

## A small fossil fish fauna, rich in *Chlamydoselachus* teeth, from the Late Pliocene of Tuscany (Siena, central Italy)

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Received 17 January 2007; revised version accepted 30 July 2008

A small elasmobranch teeth and teleost otolith assemblage from the Piacenzian-earliest Gelasian of Tuscany (Castelnuovo Berardenga Scalo, Siena province, Italy) is described. The exceptional abundance of teeth belonging to *Chlamydoselachus lawleyi* Davis, 1887 has enabled us to better define and confirm the validity of this doubtful fossil taxon. In agreement with Davis (1887) and Pfeil (1983) this species appears to differ from the living frilled shark *C. anguineus* Garman, 1884 at least by its larger size.

Palaeoecological inferences based on the ecology of *C. anguineus* together with deep water sharks such as *Centrophorus granulosus* (Bloch & Schneider, 1801) and the teleost otolith assemblage mainly characterised by macrourids and myctophids enable us to configure, in the Piacenzian to earliest Gelasian of Tuscany (Siena subbasin of the Siena-Radicofani Basin) an upper bathyal slope palaeo-environment. The occurrence of *Chlamydoselachus* in the Piacenzian-earliest Gelasian of the Mediterranean palaeo-area demonstrates the persistence of an oceanic environment not as profusely developed as during the early Zanclean (*i.e.* lower part of MPL 2 foraminiferal biozone; see Cigala Fulgosi, 1986, 1996).

Viene descritta una fauna a denti di elasmobranchi ed otoliti di teleostei rinvenuta nel Piacenziano-Gelasiano antico della Toscana (Castelnuovo Berardenga Scalo, provincia di Siena, Italia centrale). L'eccezionale abbondanza di denti di *Chlamydoselachus lawleyi* Davis, 1887 ha permesso di meglio definire questo incerto taxon fossile e di confermarne la validità. In accordo con Davis (1887) e Pfeil (1983) questa specie differisce dal vivente squalo dal collare *C. anguineus* Garman, 1884 almeno per la taglia sensibilmente più grande.

Induzioni paleoecologiche basate sull'ecologia di *Chlamydoselachus anguineus* Garman, 1884 e di squali di acque profonde come *Centrophorus granulosus* (Bloch & Schneider, 1801) e sulla associazione fossile ad otoliti di teleostei caratterizzata eminentemente da macruridi e mictofidi permette di configurare nel Piacenziano Gelasiano antico della Toscana (sub-bacino di Siena del Bacino Siena-Radicofani) un paleoambiente epibatiale di scarpata. *Chlamydoselachus* indica inoltre la persistenza nel Piacenziano Gelasiano basale della paleoarea mediterranea di una "oceanizzazione" che tuttavia non appare così intensa come quella dello Zancleano antico (*i.e.* parte inferiore della biozona a foraminiferi MPL 2; Cigala Fulgosi, 1986, 1996).

KEY WORDS: *Chlamydoselachus* fauna, Elasmobranchs, Teleosts, Teeth, Otoliths, Late Pliocene, Tuscany, Central Italy.

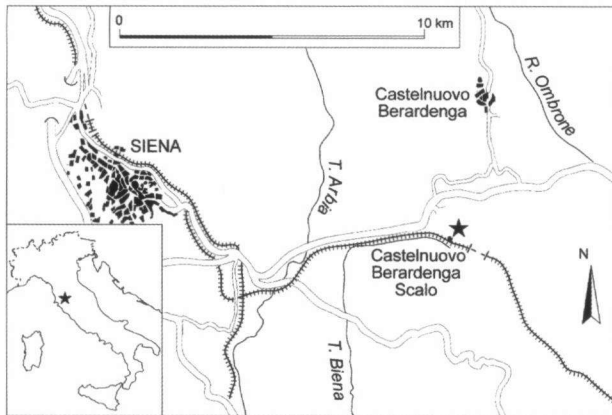
### Introduction

A small elasmobranch tooth and fish otolith fauna unusually rich in teeth of *Chlamydoselachus* is described. The teeth, together with a few hundred otoliths, were surface-collected, in recent years, by S. Casati in an open quarry near the village of Castelnuovo Berardenga Scalo, Asciano (Siena Province) (Figure 1). The quarry exploiting the clays belongs to "Laterizi Arbia SPA" and is close to the NE side of the processing plant. A first attempt to process the surface sediment in search of micro-ichtyodontoliths was unsuccessful. Due to the recent accumulation of transported material on top of the outcropping sediment this operation has not been repeated and at the present time it is

no longer possible to execute additional collecting.

Since the beginning of paleo-ichthyology the Pliocene shark fauna of Tuscany has been discussed by numerous scholars (*e.g.* Lawley, 1875, Principi, 1920). Robert Lawley in particular played an important role, both because of the pioneering and systematic use of the methodology, based on a comparison of fossils with living beings, and because of the intensity with which he focussed his attention on this fauna. An original biographical research about this author has recently been published by Manganelli *et al.* (2006). Many finds reported by Lawley, some of which were exceptional and belonged to his original collection, have unfortunately been lost.

It was Lawley (1876, pl. 1, fig. 1) who, while ignoring their



**Figure 1.** Map showing location of the outcrop with *Chlamydoselachus*, at Castelnuovo Berardenga Scalo, Siena province, Italy.

nature, published the first pictures of a fossil tooth of *Chlamydoselachus*. Garman (1884) described this unusual shark a few years later. The nine teeth Lawley collected, “two perfectly complete, and seven more or less mutilated” (“due perfettamente completi, e sette più o meno mutilati”, Lawley, 1876, p. 87), came from Orciano Pisano (Pisa province, Italy), a village at approximately 80 km from Castelnuovo Berardenga Scalo. It is also important to bear in mind that at that time the geographical references relating to the locations of the finds were not as precise as they are today and that very often other people collected and obtained these materials. According to shark teeth amateurs and collectors, the Pliocene-Pleistocene landscape around Orciano is now developed, intensively cultivated and/or urbanized. It is therefore uncertain whether we can interpret Lawley’s original finds stratigraphically (Landini, 1977). They could be generally indicated as Zanclean-Piacenzian (“Lower-Middle Pliocene”, according to Landini *et al.*, 2005 and Bianucci & Landini, 2005). Other than Lawley’s pictures, the Pliocene species *Chlamydoselachus lawleyi*, until now represented by fragments from other Mediterranean areas only (Pfeil, 1983), can be tested using this new exceptionally abundant and well-preserved material.

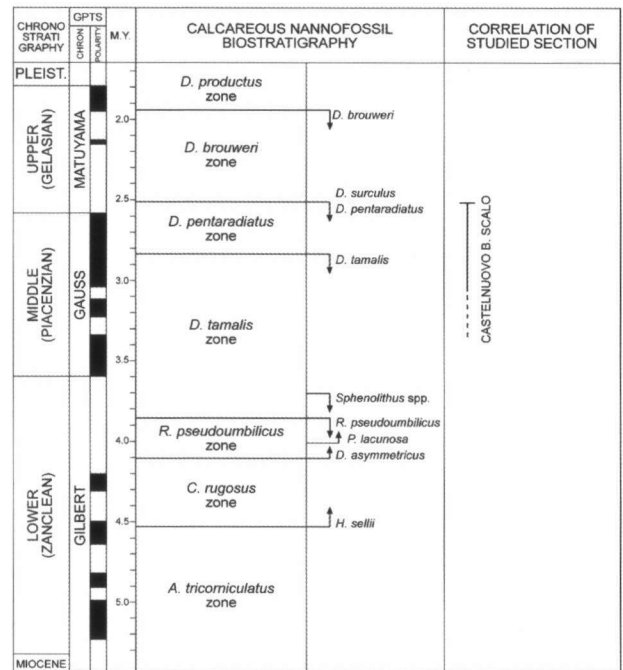
**Geological setting**

The small outcrop where the teeth and otoliths were collected is composed of muddy and silty marls comprised within the subbasin of Siena (SB), which, together with the Radicofani subbasin (RB), forms the Siena-Radicofani Basin (SRB) (Bonini, 2002, fig. 2). This basin extends in a roughly NNW-SSE direction, and the northern part (particularly the SB), is bounded by ridges mostly uplifted by W to WSW dipping thrust faults. The sedimentary succession and stratigraphy of the basin was reported by the same author who divided the succession into four main angular unconformities-bounded stratigraphic units (Bonini, 2002, fig. 4). Previously, Augugliaro (1999-2000, unpublished

thesis), using the occurrence of the planktonic foraminifer *Globorotalia aemiliana* Colalongo & Sartoni, 1967, attributed the marls of the Castelnuovo Berardenga Scalo quarry to the “Middle Pliocene”.

**Nannofossil biostratigraphy**

*Material and methods* — A semiquantitative calcareous nannofossil analysis has been done by Davide Persico. Six samples were recovered along ten topographic meters of the slope in the outcrop. The stratification on the surface of the small fossiliferous area appears indistinct. Nannofossil preservation is good and the sediment sampling is characterized by sand and clay components together with the biostratigraphic markers.



**Figure 2.** Chronostratigraphic scale and geomagnetic polarity time scale from Lourens *et al.* (1996, 2004); calcareous nannofossil biostratigraphy from Rio *et al.* (1990).

The adopted chronostratigraphic scheme (Figure 2) has been composed by the magnetostratigraphic scale of Lourens *et al.* (2004), correlated with the biostratigraphy of Rio *et al.* (1990). Calcareous nannofossils were examined using standard light microscope techniques, under crossed polarizers, transmitted light, and phase contrast light at 1250x magnification. The species considered have been distributed in five levels of abundance (Table 1).

*Results* — The recognized calcareous nannofossil assemblage characterizes a biostratigraphic interval within the *Discoaster tamalis*- and *Discoaster pentaradiatus*-zones (Figure 2).

Species	Castelnuovo B.S.6	Castelnuovo B.S.5	Castelnuovo B.S.4	Castelnuovo B.S.3	Castelnuovo B.S.2	Castelnuovo B.S.1
<i>Amaurolithus delicatus</i>		R				
<i>Braarudosphaera bigelowi</i>	F		F	R		
<i>Calcidiscus leptoporus</i>	C	C	C		C	C
<i>Coccolithus pelagicus</i>	R		R			F
<i>Discoaster asymmetricus</i>	R	R	R	R	R	
<i>Discoaster brouweri</i>	C	A	A	R	R	C
<i>Discoaster surculus</i>	C	C				R
<i>Discoaster pentaradiatus</i>	R	R	R	R	R	
<i>Discoaster tamalis</i>		R	R			
<i>Helicosphaera kamptneri/carteri</i>				R	R	
<i>Helicosphaera sellii</i>			C		R	
<i>Laternites minutus</i>				R		
<i>Pontosphaera multipora</i>				F		
<i>Pontosphaera</i> spp.						R
<i>Pseudoemiliania lacunosa</i>		C	C	C	C	C
<i>Reticulofenestra pseudoumbilica</i> (>7 µm)				R		
<i>Reticulofenestra</i> sp. (<4 µm)	C	V	V	V	A	A
<i>Sphenolithus abies</i>				R		
<i>Umbilicosphaera</i> spp.					R	

**Table 1.** Nannofossil range chart.

A = abundant (1-10 specimens per field of view),  
 C = common (1 specimen per 2-10 fields of view),  
 F = few (1 specimen per 11-100 fields of view),  
 R = rare (1 specimen per 101-1000 fields of view),  
 V = very abundant (11-100 specimens per field of view).

Generally, discoasters do not present taxonomic problems although their usefulness in the Mediterranean has been questioned because of their alleged low abundance (Rio *et al.*, 1990). However, the occurrence of a *Discoaster* assemblage with complete specimens in all the analyzed samples is an index of good preservation and a reliable assemblage.

The presence of three important markers as *D. pentaradiatus*, *D. surculus* and *D. tamalis* allow to correlate the upper part of the studied section with the interval defined at the top by the last occurrence (LO) of *D. surculus* and *D. pentaradiatus* (2.5 Ma, Figure 2). The absence of sphenoliths and the presence of *D. tamalis* allow the correlation of the section with the *D. tamalis*-Zone above the last occurrence of *Sphenolithus* spp. (3.7 Ma, Figure 2). The rare occurrence of *D. tamalis* in two of the lower samples (*i.e.* 4 and 5; Table 1) could indicate the extinction event of this species (2.8 Ma). On this basis the sampled section is attributed to the middle-late part of the Piacenzian/earliest Gelasian stage (Late Pliocene, Figure 2).

## Systematic Palaeontology

Given that the fish fauna accompanying *Chlamydoselachus* does not present particular taxonomic novelties, and that the taxa represented are nearly always Neogene chronospecies and/or lineages that can be related to living species, we shall only describe their essential characters. The synonymies, which are reduced to a minimum, are partly discussed in more or less recent works (*e.g.* Landini, 1977; Compagno, 1984, 2001; Pfeil, 1983; Ward & Galea Bonavia, 2001; Antunes & Cappetta, 2002). The dental terminology adopted is largely the one used by authors (*e.g.* Applegate, 1965; Welton, 1979; Cappetta, 1987; Compagno, 1988).

All the fossil material (S. Casati & M. Zanaga Tuscan Elasmobranch Collection, Scandicci: CZ-TES 2 and S. Casati & M. Zanaga Tuscan Otolith Collection, Scandicci: CZ-TOS 1) is deposited in the collections of the "Centro civico Ofelia Mangini, Scandicci (permanent exhibition thanks to the "Gruppo AVIS Mineralogia Paleontologia Scandicci"). Address: Piazza Vittorio Veneto n.1, 50010 Badia a Settimo, Scandicci, Firenze, Italy.

### Class Chondrichthyes

#### Subclass Elasmobranchii

#### Cohort Euselachii

#### Superorder Squalomorphii Compagno, 1973

#### Order Hexanchiformes Buen, 1926

#### Family Chlamydoselachidae Garman, 1884

#### Genus *Chlamydoselachus* Garman, 1884

### *Chlamydoselachus lawleyi* Davis, 1887

Figures 5/1-7, 6/1-6, 7/1, 2

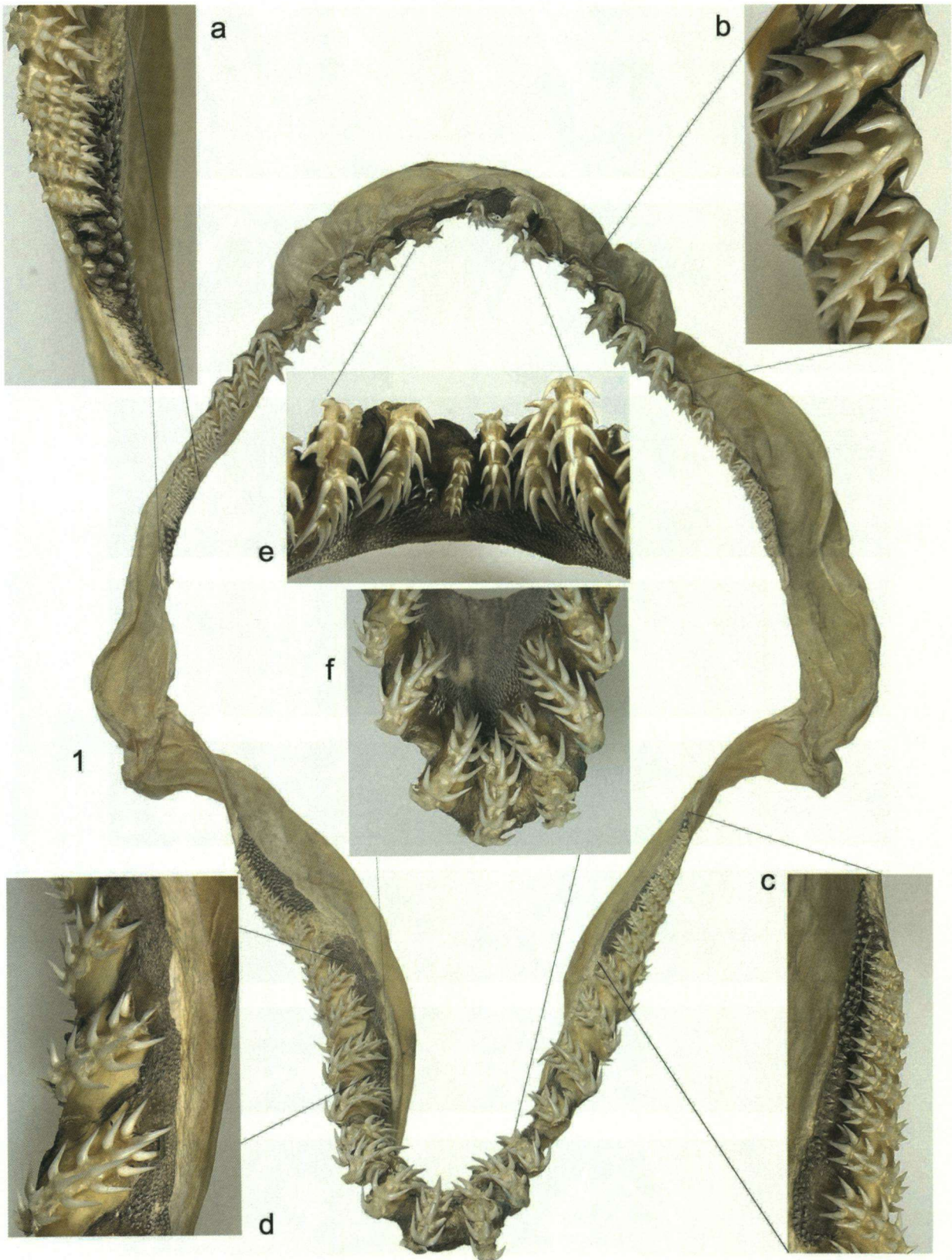
- 1876 *Incertae sedis* Lawley, p. 87, pl. 1, figs 1, 1a-c.  
 1983 *C. lawleyi* Davis – Pfeil, p. 72, pl. 35, figs 1-3.  
 1986 *C. cf. lawleyi* Davis – Cigala Fulgosi, p. 134.

*Material examined* — A hundred teeth, some of which are complete and/or lack only the cusplets, all other teeth are fragmentary (CZ-TES 2, 1-98).

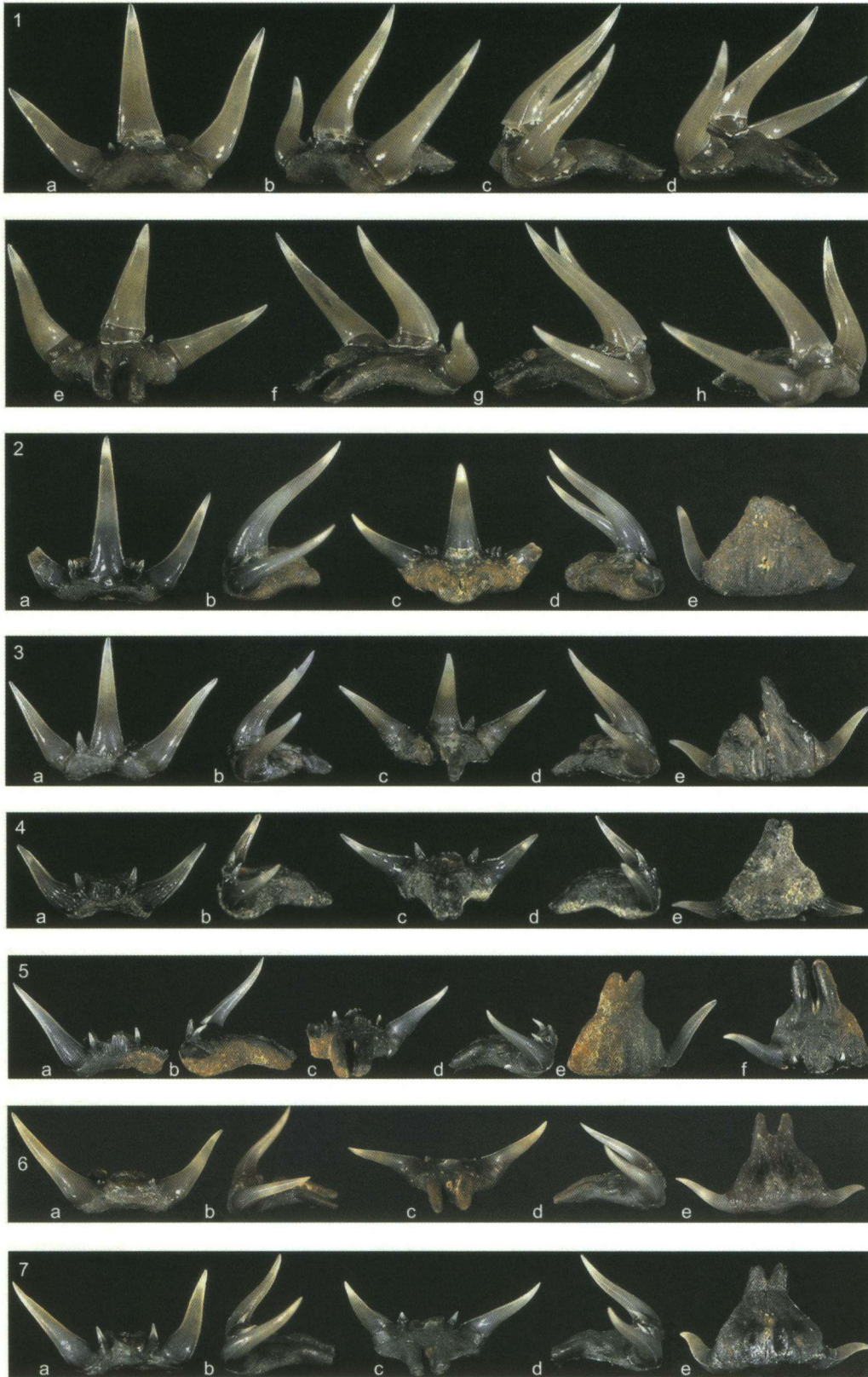
*Remarks* — The dental morphology of *Chlamydoselachus lawleyi*, which is herein studied for the first time on the basis of this copious material, matches that of the living *C. anguineus* (Gudger & Smith, 1933; Goto, 1972, 1977, 1987, 2004; Goto & Hashimoto, 1976; Pfeil 1983; Welton, 1979). We were not able to study the teeth of *C. sp. A*, an undescribed living species from Namibia (Ebert, 1990, 2003; Compagno *et al.*, 2005). This latter species, if valid, might not be easily distinguishable from *C. anguineus*, at least in consideration of its exterior features, and it would differ only on the basis of some anatomic features such as the internal structure of the chondrocranium, the vertebra, and the pectoral-fin skeletal morphology, *etc.*



**Figure 3.** 1-4. Dried head of *Chlamydoselachus anguineus* Garman, 1884. Specimen fished off Sesimbra (Lisboa, Portugal) (F. Cigala Fulgosi private collection 1, 951). 1: lateral view, x 1.1; 2: frontal view, x 0.6; 3: dorsal view, x 0.56.; 4: ventral view, x 0.62.



**Figure 4.** Jaw of *Chlamydoselachus anguineus* Garman, 1884. Female, TL 1768 mm, off Kahbara, Suruga Bay (Japan); fishing gear bottom gill nets, depth 150-180 m, 2 May 1985 (Dr. K. Yano) (F. Cigala Fulgosi private collection 1, 120), x 1; a: upper jaw (latero-posterior); b: upper jaw (antero-lateral); c: lower jaw (commissural-latero-posterior); d: lower jaw (lateral); e: upper jaw (symphyisial, anterior); f: lower jaw (symphyisial, anterior).



**Figure 5.** 1-7. *Chlamydoselachus lawleyi* Davis, 1887; 1: antero-lateral tooth (CZ-TES 2, 1); a: labial; b, d, f, h: oblique; c, g: lateral; e: lingual view, x 4.73; 2: antero-lateral tooth (CZ-TES 2, 2); a: labial; b, d: lateral; c: lingual; e: basal view, x 4.6; 3: antero-lateral tooth (CZ-TES 2, 3); a: labial; b, d: lateral; c: lingual; e: basal view, x 3.95; 4: latero-posterior tooth (CZ-TES 2, 4); a: labial; b, d: lateral; c: lingual; e: basal view, x 5.7; 5: antero-lateral tooth (CZ-TES 2, 5); a: labial; b, d: lateral; c: lingual; e: basal; f: occlusal view, x 4.2; 6: antero-lateral tooth (CZ-TES 2, 6); a: labial; b, d: lateral; c: lingual; e: occlusal view, x 4; 7: antero-lateral tooth (CZ-TES 2); a: labial; b, d: lateral; c: lingual; e: basal view, x 4.6.

As Davis (1887) first pointed out on the basis of the only tooth illustrated by Lawley, and confirmed by Pfeil (1983) on the basis of fragments and/or isolated cusps, the only difference we can perceive and/or define relates to the size of the teeth that, in the fossil species are nearly always larger. The majority of teeth found are actually twice (or one and a half times) the size of those of an adult female specimen from Japan measuring 1768 mm in length (coll. F. Cigala Fulgosi, 1 n. 120, Figure 4). The largest fossil tooth is an antero-lateral tooth (Figure 7/1) with extremely divergent mesial and distal cusps (tooth height along the median cusp axis including the base of the root = 9 mm; length of the median cusp from the apex to the enameloid base = 8 mm; maximum mesio-distal width of the root = 5.8 mm; maximum width of the tooth between the extremities of the mesial and distal cusps = 13.4 mm; median cusp angle = 40°).

The dental morphology and morphometrics of living *C. anguineus* were thoroughly examined by Welton (1979) and Pfeil (1983) and we shall therefore limit ourselves to just a few observations. When referring to isolated fossil teeth in particular, Welton found it impossible to assign these to either the upper or the lower jaw and to define with any certainty the position along the dental series. The fossil teeth regularly have secondary cusplets more or less as high as the living ones; in one specimen, which as a result is considered anomalous, there are three (Figure 5/2). The teeth of *C. lawleyi* regularly have relatively sharp and sigmoid cusps (confirming the accuracy of Lawley's illustration). The same characteristic can be observed in the dried head of a living specimen from Portugal whose sex is indeterminate (Figure 3, coll. F. Cigala Fulgosi, 1 n. 951), while in the jaw of the female specimen from Japan mentioned above (Figure 4), the cusps are slightly more robust and less sigmoid. It is likely that this resemblance between the fossils (in which this characteristic is constant), and the Portuguese specimen, cannot be ascribed to a gynandric heterodonty but to the origin from geographically close (even if chronologically distant) regions.

The rare frilled sharks have a circumglobal deep water distribution even though they are captured only sporadically and in very localised areas. These essentially demersal sharks seem to prefer the cold waters of deep and upwelling regions. This is confirmed by the frequent catches in the Suruga Bay, Japan in shallow waters (50-500), adjacent to deep regions (Kubota *et al.*, 1991). Their nocturnal ascent in the water column, almost to the surface, seems related to feeding. The diet of the frilled sharks seems to include cephalopods, other sharks and small teleosts which they seem to swallow in the same manner as snakes.

Family Hexanchidae Gray, 1851  
Genus *Hexanchus* Rafinesque, 1810

***Hexanchus griseus* (Bonnaterre, 1788)**  
Figures 7/6, 7

- 1875 *Notidanus primigenius* Agassiz – Lawley, p. 20, pl. 1, figs 1-5.
- 1875 *Notidanus gigas* Sismonda – Lawley, p. 23, pl. 1, figs 6, 6a.
- 1875 *Notidanus recurvus* Agassiz – Lawley, p. 24, pl. 2, figs 1, 1a, b.
- 1875 *Notidanus targionii* Lawley, p. 27, pl. 2, figs 3, 3a, b.
- 1875 *Notidanus meneghinii* Lawley, p. 28, pl. 2, figs 3, 3a, b, 4, 4a-c.
- 1875 *Notidanus d'anconae* Lawley, p. 29, pl. 3, figs 1, 1a, 2, 2a.
- 1875 *Notidanus problematicus* Lawley, p. 31, pl. 3, figs 3, 3a, 4, 4a.
- 1875 *Notidanus anomale* Lawley, p. 32, pl. 3, figs 5, 5a, b, 6, 6a.
- 1909 *Notidanus griseus* (Bonnaterre) – de Stefano, p. 585, pl. 18, figs 3-10.
- 1912 *Notidanus griseus* (Bonnaterre) – de Stefano, p. 54, pl. 2, fig. 30.
- 1977 *Hexanchus griseus* (Bonnaterre) – Landini, p. 96, pl. 1, figs 1-6, 8-9.
- 1996 *Hexanchus griseus* (Bonnaterre) – Mané *et al.*, p. 26, pl. 2, figs 6-7.
- 2001 *Hexanchus* sp. – Purdy *et al.*, p. 84, fig. 5.

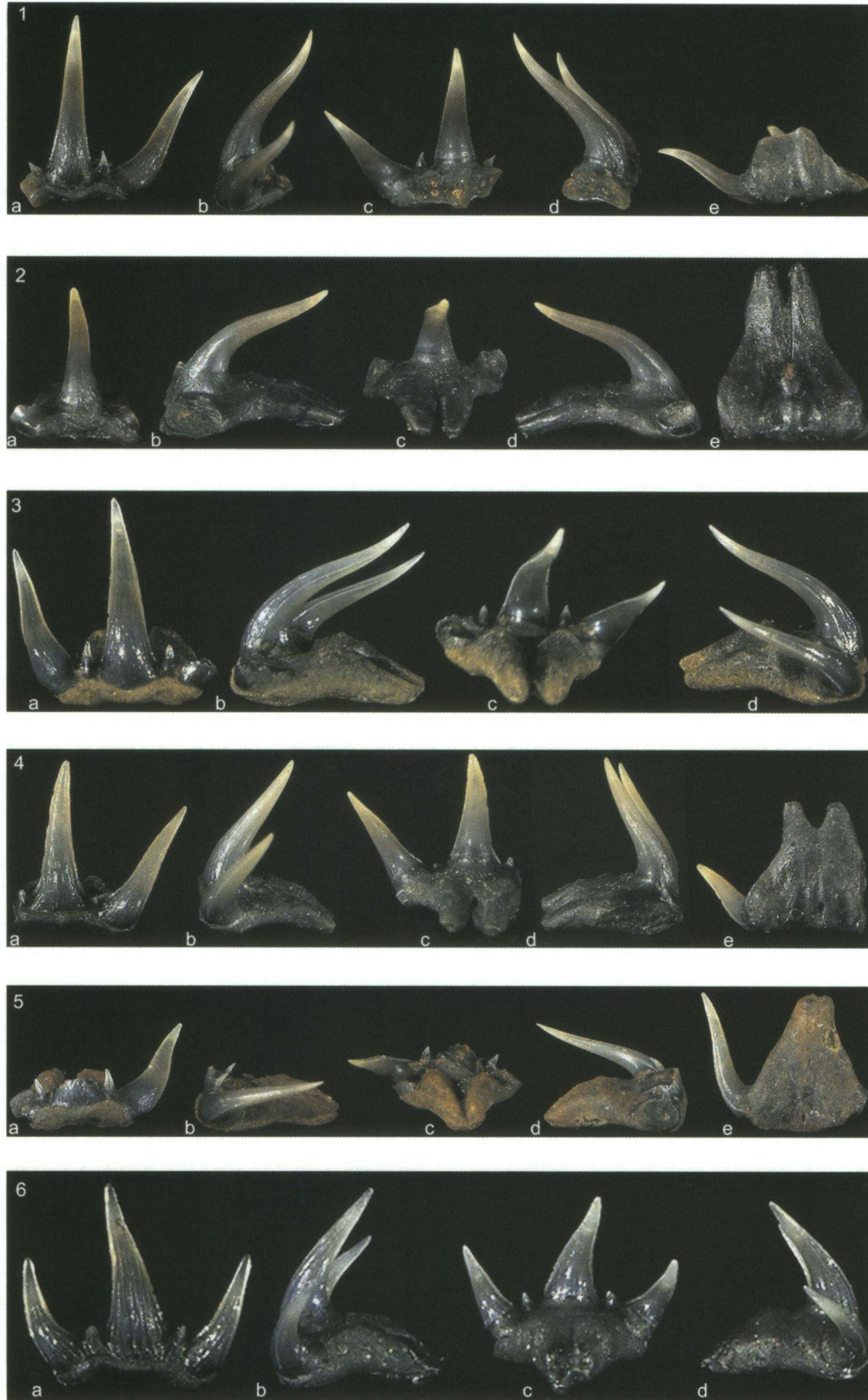
**Material examined** — Three teeth (CZ-TES 2, n. 121-123).

**Remarks** — Undoubtedly, the three teeth that were found belong to *Hexanchus griseus*, a species whose dentition, as various palaeontologists have observed, presents not only ontogenetic and gynandric heterodonty (Purdy *et al.*, 2001), but also a wide individual variability. One of the teeth (Figure 7/6), which appears rather short even though lacking the distal extremity, would appear to be the upper left eighth tooth of the symphysis. The other two, one of which is shown here (Figure 7/7), are typical lower jaw antero-lateral teeth; the illustrated tooth, relatively short and high, is probably the first of the symphysis. Landini (1977, pl. 12, figs 1-6, 8-9) illustrated several teeth from the Lawley collection.

*Hexanchus griseus* is a large-sized species linked to the bottom, and generally inhabiting both deep waters (Tortonese, 1956) (upper slopes) and fairly deep waters (continental shelf to insular shelf). It appears that, at night, when chasing its prey, this shark can reach the higher mass of water, swimming even up to the surface. Furthermore, it may be possible to find young specimens “close inshore” in shallow waters (Compagno, 1984, p. 20). This species seems to have migratory habits (Desbrosses, 1938) and in winter seems to come closer to the Sicilian coastline, reaching a depth of 300 metres (Arcidiacono, 1931).

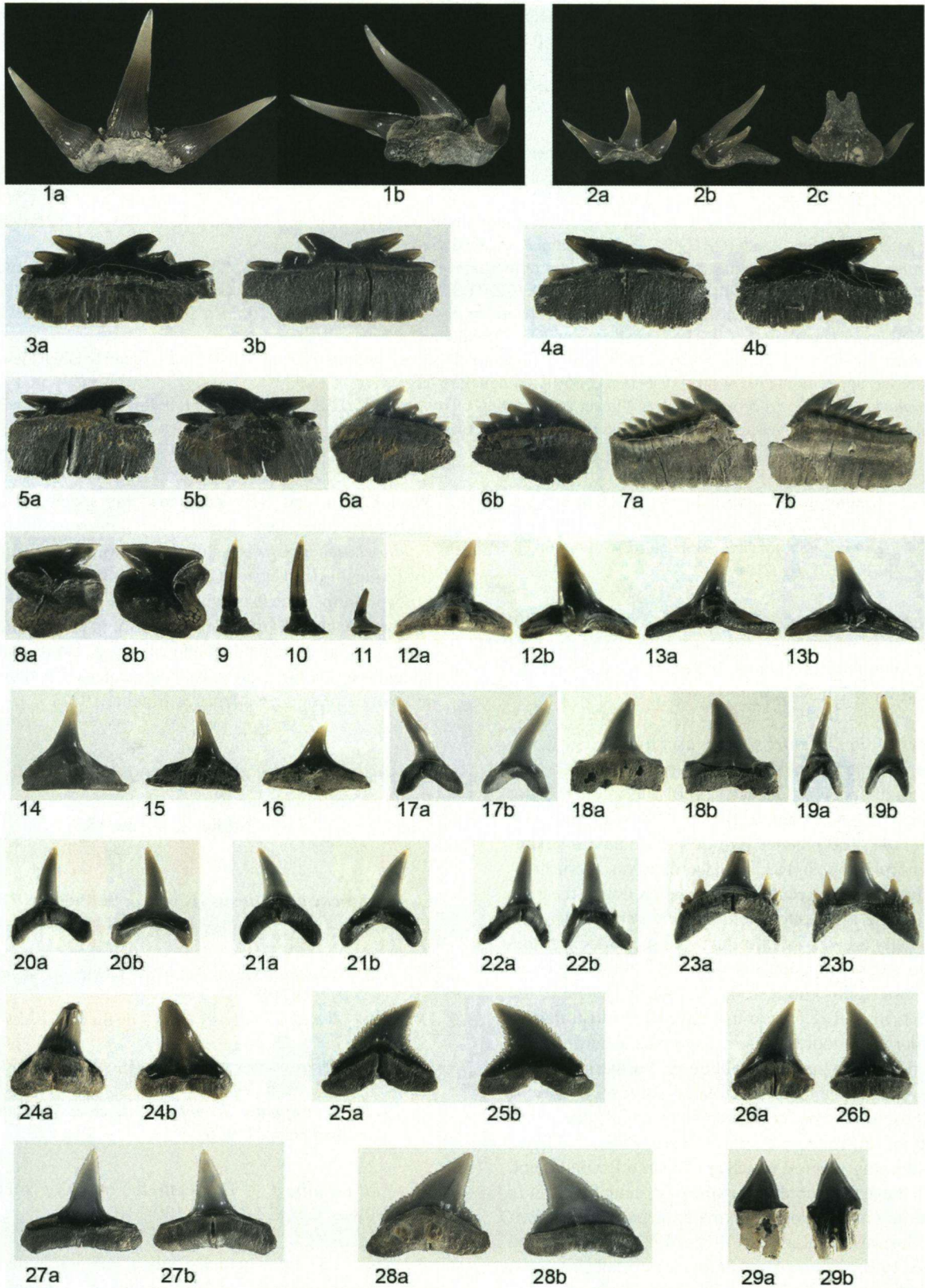
Order Echinorhiniformes Buen, 1926  
Family Echinorhinidae Gill, 1862  
Genus *Echinorhinus* Blainville, 1816

***Echinorhinus richiardi* Lawley, 1876**  
Figures 7/3-5



**Figure 6.** 1-6. *Chlamydoselachus lawleyi* Davis, 1887; 1: antero-lateral tooth (CZ-TES 2, 8); a, labial; b,d, lateral; c, lingual; e, basal view, x 4.5; 2: antero-lateral tooth (CZ-TES 2, 9); a: labial; b, d: lateral; c: lingual; e: basal view, x 5; 3: antero-lateral tooth (CZ-TES 2, 10); a: labial; b, d: lateral; c: lingual view, x 7.3; 4: antero-lateral tooth (CZ-TES 2, 11); a: labial; b, d: lateral; c: lingual; e: basal view, x 5.5; 5: antero-lateral tooth (CZ-TES 2, 12); a: labial; b, d: lateral; c: lingual; e: basal view, x 5.1; 6: posterior tooth (CZ-TES 2, 13); a: labial; b, d: lateral; c: lingual view, x 10.9.





**Figure 7.**

1-2. *Chlamydoselachus lawleyi* Davis, 1887; 1: very large antero-lateral tooth (CZ-TES 2, 14); a: labial; b: lingual-oblique view, x 3.45; 2: aberrant antero-lateral tooth (CZ-TES 2, 15); a: labial; b: lateral; c: basal view, x 2.6.  
3-5. *Echinorhinus richiardi* Lawley, 1876; 3: antero-lateral tooth (CZ-TES 2, 124); a: labial; b: lingual view, x 2.2; 4: antero-lateral tooth (CZ-TES 2, 125); a: lingual; b: labial view, x 2.8; 5: antero-lateral tooth (CZ-TES 2, 126); a: lingual; b: labial view, x 1.8.  
6-7. *Hexanchus griseus* Rafinesque, 1810; 6: left upper lateral tooth (probably, the eighth from the symphysis) (CZ-TES 2, 121); a: lingual; b: labial view, x 1.13; 7: right lower antero-lateral tooth (probably, the first) (CZ-TES 2, 122); a: labial; b: lingual view, x 0.87.

8. *Centrophorus* cf. *granulosus* (Bloch & Schneider, 1801); right lower lateral tooth (CZ-TES 2, 130); a: lingual; b: labial view, x 4.2.
- 9-11. *Pristiophorus* sp., rostral spines or rostral teeth; 9: (CZ-TES 2, 312), x 1.7; 10: (CZ-TES 2, 313), x 1.6; 11: (CZ-TES 2, 314), x 1.77.
- 12-16. *Squatina* sp., antero-lateral teeth; 12: (CZ-TES 2, 326); a: lingual; b: labial view, x 1.88; 13: (CZ-TES 2, 327); a: lingual; b: labial view, x 2.47; 14: (CZ-TES 2, 328), lingual view, x 2.74; 15: (CZ-TES 2, 329); lingual view, x 2.8; 16: (CZ-TES 2, 330); labial view, x 2.7.
- 17-19. *Isurus oxyrinchus* Rafinesque, 1810; 17: right upper anterior tooth (probably the first) (CZ-TES 2, 342); a: lingual; b: labial view, x 1.16; 18: left lower lateral tooth (CZ-TES 2, 343); a: lingual; b: labial view, x 0.87; 19: right lower anterior tooth (probably the first) (CZ-TES 2, 344); a: lingual; b: labial view, x 1.2.
- 20-21. *Alopias superciliosus* (Lowe, 1840); 20: right lower anterior tooth (CZ-TES 2, 339); a: lingual; b: labial view, x 1.2 21: right upper anterior or lateral tooth (CZ-TES 2, 340); a: lingual; b: labial view, x 1.7.
22. *Carcharias taurus* Rafinesque, 1810; left upper anterior tooth (probably the third) (CZ-TES 2, 335); a: lingual; b: labial view, x 1.
23. *Odontaspis ferox* (Risso, 1810); left upper lateral tooth (CZ-TES 2, 337); a: lingual; b: labial view, x 1.3.
- 24-25. *Prionace glauca* (Linnaeus, 1758); 24: right lower lateral tooth (4th or 5th) (CZ-TES 2, 353); a: lingual; b: labial view, x 1.83; 25: left upper lateral tooth (CZ-TES 2, 354); a: lingual; b: labial view, x 2.
- 26, 28. *Carcharhinus* cf. *plumbeus* (Nardo, 1827); 26: left upper tooth (second or third) (CZ-TES 2, 349); a: lingual; b: labial view, x 1.2; 28: left upper tooth (7th or 8th) (CZ-TES 2, 350); a: lingual; b: labial view, x 1.79.
27. *Carcharhinus* cf. *perezi* (Poey, 1876); left lower lateral tooth (6th or 7th) (CZ-TES 2, 352); a: labial; b: lingual view, x 1.68.
29. *Dalatias licha* (Bonnaterre, 1788); lower antero-lateral tooth (CZ-TES 2, 311); a: lingual; b: labial view, x 1.9.

- 1876 *Echinorhinus richiardii* Lawley, p. 41, pl. 1, figs 8, 8 a-b, pl. 2, figs 6, 6 a-d.
- 1977 *Echinorhinus brucus* (Bonnaterre) – Landini, p. 120, pl. 5, fig. 2 a-b.

**Material examined** — Five more or less complete teeth, the largest of which has a low and sub-rectangular root 1.6 cm long. All the other teeth are approximately 1 cm long, CZ-TES 2, 124-129.

**Remarks** — *Echinorhinus* teeth, usually rare, are fairly well-represented in the studied material. As described by various authors (e.g. Garrick, 1960; Bass *et al.*, 1976; Welton, 1979; Cadenat & Blache, 1981; Pfeil, 1983; Purdy *et al.*, 2001) the teeth of this genus have a hexanchoid morphology and an anaulacorhizic vascularization. Apart from the marked ontogenetic heterodonty (the teeth of the young are monocuspidate), the various types of heterodonty are very feeble. As usual in sharks, it is difficult to clearly separate fossil forms from living ones. Purdy *et al.* (2001) noticed the variability typical of the few dentitions of *E. brucus* that have been illustrated, in particular in the more or less convex mesial cutting edge of the main cusp and in its obliquity. Furthermore, it is not easy to distinguish the isolated teeth of *E. brucus* from those of *E. cookei* Pietschmann, 1928, due to the scarcity of illustrated material (see also Pfeil, 1983). The two living species, which are apparently similar and likely to have been confused in the past, actually differ in the size and morphology of skin denticles. The few denticles illustrated by Lawley (1876, pl. 2, figs 6c, d) and assigned to *E. richiardii* are similar, or even the same, as those belonging to *E. brucus*. Pliocene specimens seem to differ very little from the latter species, the only difference being the larger size of the mesial cusplet close to the main cusp. Clearly the problem is still open and *E. richiardii* can be considered a species inquirenda (Welton, 1979), in the absence of more adequate comparative material. If we consider the geographic distribution of *E. brucus* (mainly East Atlantic and Mediterranean, but also

West Pacific and New Zealand), this species is most probably a direct descendent of *E. richiardii*. *Echinorhinus brucus* is a sluggish bottom shark, primarily living in deep water (Compagno, 1984). Tortonese (1956) claims that it is widespread in the Atlantic between 400 and 900 m and usually rare in the Mediterranean. It is locally abundant and captured also in shallow water along the Senegal coast (6 specimens fished by line in a single pirogue, Cadenat & Blache, 1981).

Order Squaliformes Goodrich, 1909  
Family Centrophoridae Bleeker, 1859  
Genus *Centrophorus* Müller & Henle, 1837

***Centrophorus granulosus* (Bloch & Schneider, 1801)**  
Figure 7/8

- 1876 *Acanthias major* Agassiz – Lawley, p. 40, pl. 1, figs 19, 19b.
- 1909 *Acanthias vulgaris* Risso – de Stefano, p. 594, p. 1, figs 23, 24.
- 1972 *Centrophorus granulosus* (Bloch & Schneider) – Ledoux, p. 145, figs 5, 6.
- 1977 *Centrophorus granulosus* (Bloch & Schneider) – Landini, p. 119, fig. 4.

**Material examined** — 180 teeth, the majority from the lower jaw, CZ-TES 2, 130-310.

**Remarks** — There is actually only a very subtle distinction between the teeth of Mediterranean *Centrophorus granulosus* (Bloch & Schneider, 1801) and other *Centrophorus* species (i.e. *C. squamosus* (Bonnaterre, 1788), *C. lusitanicus* Bocage & Capello, 1864, and *C. niaukang* Teng, 1959) living in the Atlantic more or less close to Gibraltar; an identification at least has to be based on several teeth. Ledoux (1970) already dealt with various types of heterodonty in *C. granulosus* (Bloch & Schnei-

der, 1801) and *C. squamosus* (Bonnaterre, 1788), considering *C. lusitanicus* Bocage & Capello, 1864 a form or subspecies of *C. granulatus* and omitting the large oceanic species *C. niaukang* Teng, 1959. On the basis of teeth and skin denticles Cigala Fulgosi (not illustrated, 1986, 1996) recognised the oceanic deep water species *C. squamosus* in the early Zanclean (lower part of the MPL2 biozone) of the Mediterranean palaeo-area. An analysis of approximately fifty jaws of *C. granulatus* (coll. F.C.F., from Sicily channel) suggests some variation in the shape of the root edge and in cusp serration, which appears here to be more or less marked, but usually finer in *C. squamosus* (Ledoux, 1970). Furthermore, the teeth are rather small and of the same size as those found in most adult specimens from the Mediterranean (approximately 0.90-1 m TL, Cigala Fulgosi, pers. observ. of hundreds of specimens trawled off Sicily). In the Atlantic (Madeira, Senegal) sexual maturity is reached at a larger size (1300 mm TL) (Cadenat & Blache, 1981) and we presume that the maximum size reaches at least one metre and a half (Compagno, 1984). Like other species of this genus, *C. granulatus* often frequents continental slopes (upper slopes, 400-800 m sea depth) and has, as an upper limit, the marginal shelf (100- 200 m sea depth).

Family Dalatiidae Gray, 1851

Genus *Dalatias* Rafinesque, 1810

***Dalatias licha* (Bonnaterre, 1788)**

Figure 7/29

- 1876 *Scymnus majori* Lawley, p. 38, pl.1, figs 17, 17a, 17b.
- 1876 *Centrina bassanii* Lawley, p. 39, pl. 1, figs 18, 18a-e.
- 1909 *Scymnus lichia* (Cuvier) – de Stefano, p. 591, pl. 18, figs 16, 17.
- 1977 *Scymnorhinus licha* (Bonnaterre) – Landini, p. 120, pl. 1, figs 20-24.
- 1986 *Dalatias licha* (Bonnaterre) – Cigala Fulgosi, p. 135, 137, fig. 2.

*Material examined* — 1 tooth (CZ-TES 2, 311).

*Remarks* — Lower jaw tooth from a specimen of about 1 metre in length. Having collected “certainly a thousand” (“certamente un migliaio, Lawley (1876, p. 38 “Orciano, Volterra, Siena”) noted that the teeth of this species, rare in the deposit of Castelnuovo Berardenga Scalo, are very common or frequent in the Pliocene of Tuscany.

As summarised by Bigelow & Schroeder (1948), Compagno (1984) and Compagno *et al.* (2005), *Dalatias licha* is a widely ranging species locally abundant but not schooling.

It is present in warm-temperate and tropical waters up to the North Sea, Scotland and the Irish Atlantic slope, South Africa, Australia and Japan. This species prefers

waters more than 200 metres sea depth and it was captured up to 1800 metres depth. Tortonese (1956) observed that it is very rare in the Adriatic but present as a fossil in the Pliocene of the Adriatic Basin.

Order Pristiophoriformes Berg, 1958

Family Pristiophoridae Bleeker, 1859

Genus *Pristiophorus* Müller & Henle, 1837

***Pristiophorus* sp.**

Figures 7/9-11

- 1876 *Sphyræna* ? Lawley, p. 87, pl. 1, figs 2, 2a,b.

*Material examined* — 14 rostral spines (CZ-TES 2, 312-325).

*Remarks* — This genus, known since the Late Cretaceous, Late Santonian of Lebanon [*i.e.* *Pristiophorus tumidens* (Woodward, 1932) is usually represented in the fossil record by isolated rostral spines (or saw teeth or rostral teeth; “rostral spine” was used by Latham (1793) both for *Pristis* and *Pristiophorus*). Rostral spines (*e.g.* figs 7/9, 10) of approximately the same length have, in the basal part of the crown, several short and sharp plicae which in other rostral spines of Pliocene *Pristiophorus* appear as a dense crenulation (Cigala Fulgosi, pers. observ.). Lawley (1876, pl. 1, figs 2, 2a, 2b) illustrated and described two rostral spines found in the Pliocene of Orciano (Pisa, Tuscany, Italy), without realising their nature. His figures, if observed through a magnifying lens, present the same type of plicae. An undescribed deep water species, which appears rather small in size and represented by slight rostral spines with some long plicae, that might belong to *P. schroederi* Springer & Bullis, 1960 (Bahamas sawshark), was reported by Cigala Fulgosi (1986) as belonging to a psychrospheric shark fauna (Cigala Fulgosi, 1996) from the Early Pliocene of the Mediterranean Basin.

Two short and flexed rostral spines (Figure 7/11) are similar to the kind of spines found in the region beneath the eye of *Pristiophorus* species. The fossil rostral spines were compared to those of three common living species of *Pristiophorus* [*viz.* *P. cirratus* (Latham, 1794), *P. nudipinnis* Günther, 1870, and *P. japonicus* Günther, 1870, which apparently do not differ among each other, and which are different from the fossils, due to the base of their crown being from smooth to very slightly crenulated. Other undescribed living species are present in more or less restricted regions of Australia, the Indian Ocean and the Philippines (Last & Stevens; Compagno *et al.*, 2005).

With the exception of *P. nudipinnis*, which seems to inhabit the continental shelves, the majority of living *Pristiophorus* species is found in the upper slope regions, around 500-600 metres sea depth, while *P. schroederi*, which is the deepest species, is reported from 438-952 m

sea depth, living on or near the bottom (Compagno *et al.*, 2005).

Superorder Squatinomorphii Compagno, 1973  
Order Squatiniformes Buen, 1926  
Family Squatinidae Bonaparte, 1838  
*Squatina* Duméril, 1806

**Squatina** sp.

Figures 7/12-16

- 1876 *Squatina d'anconai* Lawley, p. 37, pl. 1, figs 16, 16a-e.  
1909 *Centrina salvianii* Risso – de Stefano, p. 590, pl. 17, figs 27, 28.  
1977 *Squatina squatina* (Linnaeus) – Landini, p. 121, pl. 5, fig. 6.

*Material examined* — Nine teeth (CZ-TES 2, 326-334).

*Remarks* — It is difficult to identify the various species of *Squatina* on the basis of teeth alone. Even if it were possible, the now available material is certainly insufficient. Of the nine fossil teeth found, five are illustrated (Figures 7/12-16).

*Squatina* occurs today in the Mediterranean with three species: *S. squatina* (Linnaeus, 1758), *S. aculeata* Duméril, 1829, and *S. oculata* Bonaparte, 1840, which furthermore have a respective and different distribution in the Eastern Atlantic (*i.e.* the region W of Gibraltar-the Lusitanian-boreal region for the first mentioned species and from the Mauritanian region to Angola, for the two other species). Even the bathymetry appears to follow this separation, as *S. squatina* is the species that stays closest to the coasts, while the others live to a sea depth of approximately 500 metres. Indirectly, when the fossil assemblage indicates deep waters (*e.g.* upper slope) and the *Squatina* teeth are autochthonous (“not reworked”) we can tentatively exclude the first species.

Superorder Galeomorphii Compagno, 1973  
Order Lamniformes Berg, 1958  
Family Odontaspidae Müller & Henle, 1839  
Genus *Carcharias* Rafinesque, 1810

**Carcharias taurus** Rafinesque, 1810

Figure 7/22

- 1977 *Odontaspis (Synodontaspis) acutissima* Agassiz – Landini, p. 101, pl. 1, figs 10-12.  
1996 *Odontaspis taurus* (Rafinesque) – Mané *et al.*, p. 24, pl. 1, figs 17-21.

*Material examined* — Two teeth, CZ-TES 2, 335, 336.

*Remarks* — The two teeth cannot be distinguished from

those of the living species, *Carcharias taurus*, of which six jaws were examined. One of these comes from the Sicily Channel (coll. F.C.F. 1 n. 24, 1978) two from Rocha, Punta del Diablo, Uruguay (coll. F.C.F. 1 n. 25 & 112) and three from Madagascar (coll. F.C.F. 1 n. 653, 927, 606). The dentition of this species has been repeatedly studied in order to determine both the dental terminology (*e.g.* Applegate, 1965) and the morpho-functional aspects (Taniuchi, 1970; Lucifora *et al.*, 2001). The teeth often present fine plicae or striae which appear more developed on the basal half of the crown lingual face. The illustrated tooth (Figure 7/22) seems to be a third upper left anterior tooth. The other, rather small, with an almost straight and low cusp and the base of the labial face protruding over the root, is a lower posterior tooth.

This species, which has always been rare in the Mediterranean (Doderlein, *in*: Tortonese, 1956, p. 103), could even have disappeared (apparently the last specimen, coll. F.C.F. 1 n. 24, was collected by Cigala Fulgosi in Mazara del Vallo, Sicily in 1978) and, if still present, is very rare along the North African coasts (Algeria and Tunisia waters). It concerns a species with a wide distribution (Bass *et al.*, 1975a; Cadenat & Blache, 1981; Compagno, 2001), in both coastal temperate-warm and tropical waters, and on continental shelves. It can be found in a variety of coastal habitats along sandy or rocky beaches in shallow bays and reefs and submarine caves (Compagno, 2001, p. 60). It is a piscivorous species (it eats various species of teleosts and small sharks) and can be found alone or in large aggregations or in schools during breeding (Compagno, 2001, p. 60).

Genus *Odontaspis* Agassiz, 1838

**Odontaspis ferox** (Risso, 1810)

Figure 7/23

- 1912 *Odontaspis ferox* (Risso) – de Stefano, p. 47, pl. 1, fig. 17, pl 2, figs 11, 12.  
1977 *Odontaspis ferox* (Risso) – Landini, p. 103, pl. 1, figs 13-17.  
1996 *Odontaspis ferox* (Risso) – Mané *et al.*, p. 25, pl. 1, fig. 17.  
2001 *Odontaspis ferox* (Risso) – Aguilera & de Aguilera, p. 740, figs 6/18, 6/19.  
2006 *Odontaspis ferox* (Risso) – Suarez *et al.*, p. 12, figs 4j-k.

*Material examined* — Two teeth (CZ-TES 2, 337, 338).

*Remarks* — The only complete tooth (Figure 7/23) is identical to those of the living species. The tooth morphology of this species was compared with those of twelve Recent jaws, two from the Mediterranean, *viz.* a young male (TL 215 cm) and a newborn female (TL 119 cm), and ten from the Indian Ocean, Madagascar (coll. F.C.F.). The individual variations found agree with those described in literature, *e.g.* Cadenat & Blache (1981, fig.

94). More or less high and sharp teeth might represent a slight sexual dimorphism. Some anomalies occur regarding the orientation or the flexion of the cusps.

The here illustrated tooth (Figure 7/23), which more than likely represents one of the first upper left latero-posterior teeth, has, as usual, three small lateral cusplets and at the base of the labial face of the crown several short and thick plicae. Its main cusp demonstrates distinct abrasion. Similar strong wear of the main cusp was also observed on the teeth of two or three of the more external series (at least two functional series) in three of the Recent jaws. The wear is not only common in almost all teeth, but occurs in jaws of a very different size, namely the young male from the Mediterranean (F.C.F. coll.1 n.630) and in one of the larger specimens from Madagascar (F.C.F. coll.1 n.1023). This suggests that the wear does not depend on the longer persistence of the teeth in a functional position, as one might assume in mature specimens. We might suspect that, in spite of the functional morphology and the type of diet (fish and cephalopods), these sharks feed, at least occasionally, on the carcasses of other sharks, the shagreen of which is very abrasive. The other tooth lacks the root and the proportions of the cusps suggest it could be one of the first lateral teeth.

This wide-ranging species, which is almost circumglobal and confined to deep waters (upper slopes), can swim close to drop-offs in coral reefs. Recently, large specimens of this species have been observed by eco-tourist divers in the Mediterranean (off Lebanon) and off Malpelo Island (East Pacific) (Compagno, 2001). It is generally rare, but can be locally abundant (e.g. rarely in the Sicily Channel; specimens are captured along the coasts of Madagascar). As Compagno (2001) observed, the teeth of this species are less robust in comparison to those of *Carcharias taurus* and seem to indicate an adaptation to a more homogeneous and soft prey (small fish, squid and shrimps).

Family Alopiidae Bonaparte, 1838 (emended)  
Genus *Alopias* Rafinesque, 1810

***Alopias superciliosus* (Lowe, 1840)**

Figures 7/20-21

- 1911 *Oxyrhina spallanzani* Bonaparte – de Stefano, p. 396, pl. 10, figs 20, 21.
- 1988 *Alopias superciliosus* (Lowe) – Cigala Fulgosi, p. 95, pl. 1, figs 1, 2.
- 2001 *Alopias aff. superciliosus* (Lowe) – Aguilera & de Aguilera, p. 740, figs 6/22, 23.

**Material examined** — Two teeth (CZ-TES 2, 339, 340).

**Remarks** — The two teeth cannot be distinguished from those of the living species, *Alopias superciliosus*. A comparison with some Recent jaws (coll. F.C.F.), presenting some variability also regarding the ontogenetic heterodonty, enables us to locate, at least tentatively, the

position of the fossil teeth in the jaw. Because of the pronounced sexual dimorphism occurring in this species (Bass *et al.*, 1975a, p. 39, pl. 12; Gruber & Compagno, 1981, figs 7, 8; Cigala Fulgosi, 1983, pls 2-4; 1988, pl. 1, figs 1-3), the two fossil teeth can be attributed to male specimens. In adult males the cusps are higher and sharper (narrow at the base), with a convex labial face of the crown. Because of the wide and U-shaped root, and the cusp, which is slightly bent towards the corner of the mouth, the first fossil tooth (Figure 7/20) might be the second lower right tooth beginning from the symphysis. The second (Figure 7/21), belonging to a smaller specimen, with narrow and V-shaped root, and a relatively bent cusp, might be the second upper right anterior or one of the first upper latero-posterior teeth. In the upper jaw of this species, unlike *A. vulpinus* (Bonnatere, 1788), the intermediate tooth is missing. The two anterior teeth, however, are disjunct from the latero-posteriors because they are housed in the “*dental bulla*” (*sensu* Shimada, 1998) or “*hollow*” (*sensu* Siverson, 1999, p. 52, fig. 3), which represents an important anatomic character to define the heterodonty. *A. superciliosus* was recently signalled in the Mediterranean by Compagno & Gruber (1981) on the basis of a specimen caught in the Ionian Sea. Shortly after, Cigala Fulgosi (1983) noted its occurrence in the Sicily Channel. The same author (Cigala Fulgosi, 1988) also described it from the Pliocene of Tuscany (central Italy).

*A. superciliosus* is an epipelagic species (Cadenat & Blache, 1981), virtually circumtropical, which can be found in coastal waters and over the continental shelves and also in deep seas far from land (Compagno, 2001, p. 85).

Family Cetorhinidae Gill, 1862  
Genus *Cetorhinus* Blainville, 1816

***Cetorhinus maximus* (Gunner, 1765)**

- 1876 *non det.* – Lawley, p. 89, pl. 1, figs 11, 11a-e.
- 1876 *Hannoveria aurata* van Beneden – Lawley, p. 44, pl. 1, fig. 17c.
- 1977 *Cetorhinus maximus* Gunner – Landini, p. 111, figs 18, 19.

**Material examined** — One fragmentary gill-raker (CZ-TES 2, 341).

**Remarks** — The basking shark is represented by a single fragment of a gill-raker. Gill rakers are more commonly preserved in the fossil record than the less numerous teeth, because in this shark the gill-rakers are much more numerous than teeth. On their own, these elements do not allow for a specific attribution (van den Bosch, 1984) and the identification with the living species is made indirectly here. The living *Cetorhinus maximus* (Gunner, 1765), has a long and complicated taxonomic history, which was recently synthesised by Compagno (2001), who suggested the possible existence of isolated popula-

tions with potentially restricted genetic interchange. This huge species is highly migratory and is often seen at the surface of the epipelagic zone in deep water above the slopes. Sometimes, in spring, when zooplankton blooms develop, it also moves into shallow coastal waters (Compagno, 2001, p. 93).

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

***Isurus oxyrinchus* Rafinesque, 1810**

Figures 7/17-19

- 1881 *Oxyrhina desorii* Agassiz – Lawley, p. 77, pl. 2, figs 1, 1a-b, 2, 2a-b, 3, 3a-b, 4-6, pl. 3, figs 1, 1a-b, 2, 2a-b, 3, 3a-b.
- 1899 *Oxyrhina cf. gomphodon* Müller & Henle – Vinassa de Regny, p. 82, pl. 2, fig. 10.
- 1909 *Oxyrhina spallanzani* Bonaparte – de Stefano, p. 570, pl. 16, figs 3, 8, 10, 11.
- 1912 *Oxyrhina spallanzani* Bonaparte – de Stefano, p. 49, pl. 2, fig. 19.
- 1977 *Isurus oxyrinchus* Rafinesque – Landini, p. 110, pl. 3, figs 1-8.

**Material examined** — Seven teeth (CZ-TES 2, 342-348).

**Remarks** — The morphology of the teeth matches in detail those observed on several Recent dried jaws (coll. F.C.F.) from various geographical locations. Of the three illustrated teeth the smallest two (Figures 7/17, 19) are a first lower right anterior tooth and a first upper right tooth, respectively. Their size is that of the teeth of Recent jaws of young specimens with a total length (TL) between 120 and 130 cm. The third illustrated tooth (fig. 7/18) and a fourth, smaller tooth, are likely to be two lower left lateral teeth. The last three teeth, lacking part of the root, are probably all second lower anterior teeth, two on the left and one on the right. The smallest tooth has a crown the mesial side of which measures 7.4 mm in length and it used to belong to a full-term embryo or a juvenile.

The “mako” is an extremely active and strong shark, distributed worldwide in the tropical-temperate belt offshore but also in littoral waters. This species which is epipelagic and highly migratory, following the movements of warm water masses polewards, can reach waters at least 500 metres deep (Compagno, 2001, p. 111). When young, it consumes mainly small fish and cephalopods, while large adults can attack other vertebrates such as sea turtles, other sharks and, rarely, marine mammals (dolphins).

Order Carcharhiniformes Compagno, 1973  
Family Carcharhinidae Jordan & Evermann, 1896  
Genus *Carcharhinus* Blainville, 1816

***Carcharhinus cf. plumbeus* (Nardo, 1827)**

Figures 7/26, 28

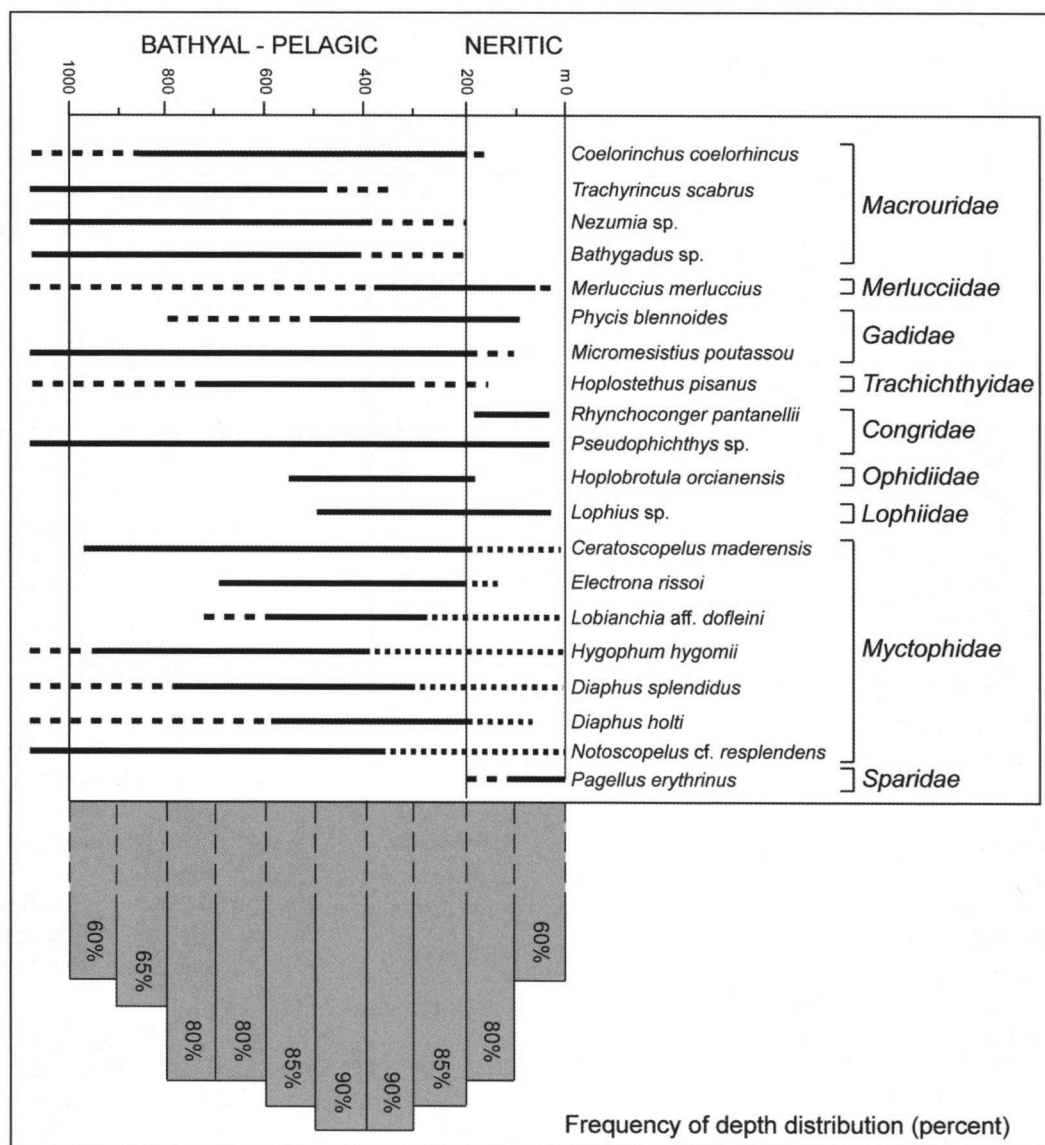
- 1996 *Carcharhinus (Prionodon) egertoni* (Agassiz) – Mané *et al.*, p. 20, pl. 1, figs 1-5, 7.
- 2001 *Carcharhinus plumbeus* (Nardo) – Purdy *et al.*, p. 154, fig. 56.

**Material examined** — Three teeth (CZ-TES 2, 349, 350, 351).

**Remarks** — The few *Carcharhinus* teeth found are insufficient for any detailed taxonomic assessment. Nonetheless, some of them (Figures 7/26, 28) are quite likely to belong to *C. plumbeus* or to the lineage of that species, the teeth of which are occasionally also found in classic Pliocene sediments of Parma and Piacenza (Cigala Fulgosi, pers. observ.). For a better assessment, the comparison was extended to other fossil material from the Pliocene of other places in Tuscany where *Carcharhinus* teeth are fairly common. The following species were recognised (pers. obs. F.C.C.): *C. obscurus* (Lesueur, 1818), *C. cf. brachyurus* (Günther, 1870), *C. cf. brevipinna* (Müller & Henle, 1839), *C. plumbeus* (Nardo, 1827), *C. cf. perezii* (Poey, 1876) and *C. cf. falciformis* (Bibron, 1839)). When the present paper was in proof, the paper of Marsili (2007) was published, in which *C. plumbeus*, *C. brachyurus*, *C. falciformis* and *C. perezii* were recognized in the Pliocene of Tuscany.

Recently Purdy *et al.* (2001, pp. 154-155, figs 55, 56), dealing with the taxonomy of *Carcharhinus*, pointed out that *C. obscurus* can be distinguished from *C. plumbeus* in having the mesial cutting edge of the upper tooth crown apically convex as well. Using this character together with the finer serration we can identify some of the teeth figured by Mané *et al.* (1996, figs 1-5, 7) as belonging to the *C. plumbeus* lineage. Two Tuscan teeth (Figures 7/26, 28) have a serration which, even though it is only fairly marked, is relatively finer than that found in *C. obscurus*. The latter, common in the Pliocene of Tuscany and in the “Lawley collection” (see Landini, 1977, pl. 4, figs 8-25) is usually called *C. egertoni* (Agassiz, 1843). Actually, it is difficult to understand to which species of the group *C. obscurus*, *C. leucas* (Valenciennes, 1839), *C. plumbeus* or *C. galapagensis* (Snodgrass & Heller, 1905) the specimens illustrated by Agassiz (1833-1843, pl. 36, figs 6, 7) might refer.

The first tooth (Figure 7/26) is narrow at the base and the mesial and distal crown edges have a style typical of the second or third upper left tooth of *C. plumbeus*, of which several Recent jaws were observed. The second (Figure 7/28), a 7th-8th upper left tooth from the symphysis, presents a notch along the mesial and distal cutting edges which render it similar to a tooth of *C. falciformis*. A closer comparison between the teeth of these two species, however, indicates that at times there are similar notches also in *C. plumbeus* and that serration at the base of the crown beneath the two notches is larger in *C. falciformis* than in *C. plumbeus*.



**Figure 8.** Present day bathymetric range of the teleost taxa represented in the Piacenzian-earliest Gelasian of Castelnuovo Berardenga Scalo (Siena, Central Italy).

This does not occur in the fossil tooth which has a more regular serration along the cutting edges. The third tooth (not illustrated) is an upper lateral tooth.

*Carcharhinus plumbeus* today seems to be the most common species of *Carcharhinus* caught in the Mediterranean (Cigala Fulgosi, pers. observ., in the Sicily Channel). This widely distributed species (see Garrick, 1982) seems locally more or less abundant in temperate-tropical waters, with a great variety of habitats. Indeed, it is found in coastal shallow waters, but even in deep waters offshore or close to oceanic reefs. Furthermore, it is common at embayments, harbours, river estuaries etc. (Compagno, 1984, p. 494).

***Carcharhinus cf. perezii* (Poey, 1876)**  
Figure 7/27

? 2001 *Carcharhinus perezii* (Poey) – Purdy *et al.*, p. 154, fig. 35b.

**Material examined** — One tooth (CZ-TES 2, 352).

**Remarks** — A comparison with some jaws (F.C.F. coll.) of this species from Brazil and other teeth from the Pliocene of Tuscany (work in progress) has led to this tentative identification. The serration is regular and develops up to the base of the crown on the mesial and distal shoulders where it becomes finer. The tooth proportions enable us to consider it as a 6th-7th lower left tooth from the symphysis. Living *Carcharhinus perezii* is a bottom coastal Atlantic species ranging from North Carolina to Venezuela-Brazil, common in the Caribbean near drop-offs on outer reefs to at least 30 metres in depth (Compagno *et al.*, 2005).

Taxa	n	%	
<i>Coelorinchus coelorhincus</i>	55	17.5	Macrouridae 49.7%
<i>Trachyrinchus scabrus</i>	97	31	
<i>Nezumia</i> sp.	2	0.6	
<i>Bathygadus</i> sp.	2	0.6	
<i>Merluccius merluccius</i>	15	4.8	Trachichthyidae 22.1%
<i>Phycis blennoides</i>	11	3.5	
<i>Micromesistius poutassou</i>	4	1.2	
<i>Hoplostethus pisanus</i>	69	22.1	
<i>Rhynchoconger pantanellii</i>	1	0.3	Myctophidae 12%
<i>Pseudophichthys</i> sp.	3	0.9	
<i>Hoplobrotula orcianensis</i>	6	1.9	
<i>Lophius</i> sp.	3	0.9	
<i>Ceratoscopelus maderensis</i>	1	0.3	Myctophidae 12%
<i>Electrona rissoi</i>	2	0.6	
<i>Lobianchia</i> aff. <i>dofleini</i>	1	0.3	
<i>Hygophum hygomii</i>	10	3.2	
<i>Diaphus splendidus</i>	20	6.4	
<i>Diaphus holti</i>	2	0.6	
<i>Notoscopelus</i> cf. <i>resplendens</i>	2	0.6	
<i>Pagellus erythrinus</i>	6	1.9	

**Table 2.** Recovered otoliths (*sagittae*) per teleost taxa with percentages of total number.

Genus *Prionace* Cantor, 1849

***Prionace glauca* (Linnaeus, 1758)**

Figures 7/24, 25

- 1876 *Prionodon subglauca* Lawley, p. 19 (pars).
- 1900 *Prionodon glaucus* Müller & Henle – Seguenza, p. 507, pl. 6, figs 37, 37a.
- 1977 *Prionace glauca* (Linneo) – Landini, p. 117, pl. 3, figs 9, 10, pl. 4, figs 1-3.

**Material examined** — 22 teeth (CZ-TES 2, 353-374).

**Remarks** — The teeth of this species are fairly common in the outcrop, although clearly less common than those of *Centrophorus* and *Chlamydoselachus*.

Their size ranges between small and modest, which indicates that we are dealing with sub-adult specimens. This also appears to be true for the rare material of *Prionace* from Early-Late Pliocene sediments of northern Italy (Cigala Fulgosi, pers. observ.).

The figured specimens represent a 4th-5th lower right tooth (Figure 7/24) and one of the last upper left lateral tooth (Figure 7/25), respectively. The teeth not illustrated here consist of five lower laterals with small narrow cusps belonging to immature specimens, three upper left laterals, and an upper right lateral tooth.

Because of its circumglobal distribution, which concerns the whole temperate-tropical range, Compagno (1984, p. 522) considered this species the widest ranging chondrichthyan. However, it appears to prefer cold waters (7-16°C),

even though it tolerates warmer regions and can be found deeper, in tropical seas (80-220 m, 12-25° C in tropical India, Compagno, 1984, p. 522).

**Otolith fauna**

Of otoliths, 312 teleostean sagittae (CZ-TOS 1, 1-312), representing 20 species (Table 2), were collected directly from the surface. For taxonomic identifications, we used various authors (*e.g.*, Koken, 1891; Bassoli, 1905; Pieragnoli, 1919; Dieni, 1968; Anfossi & Mosna, 1969, 1972, 1976, 1979; Gaemers, 1976, 1978; Gaemers & Schwarzhans, 1982; Schwarzhans, 1978a, 1978b, 1980; Nolf, 1980, 1985, 1994, 1995; Nolf & Cappetta, 1988; Nolf *et al.*, 1998; Harkonen, 1986; Landini *et al.*, 1990; Brzobohaty, 1978, 1995; Brzobohaty & Nolf, 1995, 1996, 2000; Smale *et al.*, 1995; Girone & Varola, 2001; Girone, 2003; Lloris *et al.*, 2003; Campana, 2004).

The identified species and/or genera, also the extinct ones, are summarised in Figure 8 together with the (partly interpreted) bathymetric values of the corresponding living species (compare Bini, 1967-1969; Tortonese, 1970, 1975; Wheeler, 1969; Nafpaktitis *et al.*, 1977; Nolf & Cappetta, 1988; Cohen *et al.*, 1990; Nolf & Brzobohaty, 1994; Nielsen *et al.*, 1999; Lloris *et al.*, 2003; McEachran & Fehnelm, 1998, 2005 *etc.*).

**Paleoecology**

Chondrichthyan fauna



The most significant species from a bathymetric point of view appear to be *Chlamydoselachus lawleyi* and *Centrophorus* cf. *granulosus* of which approximately 100 (28%) and 180 (51%) teeth were found, respectively. In the case of *C.* cf. *granulosus*, these meristic values are influenced by the high number of individuals represented by this bathypelagic species in deep waters (100-1200 m, locally more frequent between 400-800 m) near or at the bottom. The high density of *Chlamydoselachus*-teeth, concentrated in such a small area, is exceptional, since the living species is considered relatively rare everywhere. Kubota *et al.* (1991), however, stressed that this rarity is apparent (depending on the fishing techniques) and that at least locally this shark can be frequent (*e.g.* 139 specimens were captured in four years time in Suruga Bay, Japan, for examination of their stomach contents). Even so, we cannot exclude the possibility that some particular mechanism actually might have caused these exceptional numbers. In Suruga Bay (Kubota *et al.*, 1991, fig. 1) the sea bottom profile is steep and bathyal depths are present within short distance from the coast. Some *Chlamydoselachus* specimens were captured during night at depths between 51 and 60 metres (Kubota *et al.*, 1991), thus demonstrating the great vertical wandering of this bathybenthic to mesopelagic species. Species that may indicate an upper bathyal environment (upper slope to outer continental shelf) are *Hexanchus griseus*, *Dalatias licha*, *Echinorhinus richiardi*, *Alopias superciliosus* and *Odontaspis ferox*. The only shark species the presence of which seems to contrast with the previous picture is *Carcharhinus* cf. *perezi*, which prefers a strictly coastal environment (inshore bottom dwelling species). However, various types of batoids (*e.g.* many *Dasyatis* species, *Myliobatis* and *Pteromylaeus*) and *Notorynchus*, dwelling in the coastal region and present in other Tuscan Pliocene outcrops, are lacking. Essentially, the chondrichthyans enable us to hypothesise an upper bathyal environment probably close to the coast, and the high density of *Chlamydoselachus* could perhaps be related to some sort of upwelling (high productivity).

#### Teleostean fauna (otoliths)

The otolith assemblage (Table 2) is dominated by Macrouridae (49.7%) and to a certain degree by Myctophidae (12%). This co-occurrence was described as typical of deep habitats (*e.g.* Nolf, 1985; Nolf & Brzobohaty, 1994). In particular, benthopelagic species such as *Trachyrincus scabrus* and *Coelorinchus coelorhincus* are linked to the sea bottom and represent 31% and 17.5%, respectively, of the sagitta's collected. This is also related to the high number of individuals and specific diversity in which the macrourids naturally occur in deep habitats (Marshall, 1979). Another bathypelagic (400-600 m depth) species, *Hoplostethus pisanus* (Trachichthyidae), is also common (22.1%) in our material. The highest frequency of the represented taxa seems to be found in sea depths between 300 and 500 m (Figure 8, 90%), thus indicating an upper bathyal environment.

#### Conclusions

The fossil fish assemblage from Castelnuovo Berardenga Scalo yielded macrourids (rat-fishes, grenadiers), myctophids (lantern-fishes) and shark genera, such as *Centrophorus* and *Chlamydoselachus*, indicating a Pliocene (Piacenzian to earliest Gelasian) bathyal environment, probably located at short distance from the coast. The high number of teeth belonging to *Chlamydoselachus*, a genus which accomplishes great vertical migrations at night (Kubota *et al.*, 1991), is exceptional and might perhaps be related to some kind of upwelling, without excluding other possible causes or mechanisms, such as currents and sea bottom depressions or traps. Its teeth, generally larger than those of the living species (max. tooth width 13.5 mm, Figure 7/1), suggest an animal approximately 2.5 metres in length (the known maximum length of living *C. anguineus* is 1.96 m). Similar teeth of equivalent size were recently reported from the Early-Middle Miocene Tomioka Group, Japan (Takuwa *et al.*, 2001). On the basis of size, we identify the teeth as *C. lawleyi*, a fossil taxon which to date was known from Zanclean times, now demonstrated to persist into the Piacenzian-earliest Gelasian of the Mediterranean Basin. The presence of *Chlamydoselachus* demonstrates the persistence of a sufficiently deep connection with the Atlantic Ocean, without excluding some type of upwelling. The absence of deep water oceanic shark taxa like *Deania*, *Centrophorus squamosus*, *Scymnodon* spp., *Scymnodalatis* and *Mollisquama* (work in progress) present in the Early Zanclean (*i.e.* lower part of MPL 2 foraminiferal biozone; see Cigala Fulgosi, 1986, 1996) of other Mediterranean localities may be caused by insufficient local depths during deposition, by collecting bias, but also, and more probably, by a lesser degree of open oceanic setting of the Piacenzian-earliest Gelasian Mediterranean Basin (Cigala Fulgosi, 1996).

#### Acknowledgements

We are grateful to the director of the quarry of Castelnuovo Berardenga Scalo, Dr. Mauro Cartocci, for allowing us free access to the outcrop. Thanks are due to Mrs. E. Masini for the drawings and to Dr. Alex Orlandini (Reggio Emilia) for the photographic work (*i.e.* Figures 3-7).

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