus* (Agassiz 1843), Menesini, p. 142, pl. 7, fig. 3, (non 1, 2, 4-6)

Material & Provenance: see Menesini (1974, pl. 7, fig. 3), from the glauconite horizon within the Blue Clay– see Menesini (1974: 123).

Remarks: Of the teeth figured by Menesini, all but this fall into "*Galeocerdo*" *aduncus/contortus* grouping, referred below to *Physogaleus*. The teeth figured as *G. aduncas* from the Miocene of southern France by Cappetta (1970, pl. 12) are also *Galeocerdo cuvier*-lineage. Teeth of *Galeocerdo* and (presumed) upper teeth of *Physogaleus* (see discussion below) are difficult to separate from published figures. However, teeth figured as "*Galeocerdo* sp" by Purdy et al. 2001 appear to be a mixture of *Galeocerdo cuvier* and *Physogaleus aduncus*.

Genus *Physogaleus* Cappetta 1980

Physogaleus aduncus (Agassiz 1843) comb. nov.
No vernacular name

Synonymy: 1849 *Galeocerdo contortus* Gibbes, p. 191, pl. 25, figs 71-74.
1904 *Galeocerdo triqueter*, Eastman, p 89, pl. 32, fig. 12
1942 *Physodon triqueter* Eastman: Leriche, p. 79
1974 *Galeocerdo aduncus* (Agassiz 1843), Menesini, p. 142, pl. 7, figs 1, 2, 4-6, (non 3)
2001 *Megachasma* sp, Purdy *et al.* p. 105 fig. 21, i-m.

Material & Provenance: see Menesini (1974, p. 142)

Remarks: Apart from *Galeocerdo cuvier* Péron & Leseur 1822, there are two teeth of *Galeocerdo*-like morphology present in the Maltese material. The first, similar to Recent *Galeocerdo*, with a broad distally directed cusp, and coarsely serrated distal shoulder is normally termed *Galeocerdo aduncas*. The second has a narrower, more apically directed and slightly twisted cusp and finer distal serrations. There is a very large lingual protuberance and a flat basal surface to the tooth. This second morphology is usually referred to as *Galeocerdo contortus* Gibbes. In my experience (DJW), these two morphologies usually occur together, there are no exceptions that I am aware of. It seems reasonable to regard them as either the product of dignathic or gynandric (sexual) heterodonty in a single species. This was also the opinion of Applegate (1978: 59) but rejected by Purdy *et al.* who regarded them as separate species.

Cappetta (1980: 37) combined three Eocene species, *Physodon secundus* Winkler 1874, *Physodon tertius* Winkler 1874 and *Galeorhinus minor* Agassiz 1835 into a single species of a new genus, *Physogaleus*. This was characterised by a strong dental sexual dimorphism, particularly marked in the anterior files of the lower jaw. Males have strongly mesio-distally compressed lower teeth with tall thin backwardly-directed slightly sigmoidal crowns. Upper teeth are wider and more *Galeorhinus/Galeocerdo*-like. Winkler's (1874) types of "*Trigonodus secundus*, two small lower anterior teeth, are not lost, as inferred by Purdy *et al* 2000, they are present in the collections of the Musée royale d'Hisoire naturelle de Belgique, in Brussels, and were figured by Leriche (1905, plate 8, figs 10, 11.)

Teeth of "*Galeocerdo*" *aduncus* (including "*G.*" *contortus*) are remarkably similar to those of the Eocene species of *Physogaleus*, sufficiently similar to be referred to *Physogaleus*. Both the "aduncas" and "contortus" morphologies can be seen in middle Eocene teeth of *Physogaleus secundus*. They differ in having fine serrations superimposed on the larger serrae on the distal, and lower half of the mesial cutting edges. This character is present in *contortus, aduncus* and *cuvier*. The presence of compound serrae could be interpreted as an important character linking these three nominal species. However, complex serrae have appeared in several relatively unrelated lineages and are occasionally present in species of *Carcharhinus* including *C. plumbeus* (Nando, 1827), *C. leucas* (Valenciennes 1839), *C. obscurus* (Lesueur 1818), *C. perezii* (Poey 1876), *C. falciformis* (Bibron 1839) and *C. brachyurus* (Günther 1870) (Jim Bourdon, written comm.)

In both *Galeocerdo* and *Physogaleus*, the dentition is imbricate. That is, the teeth in the files on either side of a particular position, are slightly labial or lingual to it, and, overlap its margins, much like fish scales or roof tiles. In *Galeocerdo* overlap only occurs when the teeth are in occlusal position. However, in *Physogaleus* the imbrication, particularly in the lower jaw, is far more developed. This would suggest that, unlike *Galeocerdo*, that has a wide U-shaped slicing jaw, *Physogaleus* had a more V-shaped, pointed, grasping jaw.

The presumed upper teeth of *Physogaleus aduncus* can be separated from those of the Recent *Galeocerdo cuvier* by their more rounded, less stocky and angular roots, more arcuate, less angular root lobe separation. Purdy *et al* (2001: 146) regarded "*Galeocerdo*" *aduncas* (regarded as a separate species from *G. contortus*) as a *nomen dubium*. This was because Agassiz's holotype of *G. aduncus* is presumed lost and it is not possible from his figure to distinguish it from young specimens of *Galeocerdo cuvier*. We accept this point, but feel that, with the characters mentioned above, it is easy to separate these two nominal species. Thus, we regard the name *aduncas* as available for the combined species. From a total-dentition perspective, *Galeocerdo* has a broadly homodont dentition, whilst *Physogaleus* has a strongly heterodont dentition, a condition seen on no fossil or Recent species of *Galeocerdo*. The teeth figured as *Megachasma* sp. by Purdy *et al* (2001: fig. 21, i-m) would appear to be stocky parasymphyseal or symphyseal teeth of the "*contortus*" morphology, referred here to the lower jaw of *P. aduncus*. Many we have examined, as possible *Megachasma*, exhibit fine serrae on the mesial cutting edge.

Genus *Carcharhinus* Blainville 1816

Carcharhinus falciformis (Bibron 1839)
Silky shark

Synonymy: 1974 *Carcharhinus egertoni*, Menesini (1974, plate 7, figs 11-14).

Material as above.

Provenance: Glauconite horizon within the Blue Clay - see Menesini (1974: 123).

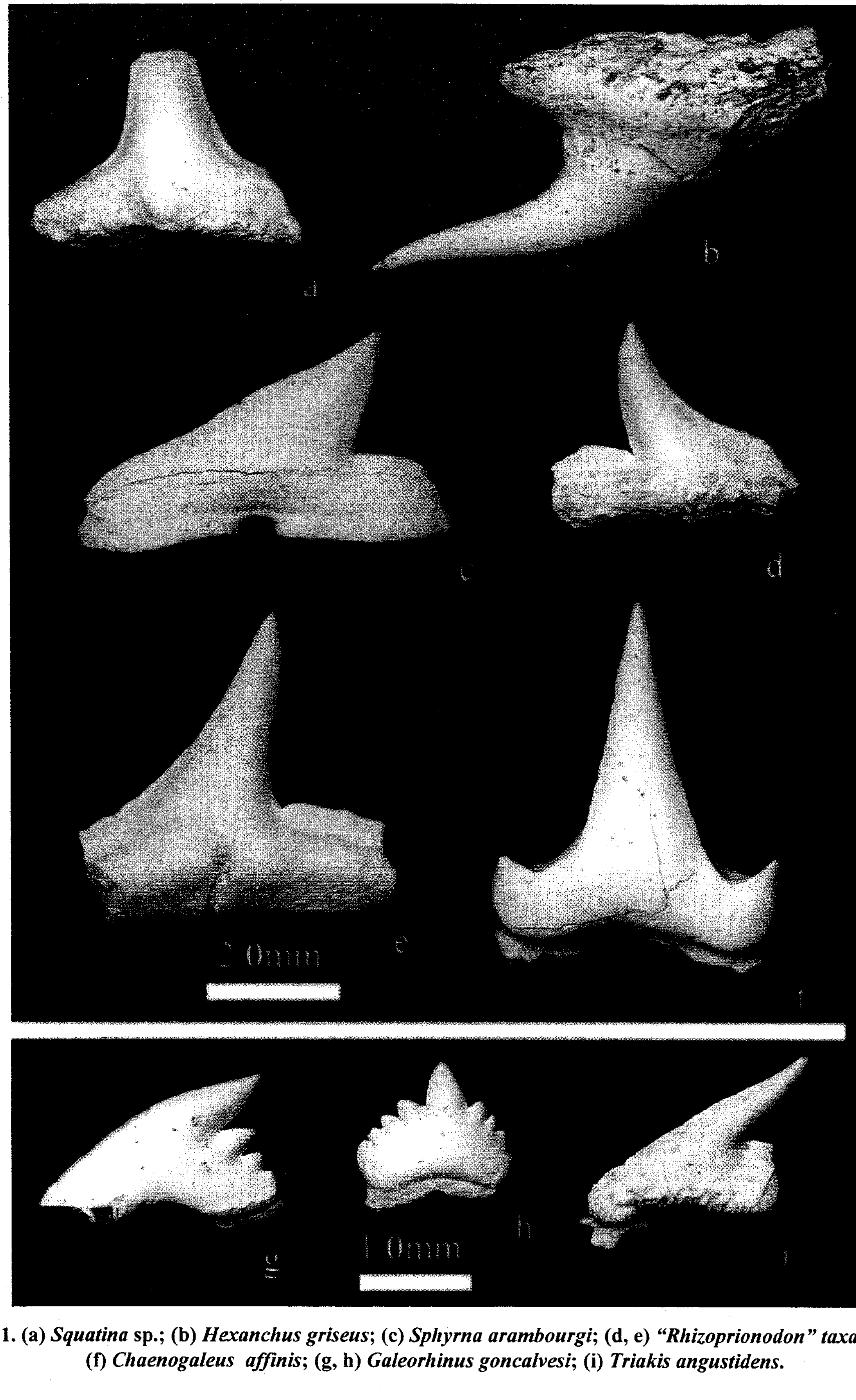

Plate 1. (a) ***Squatina*** **sp.; (b)** ***Hexanchus griseus*****; (c)** ***Sphyrna arambourgi*****; (d, e)** ***"Rhizoprionodon" taxandriae*****; (f)** ***Chaenogaleus affinis*****; (g, h)** ***Galeorhinus goncalvesi*****; (i)** ***Triakis angustidens.***

Remarks: *Carcharhinus egertoni* Agassiz 1843 tends to be used as a "dustbin" species for Miocene teeth of *Carcharhinus*. Purdy *et al* (2001: 151-152) suggest that one of Agassiz's two type specimens of *Carcharhinus egertoni* is referable to the Recent species *Carcharhinus brachyurus* (Günther 1870) (Agassiz, 1843, pl. 36, fig. 6) and the second to *Carcharhinus leucus* (Valenciennes 1839) (Agassiz, 1843, pl. 36, fig. 7). This is indeed possible, but we feel it more likely that both are teeth of *C. leucus*. The first specimen, appears to be a tooth from the right upper ? 4th or 5th row. Teeth of *Carcharhinus brachyurus* tend to have narrower crowns with a more distinct mesial and distal notch. It is very likely that several other species of *Carcharhinus* are present in the Maltese Miocene.

Genus *Negaprion* Whitley 1940

Negaprion eurybathrodon (Blake 1862)
Lemon shark

Synonymy: 1970 *Negaprion kraussi* (Probst): Cappetta, p. 52, pl. 15, figs 1-10, 12, 14-17 *non* 11, 13.
1974 *Hypoprion acanthodon* (Le Hon): Menesini, p. 148, pl. 4, figs 15-22.
1974 *Carcharhinus egertoni* (Agassiz): Menesini, p. 144, pl. 7, figs 7-10, 15.
1974 *Sphyrna prisca* Agassiz: Menesini, p. 152, pl. 7, figs 17-19.

Material & Provenance: Menesini (1974, pl. 4, figs 15-22; pl. 7, figs 7-10, 15, 17-19)

Remarks: Purdy *et al* (2001) suggest that the fossil species *Negaprion eurybathrodon* might be the senior synonym of the Recent Lemon shark, *N. brevirostris*. From looking at the Maltese specimens figured by Menesini, and Recent jaws of *N. brevirostris*, this would appear to be quite likely.

Genus *Hemipristis* Agassiz 1843

Hemipristis serra Agassiz 1843
Snaggletooth shark

Synonymy, material & provenance: see Menesini (1974, p. 132-134)

Remarks: *Hemipristis serra* teeth from Malta are quite typical and unlikely to be mistaken for any other species. The teeth of *H. serra* have an orthodont histology, a hollow pulp canal in the centre of the crown surrounded with parallel orthodont fibres, with an osteodentine root. This is the normal condition in carcharhinid sharks and some orectolobiforms. The Recent *H. elongatus* (Klunzinger 1871) is said to have an osteodont crown, the crown filled by osteodentine (Compagno, 1973, pl. 1; 1984: 171).) In fossil and Recent specimens one of us (DJW) has examined, this is usually the case. The trend in Neogene fossil shark studies is to recognise extant species from the Miocene to Recent. Because of these histological differences, we feel that the existing *status quo*; a separate species for the Miocene *Hemipristis* is justified at present.

Genus *Sphyrna* Rafinesque 1810

Sphyrna arambourgi Cappetta 1970
Hammerhead shark
Plate 1, fig c.

Material: one tooth.

Provenance: C2 Phosphorite, Ras ir-Reqqa.

Remarks: The single Maltese tooth falls within the range of variation of those described by Cappetta (1970, pl 19, figs 1-18) as *Sphyrna arambourgi* Cappetta 1970. Of the Recent species examined, these and the Maltese specimen most closely resemble teeth of *Sphyrna lewini* (Griffith & Smith 1834). There is no differentiated mesial heel, a triangular, distally directed crown and low distal cusplet separated from the crown by a distinct notch. The labial crown does not overhang the root. The cutting edge of the crown is unserrated Teeth of Recent Hammerheads range from having serrated crowns (*S. couadi* Cadinat 1950, *S. tudes* (Valenciennes 1822)), weakly serrated (*S. leweni* (Griffith & Smith 1822), *S. zygena* (Linneaus 1758)) and unserrated (*S. corona* Springer 1940, *S. media* Springer 1940, *S. tiburo* Recent species with weakly serrated crowns tend only (Linneaus 1758)), to show fine serrations in larger (= older) individuals (pers. obs. – DJW).

Genus *Rhizoprionodon* Whitley 1929

"Rhizoprionodon" taxandriae (Leriche 1926)
Sharpnose shark
Plate 1, figs. d, e.

Material: Two teeth.

Provenance: Blue Clay at Ras il-Karraba; C2 phosphorite, Ras ir-Reqqa (Gozo).

Remarks: The morphology of the teeth of *Scoliodon, Loxodon,* most species of *Rhizopriodon* and some unserrated species of *Sphyrna* species are so similar as to be virtually indistinguishable, so the referral of this species to *Rhizopriodon* is tentative.

Genus *Scyliorhinus* Blainville 1816

Scyliorhinus sp
Catshark
Plate 2, fig. a.

Material: One tooth.

Provenance: Glauconite horizon within the Blue Clay, In-Nuffara, Gozo.

Remarks: The single, incomplete tooth has a crown bearing a series of fine, apically anastomosing striae. There are two mesial lateral cusplets, the larger striated, and a single striated distal cusplet. The root is incomplete. Despite the important work of Herman *et al.,* (1990), in illustrating Recent sharks'

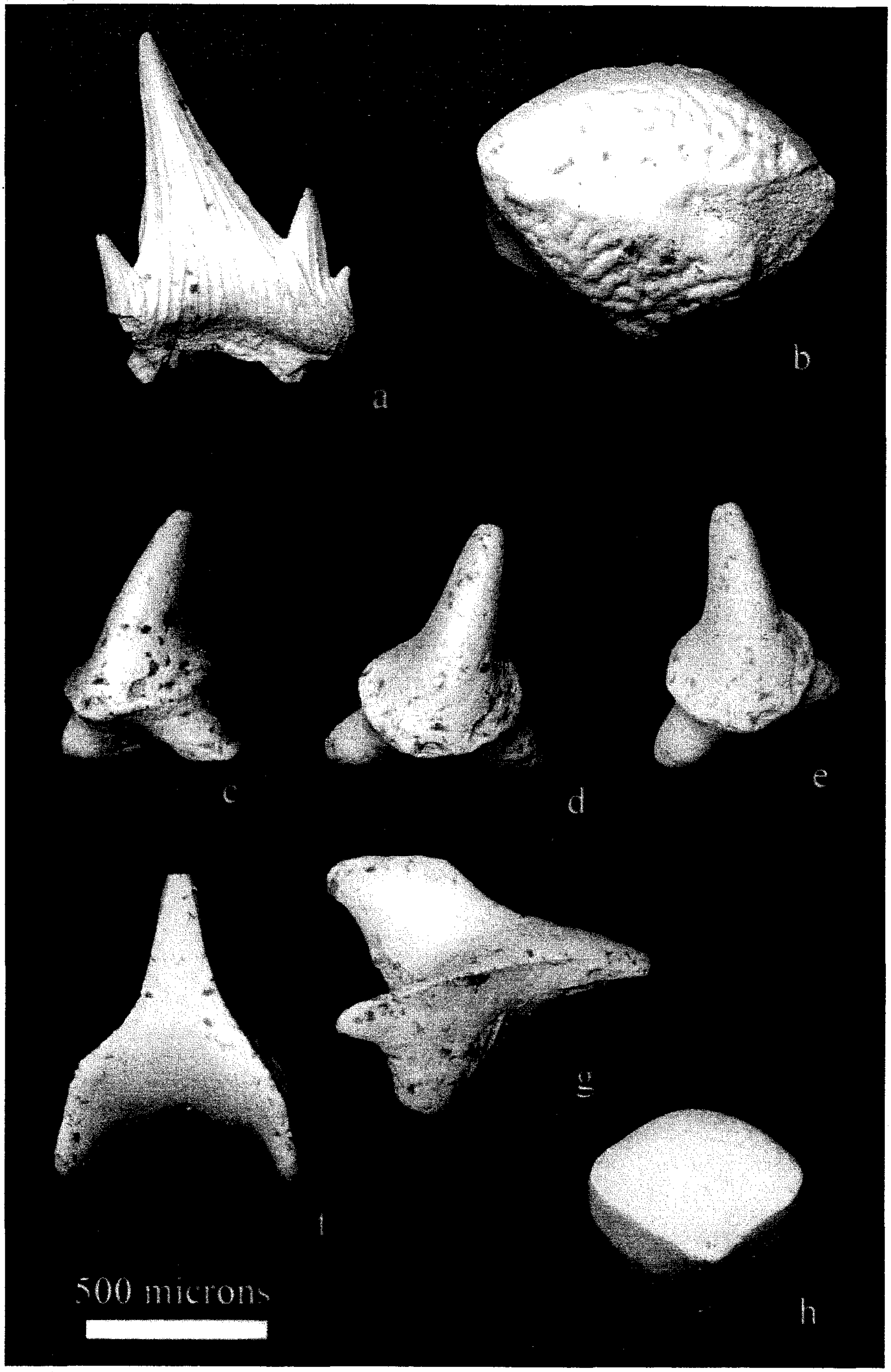

Plate 2. (a) *Scyliorhinus* sp; (b) ***Rhynchobatus pristinus***; (c – e, h) ***Raja gentili***; (f, g) ***Gymnura*** sp.

teeth, our knowledge of the specific and generic variation in the family Scyliorhinidae is sparse. This specimen bears a close resemblance to teeth of *Scyliorhinus torazame* (Tanaka 1908) figured by Herman *et al.*, (1990), but could equally belong to several other genera. Its referral to the genus *Scyliorhinus* must be provisional. It is easily separated from the Miocene species *Scyliorhinus distans* (Probst 1879) whose distal cusplets are larger and much more separate from the principal cusp.This tooth appears to be identical to that of *Scyliorhinus* sp. figured by Cappetta & Nolf (1991, pl. 3, fig. 3) from the Early Pliocene of southern France.

Genus *Chaenogaleus* Gill 1862

Chaenogaleus affinis (Probst 1879)
Hooktooth shark
Plate 1, fig. f.

Material: One tooth.

Provenance: Glauconite horizon within the Blue Clay, Nuffara, Gozo

Remarks: *Chaenogaleus affinis* is a fairly common species in the Miocene of the Mediterranean having been recorded from the south of France and Portugal (Cappetta, 1970; Antunes & Jonet, 1970). The upper teeth are *Galeorhinus*-like, with which they are usually confused, but lack a bulge in the enamel of the base of the labial crown. The lower teeth were described as *Scyliorhinus joneti* by Cappetta (1970) (Antunes *et al*, 1999).

Genus *Galeorhinus* Blainville 1816

Galeorhinus goncalvesi Antunes, Balbino & Cappetta 1999
Tope
Plate 1, figs g, h.

Material: Two teeth.

Provenance: Glauconite horizon within the Blue Clay, In-Nuffara, Gozo and at Ras il-Karraba – Malta.

Remarks: Herman *et al.* (1988) figured teeth of the Recent *Galeorhinus galeus*. The two Maltese teeth correspond very closely with these teeth and those in Recent jaws from the North Sea (DJW Coll.) The specimen in Plate 1 fig. g is a right upper lateral, whilst Plate 1 fig. h is a lower left parasymphyseal tooth.

In *Galeorhinus* parasymphyseal teeth have their crowns directed mesially, not distally. However recently Antunes *et al.* (1999) published a description of a new species of *Galeorhinus, G. goncalvesi*, from the late Miocene of Portugal. It is separated from the Recent *G. galeus*, by the rather more inflated labial crown base. The Maltese teeth show this same feature, especially the parasymphyseal, so we have referred the Maltese specimens to this species. Antunes *et al.* (1999) admit that this species is very close to the Recent *G. galeus*, so it may later transpire that it falls within the intraspecific variation and thus the synonomy of *G. galeus*. It is noteworthy that this temperate species is found in the cooler waters of the late Miocene.

Genus *Triakis* Müller & Henle 1838

Triakis angustidens Cappetta 1973
Houndshark
Plate 1, fig. i.

Material: One tooth.

Provenance: C2 phosphorite, Ras ir-Reqqa.

Remarks: This single small tooth corresponds with those figured by Cappetta (1973: 216, pl 12), from the Early Miocene of southern France, and probably from southern Portugal (Cappetta & Nolf, 1991: 59). It differs from the Early Pliocene *T. costamagnai* Cappetta & Nolf, 1991, by having a more lanceolate cusp and a more plicated labial crown base. Lateral teeth of *T. costamagnai* resemble those of the Recent species *Iago omanensis* (Norman 1939), but differ by the taller, more erect anterior teeth.

Genus *Squatina* Blainville 1806

Squatina **sp.**
Angel shark
Plate 1, fig a.

Material: one tooth.

Provenance: Glauconite horizon within the Blue Clay, Ras il-Pellegrin, Malta.

Remarks: Cappetta (1970: 77) used the species, *Squatina subserrata* Münster 1846 for specimens from southern France. The single *Squatina* tooth from Malta falls within the range of specific variation of *S. subserrata*, recorded from the Miocene of southern France (Cappetta, 1970: 77). However it also falls within the range of specific variation of almost all other Cenozoic species of *Squatina*. There are three Recent species of *Squatina* inhabiting the Mediterranean, whose teeth to are inseparable (DJW pers. obs.). Accordingly we feel that there is little value in appending a species that cannot be confidently separated from others within the genus.

Genus *Rhynchobatus* Müller & Henle 1837

Rhynchobatus pristinus (Probst 1877)
Guitarfish
Plate 2, fig. b.

Synonymy: 2001 *Rhinobatos* sp. Purdy *et al.* fig. 7d (prob. non e)

Material: One tooth.

Provenance: C2 phosphorite, Ras ir-Reqqa.

Remarks: *Rhynchobatus pristinus* is a common species in the Miocene of the Mediterranean area (Cappetta 1987: 134).

It is also common in the Miocene of N. Carolina, USA where it was figured as *Rhinobatos* sp. by Purdy *et al.* 2001. In teeth of *Rhinobatos*, the enameloid of the occlusal surface is usually smooth and there is a large lingual uvula, whereas in *Rhynchobatus*, the occlusal surface is usually ornamented with enameloid granules and the uvula is small and triangular.

Genus *Raja* Linnaeus 1758

Raja gentili Joleaud 1912
Skate
Plate 2, figs. c-e, h.

Material: Two teeth.

Provenance: Glauconite horizon within the Blue Clay, Nuffara, Gozo

Remarks: The two Maltese specimens of *Raja* correspond reasonably well with the somewhat battered teeth figured by Leriche (1927, pl. 5, figs 16-18) as *Raja gentili.* The low-crowned female tooth (Plate 2, fig. h) also corresponds well with those figured by Cappetta (1970, plate 20, figs 28-31) from southern France. A second species similar to *Raja olisiponensis* (Jonet 1968), from the Portugese Miocene, (originally described as *Narcine)*, is recorded from the Pliocene of southern France by Cappetta & Nolf, 1991. The tall-crowned male teeth are similar to those of *Raja gentili*, however the female teeth are quite different, possessing a wide, slightly domed, occlusal surface and a small lingually directed cusp reminiscent of the fossil rhinobatoid genus *Squatirhina*.

Genus *Gymnura* Van Hasselt 1823

Butterfly ray
Gymnura sp.
Plate 2, figs. f, g.

Material: One tooth.

Provenance: Glauconite horizon within the Blue Clay, Nuffara, Gozo

Remarks: Teeth of *Gymnura*, are common in the Miocene of southern France, although because of their small size, they are not usually recorded. They were described and figured, as *Pteroplatea*, a junior synonym, by Cappetta (1970: 102, pl. 20, figs 17-25).

Genus *Myliobatis* Cuvier 1817

Myliobatis sp.
Eagle ray

Material: One fragmentary tooth in the collections of the Department of Palaeontology of the Natural History Museum, London, listed by Woodward (1889:120) number 1862. A large specimen is exhhibited at the National Natural History Museum at Mdina; a second, a third and a fourth are known in separate private collections and a fifth tooth is in the private collection of the second author (CGB).

Provenance: Unknown: "... from the island of Gozo".; the second and third teeth both come from the lowermost Upper Coralline Limestone of Gnejna ; the fourth from C2 at Bahrija; the fifth tooth from the Greensand at Rdum il-Hmar.

Remarks: Teeth of *Myliobatis*, are extremely uncommon in the Miocene of Malta, despite their large size. In collections of isolated teeth of "*Myliobatis*" it is often possible to find teeth of the rays *Pteromylaeus* and *Rhinoptera*. Adams (1870) *lists Myliobates toliapicus* as occurring in the Greensand, the Blue Clay and in the Lower Coralline and with some doubt as to identification at genus level, from the Globigerina.

PALAEOECOLOGY

The larger species of lamniforms (*Carcharocles, Cosmopolotodus, Isurus Parotodus* and *Alopias*) as well as some carcharhinids (*Hemipristis*) are pelagic species and have a global distribution in the Miocene. With the limited material at our disposal, it is difficult to say anything significant about the smaller shark and ray species recovered. They are consistent with Miocene faunas elsewhere and, with their small numbers tell us little about the environment, other than that it was warm temperate to sub-tropical and relatively productive.

No deepwater species have been found, i.e. *Isistius, Centrophorus, Deanea Heptranchias Megascyliorhinus* or *Megachasma* which is consistent with deposition on a relatively shallow carbonate platform. One thing that is quite interesting, and cannot be immediately explained, is the great scarcity of *Myliobatis* and *Aetobatis* tooth-plates and the lack of *Rhinoptera* and *Plinthicus* material. The absence of small *Manta* ray teeth, which are common in southern France, could be a collecting artefact. Devil ray teeth are small and may turn up in future samples

CONCLUSIONS

By bulk sampling and by taxonomic revision, the fossil sharks and rays from the Miocene of Malta has been increased from 13 to 24 species in total. Several genera, *Alopias* and *Carcharhinus* in particular, would benefit from a closer examination and could certainly yield more species. The fact that most of the small batoids and some of the smaller carcharhinid sharks are represented by single specimens shows that more intensive bulk sampling would be most valuable. This was only intended to be a feasibility study, however the results were so promising that it was thought important to publish the results as they stood, and then proceed with a more comprehensive investigation.

The Maltese fossil shark and ray fauna recovered is very similar to that recorded from southern France by Cappetta (1970) and Portugal (Jonet, 1966; 1968; 1978; 1981). This is principally because there are very few comparable shark and ray faunas where the smaller elements, particularly rays, have been described. The Miocene fauna of North Carolina (Purdy *et al.*, 2001) contains many pelagic elements in common with the Maltese fauna, particularly the larger lamniforms (*Carcharocles, Parotodus* and *Alopias*) as well as some carcharhinids (*Hemipristis*). It is likely that many of the smaller sharks and rays will prove to be different, reflecting the current pattern of species distribution.

ACKNOWLEDGMENTS

We would like to thank Mr Arie W. Janssen (Xewkija, Gozo) for assistance in the field and for help with the stratigraphy and bibliography. Dr Noel Morris (NHM, London) also kindly helped procure photocopies of some of the more obscure references. Mr Jim Bourdon (Croton-on-Hudson, USA) contributed to the discussion on *Physogaleus* and shared with me some of his knowledge of *Carcharhinus*. Dr Mikael Siverson (University of Lund, Sweden) assisted us with some of the more contreversial systematics. The scanning electron micrographs were made with the assistance of Dr. Ian Skipper, University of Greenwich. The manuscript was greatly improved by the comments of the Editor and anonymous reviewer(s) whose time and efforts are greatly appreciated

(Accepted 20th December 2001)

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