

Uppermost Miocene Lamniform Selachians (Pisces) from the Alvalade basin (Portugal)

Miguel Telles Antunes^(1, 2, 3) & A. Cáceres Balbino^(3, 4)

(1) Academia das Ciências de Lisboa. (2) European Academy of Sciences, Arts and Humanities, Paris.

(3) Centro de Estudos Geológicos da Universidade Nova de Lisboa, Quinta da Torre, 2825-114 Caparica, Portugal. E-mail: mta@mail.fct.unl.pt

(4) Departamento de Geociências, Universidade de Évora, Apartado 94, 7002-554 Évora, Portugal. E-mail: acaceres@uevora.pt

Abstract

Key-words: Selachians; Lamniforms; Alvalade Basin; Uppermost Miocene; Paleoecology.

This paper deals with Lamniform teeth collected in deposits from the Esbarrondadoiro Formation, Alvalade Basin in Southern Portugal. The following genera were recognized: *Carcharias*, *Pseudocarcharias*, *Alopias*, *Isurus* and *Carcharocles*. The species *Carcharias acutissima* is by far the most predominant, all other taxa being rare or very rare. This situation points to neritic, tropical to subtropical, rather shallow waters not far away from the coast. This is corroborated by the rarity of the associated, mainly pelagic, taxa.

The ratio between *C. acutissima* and the remaining Lamniforms as a whole is markedly uneven between Esbarrondadoiro and the localities of Santa Margarida and Vale de Zebro. This suggests quite different environmental conditions, a matter that will require a more thorough examination taking into account all palaeontologic and geologic data.

Resumo

Palavras-chave: Seláceos; Lamníformes; Bacia de Alvalade; Miocénico terminal; Paleoecologia.

São descritos dentes de Lamníformes provenientes de depósitos da Formação de Esbarrondadoiro (Bacia de Alvalade), dos géneros *Carcharias*, *Pseudocarcharias*, *Alopias*, *Isurus* e *Carcharocles*. Verifica-se predomínio absoluto de *Carcharias acutissima*, muito frequente; todos os demais taxa são raros ou muito raros. Daí resultam ilações ambientais indicando zonas neríticas de regiões tropicais e subtropicais e águas geralmente pouco profundas, não longe da costa, o que é corroborado pela raridade das formas essencialmente pelágicas.

A relação muito desigual entre a ocorrência de *Carcharias acutissima* e a dos demais lamníformes em Esbarrondadoiro e, por outro lado, nas jazidas de Santa Margarida e Vale de Zebro evidencia condições de natureza paleoambiental bastante diferentes, que convirá analisar com base no conjunto de dados paleontológicos e geológicos.

Introduction

The Late Miocene, Esbarrondadoiro Formation (Alvalade Basin) yielded a rich and diversified assemblage of Selachian teeth, more than 10,000 at present. It represents a modern type of fauna that does not include any more typical earlier Miocene species such as *Carcharhinus priscus*, *Dasyatis rugosa* and *Aetobatus arcuatus* (Antunes *et al.*, 1999).

Lamniforms comprise seven species, or 11 % of the total number of taxa. All are pelagic forms, even if *Carcharias*, which is very common and by far the most dominant, is more often found in coastal, shallow waters ("sand sharks"). All other species are rare or very rare.

Among the Lamniforms there are large, top predators such as the mio-pliocene *Carcharocles megalodon* but not the pliocene and still extant white shark *Carcharodon carcharias*.

There are a lot of fossil Lamniforms whose systematic status at the Family level has been discussed. This results from parallel evolution (Cappetta, 1987).

According to Gluckman (1964), the Order Lamniformes comprises:

- the Superfamily Odontaspidoidea, with the families Jaekelotodontidae Gluckman, 1964, Otodontidae Gluckman, 1964, Carcharodontidae Gill, 1892, Cretoxyrhinidae Gluckman, 1958 and Odontaspidae Müller & Henle, 1841;
- the Superfamily Isuroidea, with the families Isuridae and Lamniostomatidae.

Gluckman's Systematics were revised by Herman (1977) as far as the Cretaceous and Paleocene Selachians are concerned, but with no comments about the validity and scope of some essentially neogene families (Cappetta, 1987).

Compagno (1984) ascribed to the Lamniformes 7 families with extant representatives: Lamnidae Müller & Henle, 1838; Odontaspidae Müller & Henle, 1839; Mitsukurinidae Jordan, 1898; Pseudocarchariidae Compagno, 1973; Megachasmidae Taylor, Compagno & Struhsaker, 1983; Alopiidae Bonaparte, 1838 and Cetorhinidae Gill, 1862. Here we will follow Compagno's systematics.

Systematics

Class	CHONDRICHTYES Huxley, 1880
Subclass	ELASMOBRANCHII Bonaparte, 1838
Superorder	GALEOMORPHII Compagno, 1973
Order	LAMNIFORMES Berg, 1958
Family	Odontaspidae Müller & Henle, 1839
Genus	<i>Carcharias</i> Rafinesque, 1810

Carcharias acutissima Agassiz, 1844
(Pl. 1, fig. 1-5; Pl. 2, fig. 1-5)

Material: 660 teeth.

Sites (Number of teeth): Esbarrondadoiro (432), Santa Margarida (80) and Vale de Zebro (148).

Description: this species is represented by well preserved teeth from all the sites concerned.

The parasymphysial teeth are small, with a short and thick root whose lobes are nearly fused, and with a strong internal bulge. The pointed crown is round in section, and presents a sigmoidal profile and thin cutting edges. Some parasymphysial teeth have no lateral denticles. However, in others, the crown looks deformed: the symphysial denticle is reduced or lacking, the commissural denticle being developed and placed at the crown's base.

In the anterior teeth, the crown is thin, acute, with thin cutting edges and a distinct sigmoidal profile. The convex internal surface of the crown presents an irregular, vertical striation. In some teeth the striae are very marked and occupy more than half of the surface of the crown.

As Cappetta (1970) points out, the striae are not very marked in adults and become weaker about the middle of the crown, while in young animals the striation is stronger and extends beyond half of the crown's height.

The internal side of the root is protuberant. The root has two close-by, developed branches. The internal protuberance shows (but not always) a weak furrow. Some anterior teeth have lateral denticles that are acute, circular in section and thick at the base.

In the upper lateral teeth, the crown is triangular in shape, broad at the base, flattened and somewhat bent towards the commissure. Bending increases as the teeth are more and more lateral. The root's branches are more divergent than in the anterior teeth and show a very distinct furrow. The lateral denticles are stout. In some teeth there are two pairs of denticles.

In the distal teeth, the root is thick and larger than the crown, which can be reduced into a blade. The crown is bent towards the commissure; the lateral denticles may be lacking.

The tiny intermediate teeth are very deformed in shape and mesio-distally flattened. The root is larger than the crown, whose outline is sinuous.

Discussion: *C. acutissima* teeth are often difficult to distinguish from those of the *Carcharias* sp. described by Cappetta (1970, p. 34, pl. 2, fig. 20), especially when they are small and possess a very erect crown. Teeth of this type have been ascribed to young animals (Leriche, 1910).

Carcharias cuspidata Agassiz, 1843
(Pl. 2, fig. 6)

Material: 1 tooth.

Site: Vale de Zebro.

Description: shape is triangular with a broad base. The partly destroyed crown is convex in its internal surface, the external surface being nearly flat. The root has two well developed, divergent branches and a strong internal protuberance with a central groove. There are two low and broad lateral denticles.

Discussion: the lack of striation on the internal surface of the crown; the broader, triangular crown; the strong root with very divergent branches, are characteristics that allow us to ascribe the specimen to *C. cuspidata*.

Remark: Leriche (1910) has described as *Odontaspis cuspidata* the dentition of this species, which is common in the Rupelian (Lower Oligocene) in Belgium, but is widespread in the Miocene.

Family	Pseudocarchariidae Compagno, 1973
Genus	<i>Pseudocarcharias</i> Cadenat, 1963

Pseudocarcharias cf. kamoharai (Matsubara, 1936)
(Pl. 3, fig. 1)

Material: 1 tooth.

Site: Vale de Zebro.

Description: the only specimen collected so far is a small lateral tooth.

The crown, whose profile is clearly sigmoidal, is acute, broad at its base, and a little bent towards the commissure. The cutting edges are thin. The distal talon is more developed than the mesial one, and is distinctly separate from the crown.

The root presents two divergent lobes. There is a small labial protuberance with a foramen.

Discussion: this tooth has been compared to the closely similar teeth of the extant *P. kamoharai*. It could have been reported to the genus *Carcharias* according to the morphology of the crown; however, this classification can confidently be excluded as there are no denticles, because the shape of the talon is different, and taking into account the size of the specimen.

Family Alopiidae Bonaparte, 1838
Genus *Alopias* Rafinesque, 1810

Alopias cf. *superciliosus* (Lowe, 1840)
(Pl. 3, fig. 4)

Material: 1 tooth.

Site: Vale de Zebro.

Description and discussion: one tooth is the only evidence of still another Lamniform that seems to belong to the genus *Alopias*, the thresher sharks. Among these there are two well-known extant species, the pelagic common thresher *A. vulpinus* and the large-eyed, deep water dweller *Alopias superciliosus*. Fossil species have been detected since lowermost Eocene and especially during Oligocene and Miocene. Evidence has been discussed in detail, in comparison with extant specimens (Antunes, 1970; Antunes & Jonet, 1969-1970).

The tooth in question has a moderately slender crown, smooth, only slightly bent laterally (nearly upright and symmetrical), with weak, rather faint cutting edges and a basally rounded section, the outer surface being flatter. All these characteristics indicate an anterior maxillary tooth, from the 1st or maybe the 2nd row at most. The same characteristics clearly exclude *Isurus*. The lack of lateral denticles is enough to eliminate *Carcharias* (and *Lamna*). The root presents a distinct internal protuberance with a single foramen, and moderately divergent, quite asymmetrical branches, a situation that points to being an upper tooth.

The crown seems too high for *A. vulpinus*. On the other hand, it is nearly identical to the *A. superciliosus* corresponding teeth (Antunes & Jonet, 1969-1970, pl. VIII - fig. 41 for a middle Miocene, Serravallian tooth, and fig. 27 for an extant specimen). Minor differences in shape do not seem meaningful at all. The Vale de Zebro specimen is somewhat larger than the comparison material, but this is merely related to age and size; hence its size is compatible with *A. superciliosus*.

The tooth under study can be ascribed to the genus *Alopias*. At the species level, some reserve is justified, because material is limited to a single specimen. We therefore classify it as *Alopias* cf. *superciliosus*.

The rare, if not exceptional, occurrence of a large-eyed thresher shark is interesting. Of course, from an environmental viewpoint, it would suggest rather deep, not coastal, pelagic waters, and that seems very different from the prevailing situations in the Alvalade Basin. However, there is no real contradiction, since isolated individuals eventually go astray into far from optimal environments.

Family Lamnidae Müller & Henle, 1838
Genus *Isurus* Rafinesque, 1810

Isurus desori Sismonda, 1849
(Pl. 3, fig. 2-4)

Material: 4 teeth.

Sites (Number of teeth): Esbarrondadoiro (4).

Description: the teeth ascribed to *I. desori* are characterized by an acutely pointed, rather narrow crown whose profile is slightly sigmoidal. Its cutting edges descend to the root.

The root is thick, with moderately divergent, short lobes and no lateral denticles. Some specimens show a foramen in the middle part of the internal protuberance.

Discussion: although our (maybe juvenile) specimens are smaller than those depicted by Génault (1993, p. 29, fig. 30 e 31), we can tentatively report them to *I. desori*, as all other characteristics are in agreement with this determination.

The characteristics of the crown are identical to those from the teeth ascribed to *I. desori* by Karasawa (1989, figs. 6 and 9, p. 45); the root is also very similar (*idem*, fig. 9; the root has been lost in the other specimens).

Leriche (1910) has described closely similar teeth as *Oxyrhina desori* from the Oligocene in Belgium. The same species has also been referred, by the same author, to the Belgian Miocene, but it seems rare (Leriche, 1926, p. 397).

Isurus hastalis Agassiz, 1843
(Pl. 3, fig. 5-6 and Pl. 4, fig. 1)

Material: 4 teeth.

Sites (Number of teeth): Esbarrondadoiro (2) and Santa Margarida (2).

Description: in the upper teeth, the crown is thick, triangular, and bent towards the commissure; the external surface is slightly convex; the profile is a little sigmoidal. The root is very thick; its stout branches are nearly fused and so less distinct. The internal part of the root is quite flat, and not prominent at all.

In the lower lateral teeth the crown is nearly straight, and slightly bent towards the commissure. The root has two stout branches, and its internal protuberance is nearly indistinct.

In a distal tooth, the crown is small, straight and thin. The root is much more developed than the crown, and its faintly prominent internal protuberance supports two lateral talons.

Discussion: in general, teeth from *I. hastalis* can be easily identified owing to their large size, to the crown's triangular (especially in upper teeth) outline, and because the crown is rather flat.

A very worn specimen has been regarded as an *I. hastalis* mandibular tooth. Even if some of its characteristics are not distinct, it is similar enough to the tooth described by Cappetta (1970, pl. 5, fig. 5 and 8) that our classification seems justified.

Família Otodontidae Glückman, 1964

Género *Carcharocles* Jordan & Hannibal, 1923

Carcharocles megalodon (Agassiz, 1843)
(Pl. 4, fig. 2)

Material: 2 teeth.

Sites (Number of teeth): Vale de Zebro (1) and Santa Margarida (1).

Description: a single tooth fragment, reduced to a part of the crown, has been collected at Vale de Zebro. Another, nearly complete tooth (M. T. Antunes collection) was found at Santa Margarida.

According to Cappetta (1987), the large size of the *C. megalodon* teeth helped their detection and therefore has contributed to the fact that the species has been recognized everywhere: in North America (Eastman, 1904; Fowler, 1911; Leriche, 1942); Europe (Leriche, 1926, 1927; Leriche *et al.*, 1957; Menesini, 1969, 1974); Australia (Chapman & Pritchard, 1904; Chapman & Cudmore, 1924); New Zealand (Keyes, 1972); Japan (Goto, 1972); India (Leriche & Casier, 1954); the West Indies (Casier, 1958); Western Africa and especially in Angola (Darteville & Casier, 1959; Antunes, 1978); Northern Africa (Arambourg, 1927); etc.

Remarks: *C. megalodon* teeth are very rare in comparison with those of other selachians. However, as a top predator it surely had to be scarce (Antunes & Jonet, 1970, p. 144). The data from the Alvalade Basin corroborate this viewpoint.

Conclusions

The order Lamniformes is represented in the uppermost Miocene of the Alvalade basin by the following taxa (Table 1).

As is obvious, only *Carcharias acutissima* is very common, all other species being rare or very rare. No meaningful statistics can be elaborated. The only possible environmental conclusion must therefore rely on *Carcharias acutissima*. The behaviour of the extant, very closely allied *Carcharias taurus* is well-known; it lives in the neritic zone of warm and subtropical regions. The fossil representatives therefore unmistakably point to rather shallow, warm to moderately warm waters, often close by the coast. Furthermore, the ratio *C. acutissima*/the sum of others shows different values between Esbarrondadoiro and the remaining sites (Santa Margarida, Vale de Zebro), whose corresponding values are closer and not very different between themselves. This suggests environmental differences that should be better analysed, taking into account the palaeontological and geologic data as a whole.

The rarity of pelagic forms such as *Alopias*, *Isurus* and *Carcharocles* point to the existence in the concerned area of a rather narrow gulf between lands in uppermost Miocene (Messinian) times, in contrast to the Tortonian, upper Miocene situation in the Lisbon area of open sea. In the Alvalade Basin, Carcharhiniformes largely prevail over Lamniformes (Antunes *et al.*, 1999).

As far as chronology is concerned, the absence of *Carcharodon carcharias* (whose first appearance is in Pliocene and still survives), the progressive character of the *Carcharhinus* teeth, as well as the absolute lack of stenotherm, warm water forms such as *Hemipristis*, corroborate the dating of the Esbarrondadoiro Formation based on small mammals (Antunes & Mein, 1989): it is older than Pliocene and later than Tortonian (and for even stronger reasons, than still earlier Miocene levels), and hence uppermost Miocene, Messinian.

Table 1

Lamniformes from the Alvalade basin (Uppermost Miocene)
Localities: Esb., Esbarrondadoiro; S.M., Santa Margarida; V.Z., Vale de Zebro.

Taxa	Number of teeth (Localities)			Totals
<i>Carcharias acutissima</i>	432 (Esb.)	80 (S.M.)	148 (V.Z.)	660
<i>Carcharias cuspidata</i>	1 (V.Z.)			1
<i>Pseudocarcharias cf. kamoharai</i>	1 (V.Z.)			1
<i>Alopias cf. superciliosus</i>	1 (V.Z.)			1
<i>Isurus desori</i>	4 (Esb.)			4
<i>Isurus hastalis</i>	2 (Esb.)	2 (S.M.)		4
<i>Carcharocles megalodon</i>	1 (S.M.)	1 (V.Z.)		2
Ratio <i>C. acutissima</i>/the sum of others	72 (Esb.)	26.7 (S.M.)	37 (V.Z.)	Σ= 673

References

- Antunes, M. Telles (1970) – Présence de *Alopias superciliosus* (Lowe) dans les mers du Portugal/ Remarques sur les *Alopias* (Selachii) récents et fossiles. *Arquivos do Museu Bocage*, 2ª Série, II(19): 365-378, 2 pl.
- Antunes, M. Telles (1978) - Faunes ichthyologiques du Néogène supérieur d'Angola, leur âge, remarques sur le Pliocène marin en Afrique australe. *Ciências da Terra (UNL)*, Lisboa, 4: 59-90, 3 pl.
- Antunes, M. Telles & Jonet, S. (1970) – Requins de l'Helvétien supérieur et du Tortonien de Lisbonne. *Revista Faculdade Ciências Lisboa*, 2ª série, C, 16(1): 119- 280, 20 pl.
- Antunes, M. Telles; Balbino, A. Cáceres & Cappetta, H.-C. (1999) - A new shark, *Galeorhinus gonçalvesi* (Triakidae, Carcharhiniformes) from the uppermost Miocene of Portugal. *Tertiary Research*, Leiden, 19 (3-4): 105-110.
- Antunes, M. Telles; Balbino, A. Cáceres & Cappetta, H.C. (1999) - Sélaciens du Miocène terminal du bassin d'Alvalade (Portugal). Essai de synthèse. *Ciências da Terra (UNL)*, Lisboa, 13: 115-129.
- Arambourg, C (1927) – Les Poissons fossiles d'Oran. *Matériaux Carte Géologique Algérie*, 1ère série, 6, 298 p., 46 pl.
- Balbino, A. Cáceres (1995) - *Seláceos (Pisces) do Miocénico terminal da Bacia de Alvalade (Portugal)/ Sistemática, Ecologia, Paleoaambientes, comparação com faunas actuais*. Dissertação Doutoramento, Universidade Évora, 200 p., 38 pl.
- Balbino, A. Cáceres & Cappetta, H.-C. (2000) - *Paragaleus antunesi* (Hemigaleidae, Carcharhiniformes) a new shark species from the latest Miocene of Portugal. *Tertiary Research*, Leiden, 20 (1-4): 1-6, 2 pl.
- Cappetta, H.-C. (1970) – Les Sélaciens du Miocène de la région de Montpellier. *Palaeovertebrata*, Mémoire extraordinaire, 139 p., 27 pl.
- Cappetta, H.-C. (1987) - Mesozoic and Cenozoic Elasmobranchii Chondrichthyes II. *Gustav Fischer Verlag*, Stuttgart, 193 p.
- Cappetta, H.-C. & Nolf, D. (1991) - Les Sélaciens du Pliocène inférieur de Le-Puget-sur-Argens (Sud-Est de la France). *Palaeontographica*, Abt. A., Stuttgart, 218: 49-67, Lfg.1-3.
- Cappetta, H.-C. & Ward, D. J. (1977) – A new Eocene shark from the London Clay of Essex. *Paleontology*, London, 20 (1): 195 – 202, pl. 26 – 27.
- Compagno, L. J. V. (1973) - Interrelationships of living elasmobranchs. In P. H. Greenwood; R. S. Miles & C. Patterson eds., Interrelationships of fishes. *Zoological Journal Linnean Society*, Suppl. n°1, 53: 15-61, 5 fig., 2 pl.
- Compagno, L. J. V. (1984) – FAO species catalogue. Vol. 4 Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1 Hexanchiformes to Lamniformes. *FAO Fish. Synop.*, 125, 4 (1): 249 p.; Part 2 Carcharhiniformes, *FAO fish. Synop.*, 125 (2): 251-655.
- Darteville, E. & Casier, E. (1943) – Les Poissons fossiles du Bas-Congo et des regions voisines (Première partie). *Annales Musée Royal Congo Belge*, Tervuren, A, série III, II(1): 1-200, pl. I-XVI.
- Darteville, E. & Casier, E. (1959) – Les Poissons fossiles du Bas-Congo et des regions voisines (Troisième partie). *Annales Musée Royal Congo Belge*, Tervuren, A, série III, II(3): 257-568, pl. XXIII-XXXIX.
- Genault, B. (1993) – Contribution à l' étude des Élasmobranches oligocènes du bassin de Paris/ Découverte de deux Horizons à Élasmobranches dans le Stampien (Sables de Fontainebleau) de la feuille géologique de Chartres. *Cossmanniana*, Paris, 2: 13-36, 70 fig.
- Karasawa, H. (1989) – Late Cenozoic Elasmobranchs from the Hokusiku district, central Japan. *Science Reports Kanazawa University*, 34(1): 34-57.
- Leriche, M. (1910) – Les poissons oligocènes de la Belgique. *Mém. Mus. Roy. Hist. Nat. Belgique*, 20: 229-363, 15 pl. (XIII-XXVII).
- Leriche, M. (1926) – Les poissons néogènes de la Belgique. *Mém. Mus. Roy. Hist. Nat. Belgique*, 32: 365-472, 13 pl. (XXVIII –XLI).

Plate 1

Fig. 1-5 – *Carcharias acutissima* Agassiz, 1844.

Fig. 1 – Parasymphysial tooth, x 4: labial (a) and lingual (b) views, distal profile (c), and mesial profile (d).

Fig. 2 – Parasymphysial tooth, x 4: profile.

Fig. 3 – Anterior (mesial) tooth, x 3: labial (a) and lingual (b) views, distal profile (c).

Fig. 4-5 – Intermediate teeth, x 3. Labial (a) and lingual (b) views.

All specimens from Esbarrondadoiro.

PLATE 1



Plate 2

Fig. 1-5 – *Carcharias acutissima* Agassiz, 1844.

Lateral posterior (distal) teeth.

Fig. 1 – labial (a) and lingual (b) views, x 3.

Fig. 2 – labial (a) and lingual (b) views, x 3.

Fig. 3 – labial (a) and lingual (b) views, x 4.

Fig. 4 – labial (a) and lingual (b) views, x 5.

Fig. 5 – labial (a) and lingual (b) views, x 5.

Fig. 6 – *Carcharias cuspidata* Agassiz, 1843.

Anterior (mesial) tooth, x 2: lingual (a) and labial (b) views.

All specimens from Esbarrondadoiro.

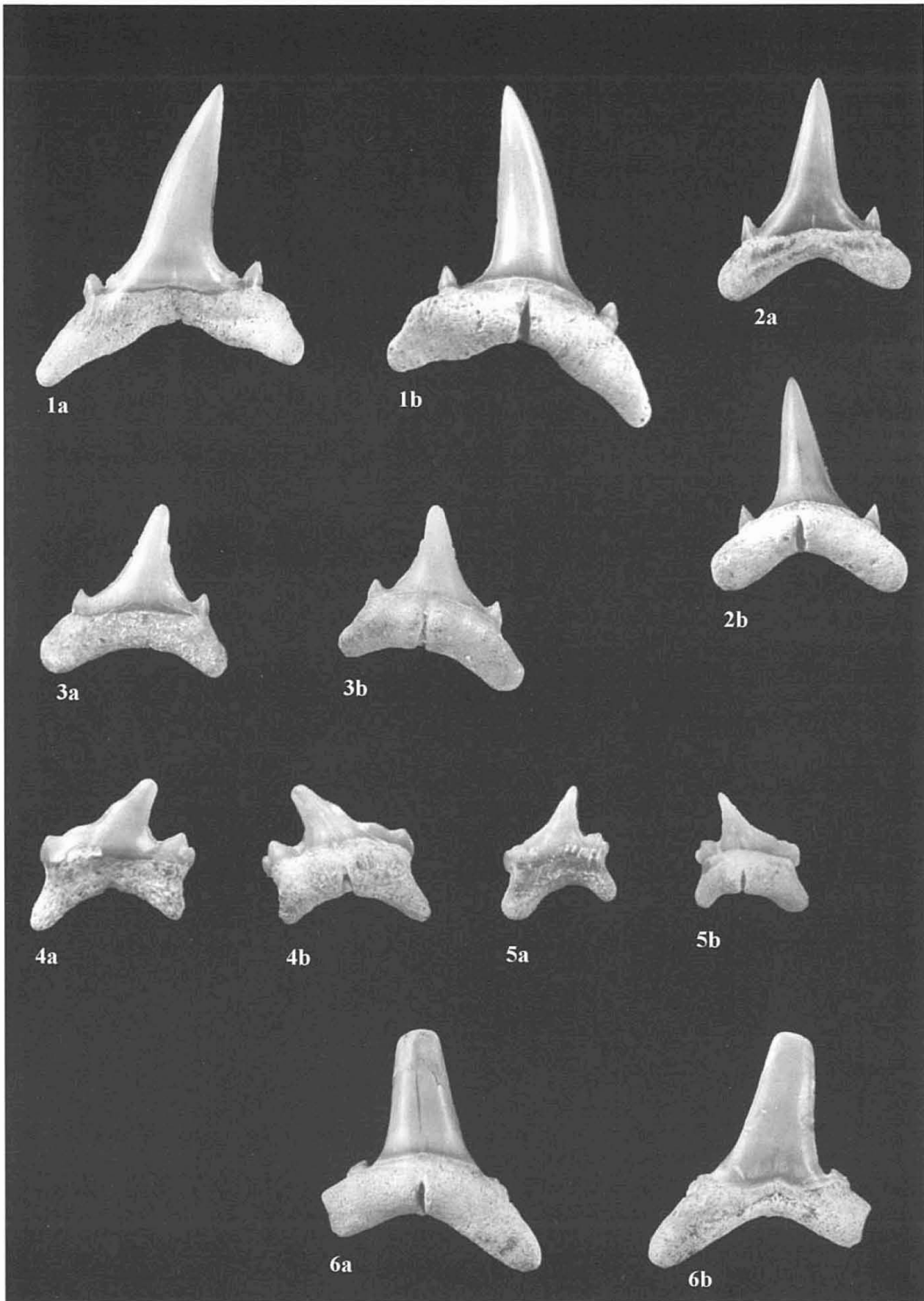


Plate 3

Fig. 1 – *Pseudocarcharias* cf. *kamoharai* (Matsubara, 1936).
Lateral (distal) tooth, x 3: labial (a) and lingual (b) views, profile (c).
Site: Vale de Zebro.

Fig. 2 – *Alopias* cf. *supercilius* (Lowe, 1840).
Anterior (mesial) tooth, x 2: labial (a) and lingual (b) views.
Site: Vale de Zebro.

Fig. 3-4 – *Isurus desori* Sismonda, 1849.
Lateral teeth, x 2.

Fig. 3 – labial (a) and lingual (b) views.

Fig. 4 – labial (a) and lingual (b) views.

Site: Esbarrondadoiro.

Fig. 5-6 – *Isurus hastalis* Agassiz, 1843.
Lateral teeth.

Fig. 5 – labial (a) and lingual (b) views, x 1.5.

Fig. 6 – labial (a) and lingual (b) views, x 2.

Sites: 5, Esbarrondadoiro; 6, Santa Margarida.

PLATE 3

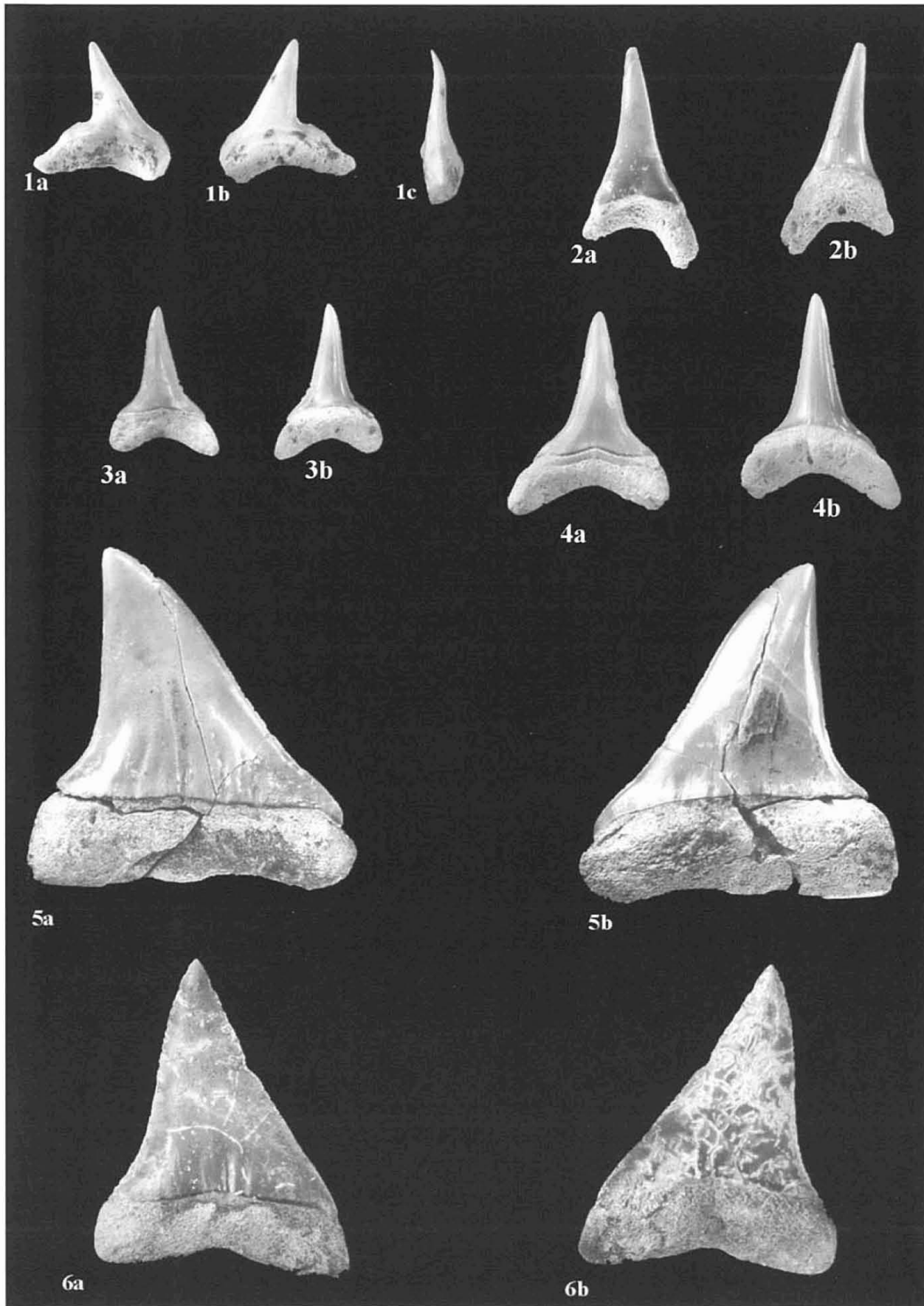


Plate 4

Fig. 1 – *Isurus hastalis* Agassiz, 1843.

Lateral (distal) tooth, x 4: labial (a) and lingual (b) views.

Site: Santa Margarida.

Fig. 2 – *Carcharocles megalodon* (Agassiz, 1843).

Fragment of lateral tooth, x 2.

Site: Vale de Zebro.

PLATE 4

