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| Bollettino della Società Paleontologica Italiana | 34 (3), 1995 | ISSN 0375-7633 | 301-322 | 6 pls. | Modena, Aprile 1996 |
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## Rare oceanic deep water squaloid sharks from the Lower Pliocene of the Northern Apennines (Parma Province, Italy)

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**KEY WORDS** – *Chondrichthyes*, Taxonomy, Paleocology, Paleobiogeography, Odontology, Lower Pliocene, Paleomediterranean, Recent species.

**ABSTRACT** – Three rare species of oceanic deep water squaloid sharks: *Scymnodalatias* aff. *garricki* Kukuev & Konvalenko, 1988, *Zameus squamulosus* (Günther, 1877) and *Scymnodon ringens* Bocage & Capello, 1864, are recorded from a Lower Pliocene outcrop (lower part of the MPL 2 foraminiferal biozone) in the Northern Apennines (S. Andrea Bagni, Parma, Adriatic paleo-area, Italy).

*Scymnodon ringens* is a rare taxon in its fossil state, while the other two species are the first fossil occurrences.

Study of the largest group of teeth shows a close affinity with those of the living species *Scymnodalatias garricki*, of which the only holotype, caught in the water mass above the North Atlantic Ridge, a little north of the latitude of Gibraltar, is known. The teeth of the holotype are accurately described; some aspects of its body morphology are also reconsidered. The matching of the fossil teeth with those of *S. garricki*, whose variability range is unknown, receives further support from the relative geographical proximity between the distribution area of the living species and the Mediterranean paleo-area. Its taxonomic relationship with the two other species of the same genus from the southern hemisphere i.e. *S. sherwoodi* (Archey, 1921) and *S. albicauda* Taniuchi & Garrick, 1986, needs to be better defined, since current knowledge is based on one and on few specimens respectively.

While some fossil teeth may be attributed to *Scymnodalatias*, they show some slight differences from those of the *S. garricki* holotype. Until further data is produced, they may be interpreted for the moment as an expression of individual variability or, more probably, of gynandric heterodonty. When the living populations have been satisfactorily checked, the lesser width of the apron, which appears to characterize the lower fossil teeth, might prove to be a diagnostic character for a new fossil taxon. Without going any further into the meaning of the fossil fauna as a whole, these taxa alone show the presence in the Adriatic paleo-area, during the early Pliocene (lower part of MPL 2 biozone), of psychrospheric water masses (upper psychrosphere) of Atlantic origin and of a phase of maximum «oceanization» in the Mediterranean basin. Furthermore, considering other elements of the fauna, it appears evident that a stabilized open and deep sea eco-system occurred again after the Messinian salinity crisis. Although wider areas must be studied in order to exclude local causes, the apparent brief presence in the Lower Pliocene of these Atlantic immigrants (or reimmigrants after the Messinian salinity crisis) suggests that their disappearance from the basin might not have been caused by later known climatic deteriorations (intra-Pliocene and Quaternary), but mainly by the early failing of a sufficiently open and deep Atlantic-Mediterranean connection in the paleo-area of Gibraltar, and therefore of the conditions of maximum «oceanization» in the basin.

In the Appendix, the teeth of the holotype of *Mollisquama parini* Dolganov, 1984 are also described. Furthermore, it appears that *Scymnodalatias oligodon* Kukuev & Konvalenko, 1988 is invalid, since the holotype shows features of *Centroscymnus*.

**RIASSUNTO** – [Rari squali squaloidi oceanici di acque profonde del Pliocene inferiore dell'Appennino Settentrionale (Provincia di Parma, Italia)] – Tre rare specie di squali squaloidi oceanici di acque profonde: *Scymnodalatias* aff. *garricki* Kukuev & Konvalenko, 1988, *Zameus squamulosus* (Günther, 1877) e *Scymnodon ringens* Bocage & Capello, 1864, vengono segnalate in un affioramento di Pliocene inferiore (parte inferiore della biozona a foraminiferi MPL 2) dell'Appennino Settentrionale (S. Andrea Bagni, Parma, paleo-area adriatica, Italia).

*Scymnodon ringens* continua ad essere un taxon raro allo stato fossile, le altre due specie costituiscono il primo rinvenimento.

Un'accurata osservazione del lotto più numeroso di denti evidenzia con relativa sicurezza la stretta affinità con la specie attuale *Scymnodalatias garricki*, di cui è noto il solo olotipo catturato nella massa d'acqua sovrastante la Dorsale Nord Atlantica, poco a nord della latitudine di Gibilterra. I denti dell'olotipo vengono accuratamente descritti; sono reconsiderati inoltre alcuni aspetti della morfologia corporea.

L'accostamento dei denti fossili a quelli di *S. garricki*, il cui «range» di variabilità è sconosciuto, trova un ulteriore sostegno nella relativa vicinanza geografica fra l'areale di distribuzione della specie attuale e la paleo-area mediterranea. I suoi rapporti tassonomici con le altre due specie congeneri dell'emisfero australe, *S. sherwoodi* (Archey, 1921) e *S. albicauda* Taniuchi & Garrick, 1986, sono tuttavia in attesa di una miglior definizione, attualmente basata rispettivamente su uno e su pochi esemplari.

Alcuni denti fossili, pur ascrivibili a *Scymnodalatias*, mostrano lievi differenze da quelli dell'olotipo di *S. garricki*. In attesa di ulteriori dati esse sono per ora interpretabili come espressione di variabilità individuale o, più probabilmente, di eterodontia gynandrica. Quando disporremo di un sufficiente controllo sulle popolazioni attuali la minor larghezza dell'apron, che sembra caratterizzare i denti inferiori fossili, potrebbe costituire un elemento discriminante anche valido per l'istituzione di un nuovo taxon fossile.

Senza penetrare profondamente nel significato della fauna fossile nel suo complesso, questi taxa, da soli, dimostrano la presenza nel Pliocene inferiore (parte inferiore della biozona MPL 2) della paleo-area adriatica, di masse d'acqua psicrosferica (psicrosfera superiore) di origine atlantica e di una fase di massima «oceanizzazione» nel bacino del Mediterraneo. Considerando inoltre altri elementi della fauna risulta evidente l'avvenuto ricostituirsi, dopo la crisi di salinità messiniana, di un ecosistema stabilizzato di mare aperto e profondo. L'apparente breve presenza nel Pliocene inferiore di questi immigrati atlantici (o reimmigrati dopo la crisi di salinità messiniana), anche se da controllarsi su aree più ampie per escludere cause locali, lascia ipotizzare che la loro scomparsa dal bacino potrebbe non essere stata causata dai noti deterioramenti climatici più tardivi (intra-pliocenici e quaternari), ma, eminentemente, dal precoce venir meno di una connessione Atlantico-Mediterraneo sufficientemente aperta e profonda nella paleo-area di Gibilterra e quindi delle condizioni di massima «oceanizzazione» nel bacino.

In appendice al lavoro vengono descritti i denti dell'olotipo di *Mollisquama parini* Dolganov, 1984. Sembra inoltre da invalidare *Scymnodalatias oligodon* Kukuev & Konvalenko, 1988, il cui olotipo mostra caratteri di *Centroscymnus*.

## INTRODUCTION

Due to their small size, poor collecting techniques and the little importance afforded them in systematics, the teeth of both fossil and living squaloid sharks have been practically neglected in the past. Lawley (1876, pl. 1, figs 17a, b, 18) recognised the need to make a comparison with living specimens, and was one of the first authors to record some small teeth of *Dalatias licha* (Bonaterre, 1788) from the Tuscan Pliocene, which he named *Scymnus Majori* and *Centrina Bassanii*.

The fundamental and pioneering work of Casier (1947 a, b, c; 1961) on selachian tooth vascularization and the studies of Ledoux (1970, 1972), who gave the first detailed descriptions of the teeth of numerous squaloid species, have, in the last ten years, stimulated further research into the systematics and paleontology of this group, which is diversified at least from the late Mesozoic (e.g. Thies & Muller, 1993; Siverson, 1993).

As far as the Mediterranean paleo-area is concerned, apart from the author's studies (Cigala Fulgosi, 1986; 1988), Cappetta & Nolf (1991) described a small fauna with *Centrophorus*, *Deania*, *Scymnorhinus*, batoids etc. from the Lower Pliocene of south-eastern France.

With a more systematic objective, focussed on the tooth characters, Herman, Hovestadt-Euler & Hovestadt (1989, 1993) described and illustrated the teeth of some of the living squaloid species using SEM photographs.

The present work follows on from two short notes (Cigala Fulgosi, 1986; 1988) on a rich deep water squaloid shark fauna from the Lower Pliocene of the Mediterranean paleo-area. The fossils, which are small, were obtained partly by surface collecting and partly disaggregating with  $H_2O_2$  and sifting about 5 tons of sediment. After a first sifting through 63 micron mesh the final residue was obtained by dry sifting with a 420 micron mesh. The arduous task of accomplishing this work, together with the hard task of collecting the sediment on an uneven and difficult ground, took about 15 years.

The aim of this account is to discuss and illustrate some rare fossil teeth of the squaloid shark species *Scymnodalatias* aff. *garricki* Kukuev & Konovalenko, 1988, *Zameus squamulosus* (Günther, 1877) and *Scymnodon ringens* Bocage & Capello, 1864, together with paleoecological and paleobiogeographical inferences and specifications on the morphology of the living species. Studies, as well as new acquisitions, of these poorly known species are mainly thanks to Garrick (1956), Yano & Tanaka (1983), Taniuchi & Garrick (1986),

Dolganov (1984) and Kukuev & Konovalenko (1988), some resulting from Russian and Japanese oceanic cruises.

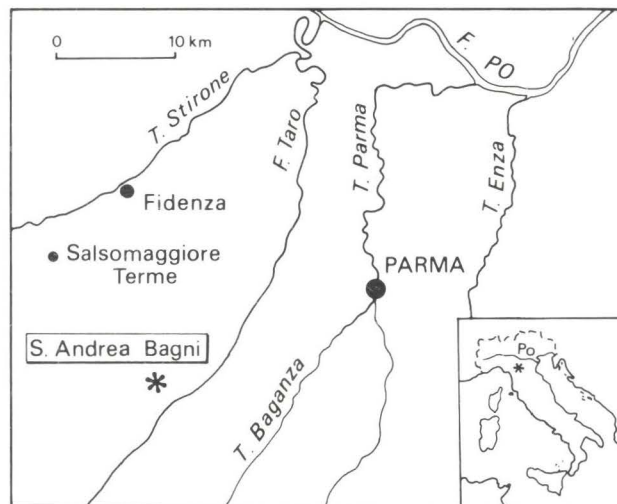
Although not strictly relating to the fossil fauna, comments will be made on *Scymnodalatias oligodon* Kukuev & Konovalenko, 1988, and the teeth of the holotype of *Mollisquama parini* Dolganov, 1984, will be described.

Other squaloid sharks of the fauna of the same locality, such as *Centrophorus*, *Deania*, *Scyliorhinidae*, *Etmopterus*, etc., will be discussed in subsequent notes.

The fossil specimens (MPP, FCF Coll., n. 120, 2-35) are preserved in the «Museo Paleontologico Parmense» (MPP), F. Cigala Fulgosi Collection (FCF), «Istituto di Geologia, Paleontologia e Geografia», University of Parma, Italy.

## GEOLOGICAL AND STRATIGRAPHIC SETTING

The material described comes from a short section (about 25 m thick) near the village of S. Andrea Bagni (Text-fig. 1) (Parma Province, Northern Apennines). The section, observed by Cigala Fulgosi (1986), is made up of silty argillaceous pelites, «blue clays» *sensu lato*, slightly more marly at the base, and showing indistinct bedding. Some evidence of bedding is seen in the alternation of light and dark bands (Cigala Fulgosi, 1986), probably in connection with the fluctuation of the amount of  $CaCO_3$  and pyrites, which sometimes characterizes the basal terrigenous facies of P<sub>1</sub> («Lower» Pliocene Cycle, Ricci Lucchi *et al.*, 1982) and reflecting a pelagic trend. There is some controversy among biostratigraphers as to the



Text-fig. 1 - Map of the S. Andrea Bagni area (Parma Province, Italy) with location of the Lower Pliocene outcrop.

presence-absence of the biozone MPL 1 in the Northern Apennines (e.g. Iaccarino & Papani, 1979; Channell, *et al.*, 1994) above the Messinian «Lago mare» sediments, in relation to the supposedly non-depositional hiatus that would appear to characterize the Mio-Pliocene boundary in the area. In the limited area of the section, the Mio-Pliocene boundary is not visible, but it can probably be found just a few metres below the outcrop (*i.e.* the base of the section).

In any case, Channell, *et al.* (1994) published an integrated magnetic and biostratigraphic account of the S. Andrea section. Inferences based on calcareous plankton assemblage, consistent with a normal polarity zone, (correlated to the Thvera subchron) overlain by a reversed polarity zone, allow the authors to assign the section to the lower part of the MPL 2 biozone (Cita, 1973, 1975; Rio, Sprovieri & Raffi, 1984) (Text-fig. 2). Macro mollusc shells are apparently absent or rare at the base of the section but they appear, at first sporadically, some metres above where the rich deep water shark fauna disappears. The fish fauna (shark teeth and scales and teleost disarticulated bones, teeth and otoliths) was collected in the basal part and was concentrated in some small scattered lenses (possibly some decimetres in width and < 1-2 centimetres thick) containing together with foraminifera, cidaroid

spines and plates and very small deep water molluscs. Deep water and small cup-shaped solitary corals are scattered on the ground.

Other vertebrate remains were found by the author some metres above the base of the outcrop: in particular, a fragmented skull of kogiinae (Cetacea: Odontoceti) and badly preserved remains (not recovered) of a marine turtle.

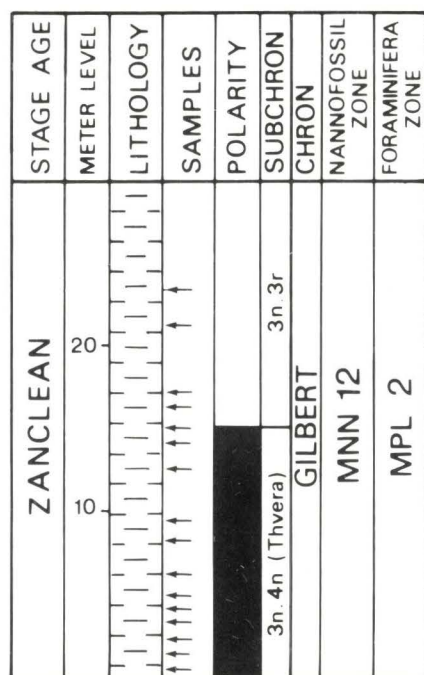
#### SQUALOID SYSTEMATICS WITH REFERENCE TO THE TAXA CONSIDERED

After a number of contributions from the classical work of Bigelow & Schroeder (1957) to the recent studies of Compagno (1973, 1977 and 1984) squaloid shark systematics continue to be a difficult subject, hindered by parallelisms.

Compagno (1973) divided the family Squalidae (including *Oxynotus*) into 6 subfamilies: Etmopterinae Fowler, 1934 for *Aculeola*, *Centroscyllum* and *Etmopterus*; Squalinae Bonaparte, 1834 for *Centrophorus*, *Cirrhigaleus* and *Squalus*; Deaniinae for *Deania*; Oxynotinae Gill for *Oxynotus*; Somniosinae Jordan, 1888 for *Centroscyrnus*, *Enchiridiodon*?, *Scymnodon* and *Somniosus*; Dalatiinae Gray, 1851 for *Dalatis*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscyrnoides*?, *Isistius*, *Scymnodalatis* and *Squaliolus*. Subsequently (1984, Part 1, pp. 28-29) he modified his opinion suggesting that *Deania* be included in Squalinae and *Scymnodalatis* removed from Dalatiinae and that it should be placed in a common group for Somniosinae and Oxynotinae. Pending completion of his work on squaloid morphology he preferred to include «the squaloid genera other than *Echinorhinus* and *Oxynotus* in a single family, Squalidae, without subdivision, and retain the family Oxynotidae for *Oxynotus*» (Compagno 1984, Part 1, pp. 28-29).

Regarding the concept of subfamily subdivision, Compagno's opinion (1973) generally agrees with the proposal of Herman, Hovestadt-Euler & Hovestadt (1989, 1993), who grouped the squaloid genera into eight subfamilies, basing their opinions on odontological characters (root vascularization and morphology).

Considering a number of characters, Yano & Tanaka (1984) reviewed *Scymnodon* and synonymized *Scymnodon obscurus* (Vaillant, 1888) with *Scymnodon squamulosus* (Günther, 1877). At a later date, Taniuchi & Garrick (1986) dealt with *Scymnodalatis*, discussing the relationships with such very close genera as *Scymnodon*, *Zameus*, and *Centroscyrnus*. These authors maintain *Scymnodon* and *Scymnodalatis* as distinct genera and resurrect *Zameus* Jordan & Fowler, 1903 to include



Text-fig. 2 - Lithology, biostratigraphy and polarity interpretation for the S. Andrea Bagni section (redrawn from Channell *et al.*, 1994).

*squamulosus*. Recently Herman, Hovestadt-Euler & Hovestadt (1989, 1993) proposed that *Scymnodalatias* and *Zameus* be considered as synonyms of *Scymnodon* on the basis of strong affinities in root vascularization and morphology. Although this opinion is stimulating, yet simplifying, and pending on the results of further studies, I agree with Taniuchi & Garrick (1986) in their conclusion.

*Scymnodon obscurus* (Vaillant, 1888) is considered here as a synonym of *squamulosus* (Günther, 1877) also taking into account any differences between such remote populations. The fossil specimens of the Mediterranean paleo-area are indeed, more «naturally» connected to the living Atlantic populations (*S. obscurus sensu stricto*).

#### RECENT SPECIMENS DIRECTLY EXAMINED

*Scymnodon obscurus* (Vaillant, 1888)

male, 384 mm TL, Station 41, Villa Ana, 14° 19' N, 17° 35' W, 650 m deep, Senegal, by courtesy of B. Seret.

*Scymnodon ringens* Bocage & Capello, 1864

female, 800 mm TL, North Atlantic, by courtesy of J. Herman.

juvenile male, 307 mm TL, West Bretagne.

*Centroscymnus crepidater* (Bocage & Capello, 1864)

male, 670 mm TL, New Zealand, by courtesy of Prof. J.A.F. Garrick.

females, 84 and 83 cm TL, North Atlantic, by courtesy of J. Herman.

male, 65 cm TL, North Atlantic, by courtesy of J. Herman.

*Scymnodalatias albicauda* Taniuchi & Garrick, 1986

holotype, female, 914 mm TL, 45° S, 92° E, 150-200 m deep, Southern Indian Ocean, March 8, 1967, tuna long line vessel No. 35, Shotoku-maru, Dept. Fish. Univ. M., Univ. of Tokyo (FUMT) P-197.

*Scymnodalatias garricki* Kukuev & Konovalenko, 1988

holotype, male, 377 mm TL, 40° 22' N, 30° 10' W, North Atlantic Ridge, 300 m deep, 1977, PTM «Bachcisarai» SIN No. 48190.

*Mollisquama parini* Dolganov, 1984

holotype, female, 400 mm TL, 21° 32' S, 81° 38' W, Nasca submarine Ridge, Peru, 15-10-1979, scientific vessel «Ichtandr», 330 m deep, SIN 45988.

*Scymnodalatias oligodon* Kukuev & Konovalenko, 1988

holotype, male, 260 mm TL, 33° 31' S, 96° 07' W, South-eastern Pacific Ocean, 0-200 m deep, November 1985, PTMC «Novoceboksarsk», SIN No. 48191.

*Centroscymnus owstoni* Garman, 1906

female, 1104 mm TL, off Yui, Japan, by courtesy of Yuki Tanaka.

*Centroscymnus cryptacanthus* Regan, 1906

holotype, adult male, 780 mm TL, Madeira, BM-NH 1865.5.20.4.

*Centroscymnus coelolepis* Bocage & Capello, 1864

female, 114 cm TL, North Atlantic, by courtesy of J. Herman.

#### OBSERVATIONS ON RECENT SPECIES

*Scymnodalatias garricki* Kukuev &

Konovalenko, 1988

The only specimen is the holotype, a male about 377 mm TL possibly stored in Kaliningrad, although I observed it in the Zoological Institute Museum, Academy of Sciences, Saint Petersburg, SIN n. 48190.

*Body morphology* – Small shark (Text-fig. 3), apparently immature, with relatively short claspers as in *Scymnodalatias sherwoodi* (Archev, 1921) but with relatively long and needle-like spurs, not short and subterminal as described by Garrick (1956, p. 556) for *S. sherwoodi*.

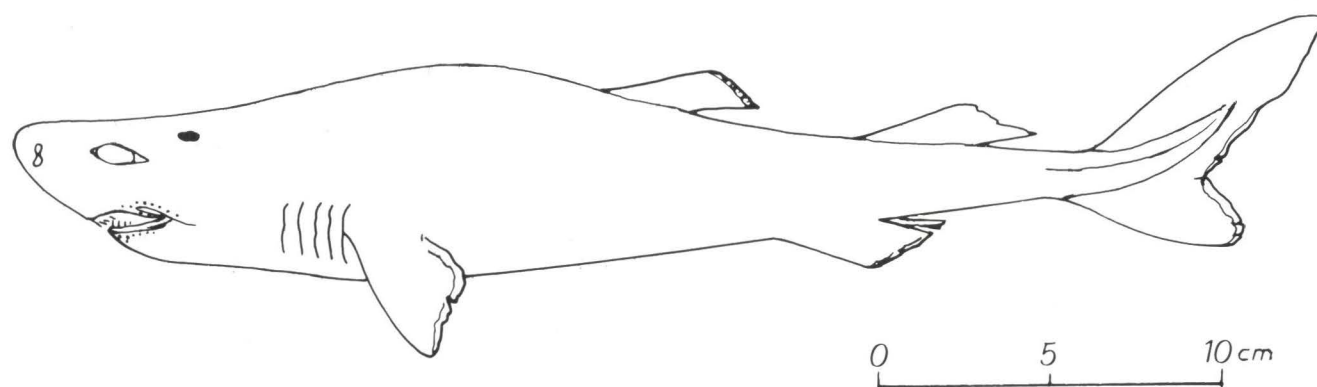
Dorsal fins without spines as in *Scymnodalatias*.

The snout is slightly bulbous, not acute as in *S. sherwoodi* and *S. albicauda* Taniuchi & Garrick, 1986. In lateral and dorsal view it shows a rounded contour without the angles drawn by Kukuev & Konovalenko (1988, fig. 18) not triangular as in the drawing by Garrick (1956, text-fig. 1, B-C) for *S. sherwoodi*.

Pectoral fins relatively small, like *S. sherwoodi*, with outer apex not acute as in the other two species of the genus but fairly rounded, even if less than in *Zameus*.

The proportional dimensions of the body apparently fall within the range of variation of *Scymnodalatias* if compared with data reported by Taniuchi & Garrick (1986, tab. 1). The first dorsal position (snout apex to first dorsal origin in percentage of TL: 46.6) is similar but slightly more posterior than in *S. albicauda* and *S. sherwoodi* (44.0, 41.0, 44.7), but it proves to be decidedly further back than in *Zameus squamulosus* (38.7, 38.1).

Even considering a margin of error due to the deformation of the specimen preserved, the dorsal profile of the body (Text-fig. 3), as described by Kukuev & Konovalenko (1988, p. 315 and fig. 1a) as well, is slightly flattened on the head and becomes strongly arcuated in the region between the posterior inner tip of the pectorals and the begin-



Text-fig. 3 - *Scymnodalatias garricki* Kukuev & Konovalenko, 1988; holotype, male, 377 mm TL; lateral profile. The body proportions are in part obtained by measuring. (Redrawn by the author).

ning of the first dorsal. The scales from the side of the trunk are leaf-like with three longitudinal ridges ending posteriorly with three cusps. The median ridge is the longest. Arcuated transverse ridges (microsculpture) are present, of the same type as in *Scymnodalatias* and *Zameus*, but in this last genus, the pattern is complicated by a more dense net of ramifications of the transverse ridges. The longitudinal ridges are dorsally concave along their entire length as in *Scymnodalatias*.

**Odontology** – The dentition (Pl. 1, figs 1-9) shows a strong dignathic heterodonty, a weak gradient monognathic heterodonty and an anaulacorhizid root vascularization.

The dental formula  $\frac{26-26}{15-15}$  differs from that

reported by the authors of the species (Kukuev & Konovalenko, 1988, p. 315) since they did not count the teeth that are more inner in the mouth and they did not specify the lower symphyseal row.

**Upper teeth:** upper anterior tooth (Pl. 1, figs 2a, b) with very acute straight cusp (needle-like). Parasymphyseal tooth (Pl. 1, figs 1a, b) occurs with about the same features but is slightly shorter than the anteriors and with a different ratio root height/lobe length. The roots are bilobate with peculiarly very long lobes, recalling the *Odontaspis* root profile, rounded or ovoid in section. The lingual and labial faces of the crown are strongly convex. The labial face brings a relatively long subcentral cutting edge, slightly lateral in the anterior tooth figured (Pl. 1, figs 2a, b) which is followed basally by a flat triangular surface of bifurcated enameloid at the crown base. A large basal foramen occurs centrally where the two lobes of the root converge. Another large foramen occurs in the latero-proximal part of the two root lobes while a smaller foramen is found on the lingual bulge of the root near the crown-root

junction. In lateral view, the crown is well flexed forward and slightly sigmoid at the top. The lingual profile of the tooth, in the region where the basal part of the crown joins the root, forms an angle of 90° (see the fossil tooth in Pl. 5, fig. 1c). Some scattered small foramina can occur. Along the file, towards the commissure, the teeth change their morphology in the manner of the other species of *Scymnodalatias* (e.g. *S. sherwoodi*, Garrick, 1956, text-fig. 1, F - I). The 14th tooth (latero-posterior) (Pl. 1, figs 5a, b) shows a massive polygonal root with short lobes and, considering the fact that the enameloid capsule has worn away, the crown appears to be straight, although inclined towards the commissure. Posterior teeth (Pl. 1, figs 3, 4a, b) with longitudinally expanded root and crown inclined towards the commissure. In the commissural tooth (Pl. 1, figs 6a, b) the crown is still relatively high and the root is like a rounded plate.

**Lower teeth:** apart from the symphyseal which has not been figured, the anterior teeth (Pl. 1, figs 7a, b) have a subrectangular blade-like root slightly shorter than the crown. The first anteriors show a straight crown which becomes inclined towards the commissure in the following teeth of the file. There is a weaker gradient of monognathic heterodonty than in the upper tooth file. The cusp shows a characteristic and marked widening at the base and becomes very acute at the apex. The lingual and labial faces of the cusp are notably convex. The uvula is absent as well as a true ornamentation at the base of the enameloid. The apron is relatively wide and flattened, and does not overhang the root. On the lingual face (Pl. 1, fig. 7b) the root forms a strongly convex longitudinal ridge bearing a central and a mesial foramen. A basal sulcus occurs in the fifth anterior tooth (Pl. 1, figs 7a, b) but it is lacking or reduced to a small foramen in the latero-posterior tooth (Pl. 1, fig. 8b). On the labial face of the lower

tooth root and around the apron a variable number of foramina is present (Pl. 1, figs 8a, 9a); in particular, the longest of them, laterally to the apron, have an elliptical contour and a herring-bone pattern, ending in a short depression. The latero-posterior tooth cusp (Pl. 1, figs 8a, b) has a beaked profile and widens at the base. The commissural tooth (Pl. 1, figs 9a, b) is wide with a strongly inclined mesial cutting edge. On this tooth three large foramina occur on the distal part of the root together with scattered foramina around the apron.

*Comments and differences with the other species of Scymnodalatias* – Apart from the number of teeth that were erroneously reported by Kukuev & Konovalenko (1988, p. 315) for this species, which, in actual fact, is similar to that of *S. sherwoodi* (Garrick, 1956, p. 568) and *S. albicauda* (Taniuchi & Garrick, 1986, p. 121) the differential morphological characters listed by Kukuev & Konovalenko (1988, p. 317) seem to show that *S. garricki* is a valid and separate species. This opinion is further strengthened by the slightly bulbous snout and by the relatively long and not subterminal clasper's spurs. Essentially the tooth morphology and vascularization in the known species of *Scymnodalatias* are very similar. The observations below are impeded at the present time since it is not possible to check the gynandric and ontogenetic heterodonty and individual variation; furthermore, I did not directly observe the dentition of *S. sherwoodi*, since I based my examination on the presumably accurate figure of Garrick (1956, text-fig. 1, F - J).

In *S. garricki* the anterior upper teeth, in labial view (Pl. 1, fig. 2a), appear to be relatively symmetrical with a straight crown and a subcentral cutting edge; the root lobes are very long and ovoid in section. In *S. albicauda* and *S. sherwoodi* (see Herman, Hovestadt-Euler & Hovestadt, 1989, pl. 17;

Garrick, 1956, text-fig. 1, F, G) the crown is more or less twisted and in the first species sigmoid in lingual and labial view. A possible sexual dimorphism that might explain these differences may not be justified considering the fact that, although there are relatively few specimens, the upper fossil teeth found consistently show straight and symmetrical crowns as in the holotype of *S. garricki*.

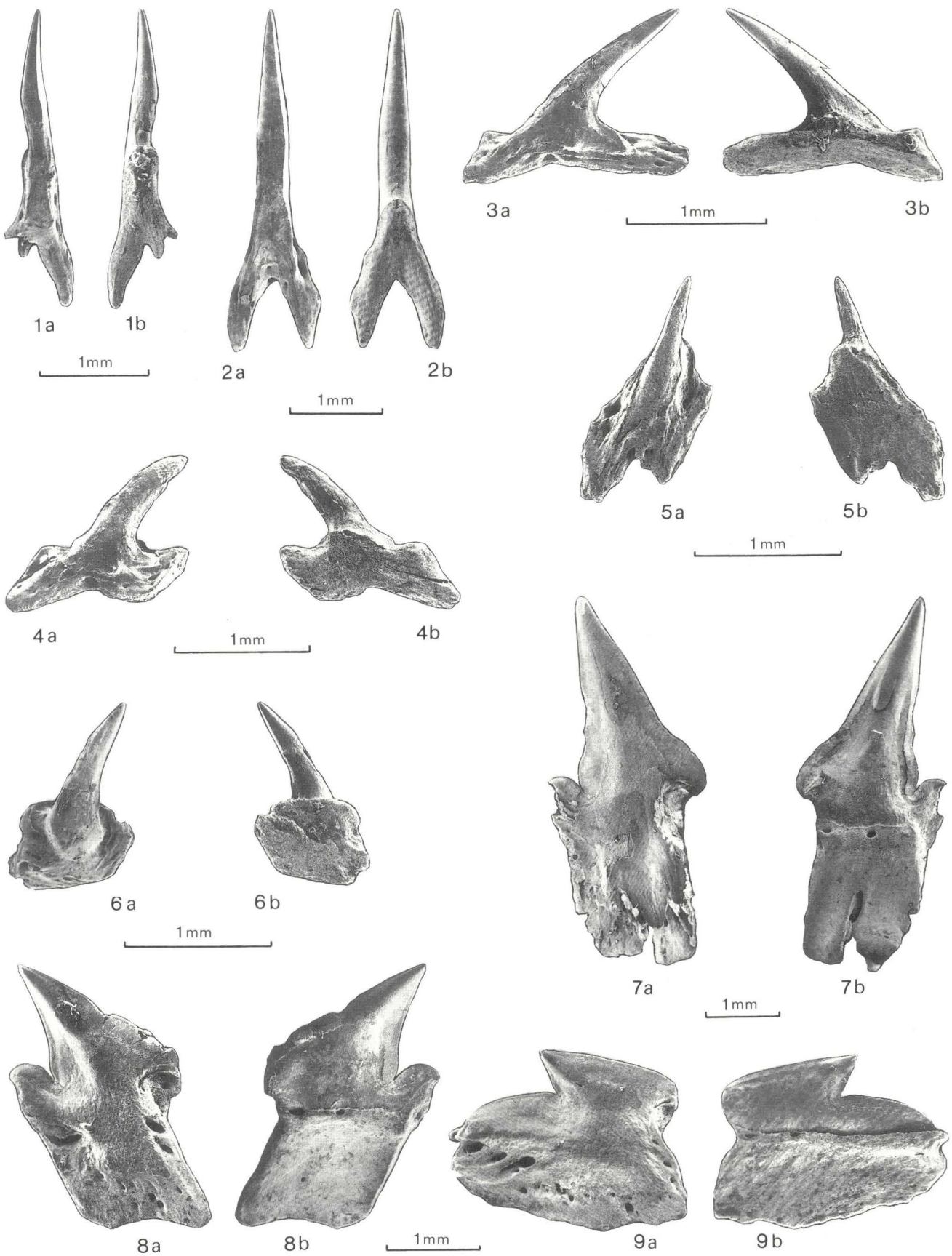
The root lobes are notably shorter in *S. albicauda* and *S. sherwoodi* than in *S. garricki* considering the root proportions (root height/lobe length). Another, possibly less significant difference, concerns the region of the root where the two lobes converge in proximity of the central foramen. Here the two lobes form a marked angle and a well defined furrow in *S. albicauda* and *S. sherwoodi* (Herman, Hovestadt-Euler & Hovestadt, 1989, pl. 17; Garrick, 1956, text-fig. 1, F, G, K, L) which are absent or only slightly sketched in *S. garricki* (Pl. 1, figs 1a, b, 2a, b). Considering just the lower teeth, the differences among these three species appear to be more difficult to define and could fall in the variation range of a single species. In the holotype of *S. albicauda*, apart from the fact that the enameloid has partly worn away by the formalin, the lower tooth crown shows a profile very similar to that of *S. garricki*. The apron is uniformly flat and wide while in the specimen of the same species illustrated by Herman, Hovestadt-Euler & Hovestadt (1989, pl. 17), this is a little narrow at the top and widened at the base where enameloid folds can also be observed.

*Zameus squamulosus* (Günther, 1877) and  
*Scymnodon ringens* Bocage & Capello, 1864

The dentition of these species was recently described and illustrated by Herman, Hovestadt-Euler & Hovestadt (1989, text-pl. 14, pl. 16; 1993, text-pls 1, 2, pls 49, 50) who show separately the dental series of *S. squamulosus* (specimen from Japan)

#### EXPLANATION OF PLATE 1

- Figs 1-9 - *Scymnodalatias garricki* Kukuev & Konovalenko, 1988. Holotype, Recent, male, 377 mm TL, 40° 22' N, 30° 10' W, North Atlantic Ridge, SIN no. 48190.
- 1) upper parasymphysial tooth;
  - 2) 3rd left upper anterior tooth;
  - 3) right upper posterior tooth;
  - 4) right upper posterior tooth;
  - 5) 14th right upper latero-posterior tooth;
  - 6) right upper commissural tooth;
  - 7) 5th right lower anterior tooth;
  - 8) right lower latero-posterior tooth;
  - 9) right lower commissural tooth;
- a) labial and b) lingual views; scale bar = 1 mm.



and *S. obscurus* (Senegal). Because of this, I limit myself to the description of fossil teeth (Pl. 5, figs 8-10, Pl. 6, figs 1-6) comparing them also to those of a specimen of *S. obscurus* from Senegal (Pl. 2, figs 1-11).

#### SYSTEMATIC PALAEOLOGY

Class CHONDRICHTYES  
 Subclass ELASMOBRANCHII  
 Cohort EUSELACHII  
 Superorder SQUALOMORPHII  
 Order SQUALIFORMES  
 Family SQUALIDAE  
 Genus SCYMNODALATIAS Garrick, 1956  
 SCYMNODALATIAS aff. GARRICKI Kukuev &  
 Konovalenko, 1988  
 Pl. 3, figs 1-9; Pl. 4, figs 1-9; Pl. 5, figs 1-7

*Material and description* – MPP, n. 120-2. FCF Coll. (Pl. 3, figs 1a, b). Left upper anterior tooth. The rounded root lobes, which form a tight angle, indicate that the tooth is very close to the symphysis (possibly the first anterior). The different ratio root height/lobe length excludes the parasymphysial (see Pl. 1, figs 1a, b for comparison). On the labial face of the crown, the cutting edge is subcentral and develops in the upper 2/3 section of the cusp (Pl. 3, fig. 1a).

MPP, n. 120-3, FCF Coll. (Pl. 5, figs 1a, b, c). Left upper anterior tooth. This tooth shows the typical morphology of the first anteriors as observed in the holotype of *S. garricki* (Pl. 1, figs 2a, b). On the labial face of the crown, the cutting edge is subcentral, slightly shifted on the mesial side. The lower third section of the labial face of the crown has a triangular surface of enameloid which narrows at

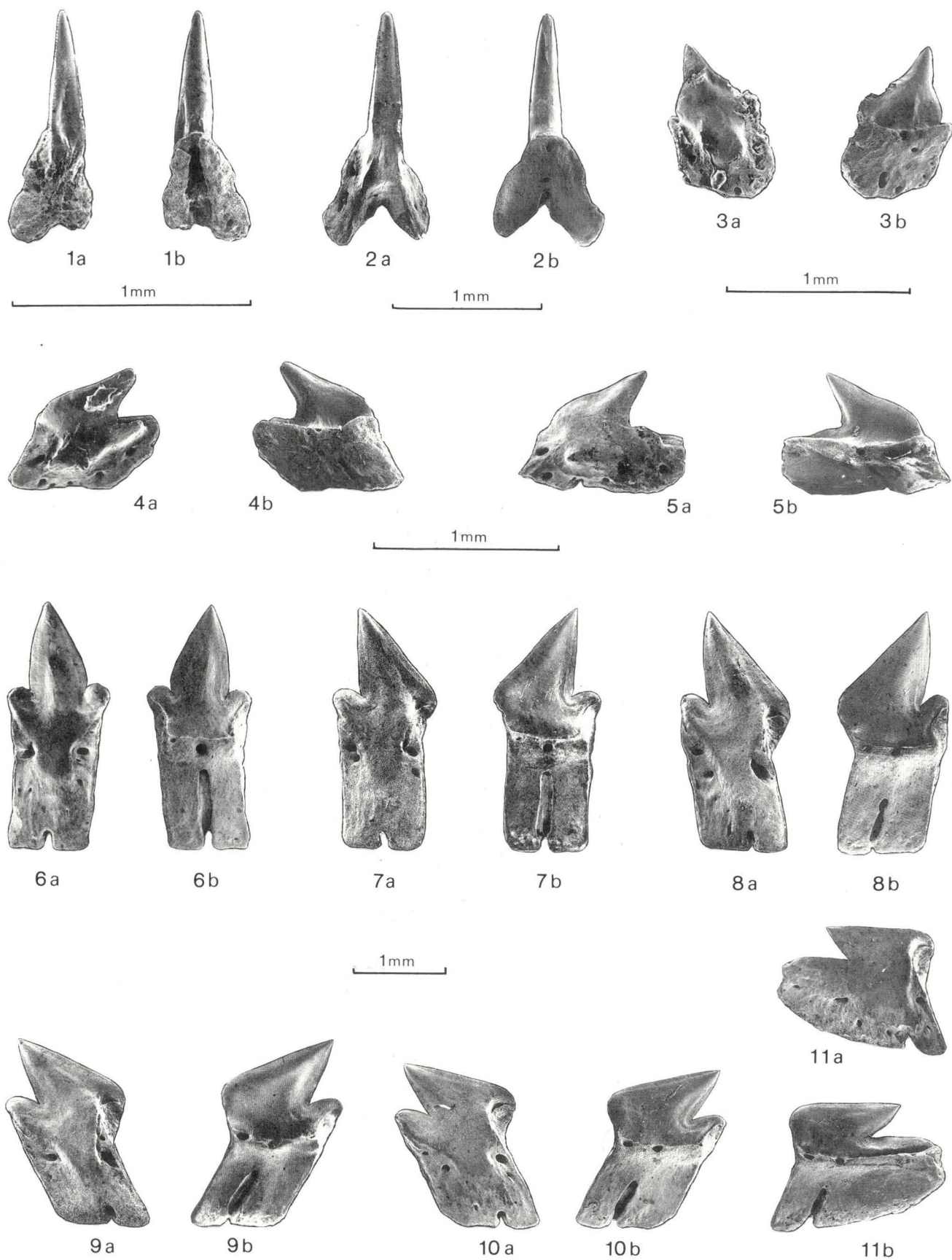
the top and ends where the cutting edge begins. At the base, it forms a slight central depression above the large central foramen (Pl. 5, fig. 1a). In lateral view (Pl. 5, fig. 1c) the cusp is flexed forward and sigmoid at the top. On the sides of the root lobes a slight groove is noted which leads to a large oval foramen near the crown base. Few scattered foramina occur around the central foramen (Pl. 5, fig. 1a) together with an opened and short sulcus. The root lobes are regularly convex starting from the lingual bulge of the root where a small central foramen is present near the enameloid-root junction (Pl. 5, fig. 1b).

MPP, n. 120-4, FCF Coll. (Pl. 3, figs 5a, b). Right lower antero-lateral tooth. The tooth is slender since its height is 3 times the width of the crown. The height of the crown (measured at the base of the enameloid on the lingual face) is slightly larger than the height of the root. The cusp is characteristically acute and narrow at the apex (in the upper 2/3 section) while it widens and becomes bell-shaped in the lower third part. The labial and lingual cusp faces are strongly convex especially at the apex. The apron (Pl. 3, fig. 5a) is relatively long and narrow, slightly overhanging the mesial and distal parts of the root. The base of the apron widens slightly. On the root, on both sides of the apron, there are some large foramina with a characteristically elliptic contour and herring-bone pattern [this feature is observed better in other teeth (e.g. Pl. 3, fig. 3a; Pl. 4, fig. 2a)]. Around the lower part of the apron some scattered foramina occur. The root base, on the lingual face, shows a short sulcus above which there is an elongated median aperture. The root is subrectangular with subparallel distal and mesial edges, slightly inclined towards the commissure. On the lingual face (Pl. 3, fig. 5b) the root has a strongly convex longitudinal ridge with a central aperture

#### EXPLANATION OF PLATE 2

Figs 1-11 - *Scymnodon obscurus* (Vaillant, 1888) synonymized with *Zameus squamulosus* (Günther, 1877). Recent, male, 384 mm TL, Station 41, Villa Ana, 14° 19' N, 17° 35' W, 650 m deep, Senegal.

- 1) left upper parasymphysial tooth;
  - 2) 4th right upper anterior tooth;
  - 3) 12th left upper tooth (latero-posterior);
  - 4) 23rd right upper tooth (latero-posterior);
  - 5) 26th right upper tooth (commissural);
  - 6) lower symphysial tooth;
  - 7) 1st right lower anterior tooth;
  - 8) 7th right lower tooth (antero-lateral);
  - 9) 17th right lower tooth (lateral);
  - 10) 18th right lower tooth (lateral);
  - 11) 19th right lower tooth (commissural);
- a) labial and b) lingual views; scale bar = 1 mm.



and a larger mesial one. In correspondence to these foramina and to the crown distal blade the base of the enameloid is depressed and undulated.

MPP, n. 120-5, FCF Coll. (Pl. 3, figs 3a, b). Left lower anterior tooth with characters similar to the preceding one but with a slightly more erect cusp. The widening of the profile of the mesial and distal cutting edges at the base of the cusp is very marked and characteristic, likewise the apron and the style of the foramina on the labial face of the tooth.

MPP, n. 120-6, FCF Coll. (Pl. 3, figs 9a, b). Left lower anterior tooth lacking the lower part of the root. This tooth is large and similar to the corresponding tooth of the holotype (Pl. 1, figs 7a, b). The cusp is strongly convex and acute in the upper 2/3 section.

MPP, n. 120-7, FCF Coll. (Pl. 4, figs 2a, b). Right lower lateral tooth with the typical morphology described above. The tooth is slightly larger in proportion to the preceding ones.

MPP, n. 120-8, FCF Coll. (Pl. 4, figs 9a, b). Right lower latero-posterior tooth. The tooth is wider and more inclined than the preceding ones. The cusp is wide at the base and the profile of the mesial and cutting edges more regular (slightly concave).

MPP, n. 120-9, FCF Coll. (Pl. 4, figs 8a, b). Left lower lateral tooth similar to the preceding one but placed slightly more mesially along the tooth file.

MPP, n. 120-10, FCF Coll. (Pl. 4, figs 3a, b). Left lower latero-posterior tooth. This specimen shows the apex of the cusp inclined towards the commissure and beaked matching with the lower latero-posterior of the holotype (Pl. 1, figs 8a, b).

MPP, n. 120-11, FCF Coll. (Pl. 3, figs 2a, b). Lower symphyseal tooth. The tooth is symmetrical and slender. Its proportions, vascularization and the form of the apron seem to indicate that the tooth belongs to the same species of shark.

MPP, n. 120-12, FCF Coll. (Pl. 4, figs 1a, b). Left lower lateral tooth. Tooth with the same vascularization pattern and root as the above

described ones. The cusp, however, has subrectilinear cutting edges, lacking a marked widening at the base. Considering the fact that intermediate situations are observed in other teeth, a tentative interpretation of this form may be made as an expression of variability or, more probably, of sexual dimorphism.

MPP, n. 120-13, FCF Coll. (Pl. 3, figs 4a, b). Left lower anterior tooth. The tooth matches the characteristics of the specimen of Pl. 3, figs 3a, b. It differs in having a large aperture produced by the fusion of smaller foramina on the mesial and distal parts of the root, lateral to the apron.

MPP, n. 120-14...22 (Pl. 3, figs 6a, b; 8a, b; Pl. 4, figs 4a, b, 5a, b, 7a, b; Pl. 5, figs 3a, b, 4a, b, 5a, b, 7a, b). Lower lateral teeth. This group of teeth includes specimens that show a certain degree of variability in the profile of the mesial and distal cutting edges of the cusp, and occupy more or less lateral positions along the file. In particular, the tooth of Pl. 5, figs 3a, b has a wider apron, slightly ornamented at the base.

MPP, n. 120-23, FCF Coll. (Pl. 5, figs 2a, b). Left lower anterior tooth. The profile of the cusp is characterized by the typical marked widening at the base, well matching similar specimens described above (Pl. 3, figs 3, 4a, b).

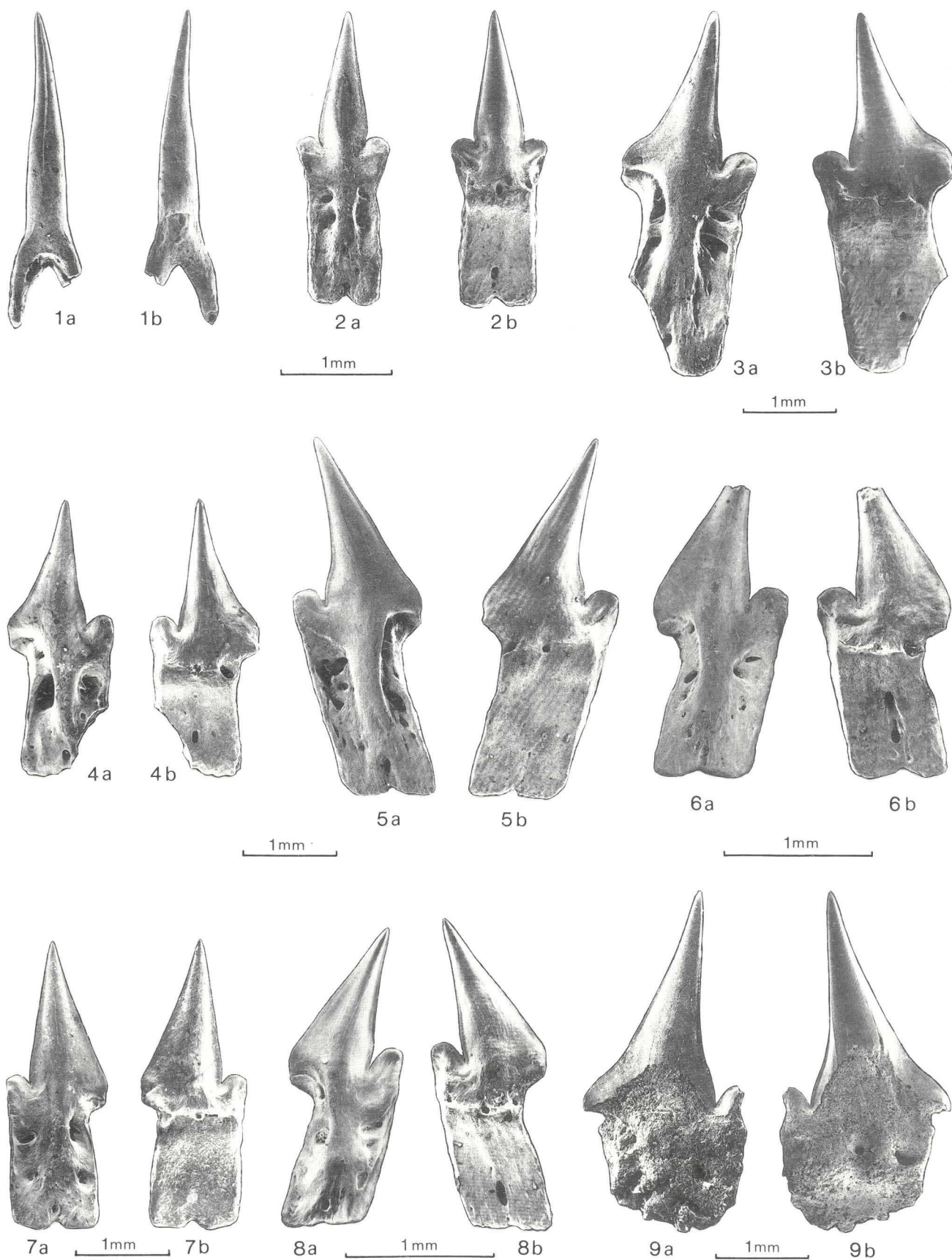
MPP, n. 120-24, FCF Coll. (Pl. 3, figs 7a, b). Right lower anterior tooth. If compared with the above described tooth (Pl. 5, figs 2a, b) this specimen shows the profile of the crown cutting edges without the marked widening at the base. The difference may be interpreted as an expression of sexual dimorphism.

MPP, n. 120-25, FCF Coll. (Pl. 5, figs 6a, b). Right lower latero-posterior tooth. Large specimen with beaked cusp strongly bell-shaped at the base. On the basal face of the root, a sulcus followed by a long groove occurs. Apart from the position along the tooth file, the specimen matches closely the above described anterior tooth style (Pl. 5, figs 2a, b) and in the same way it harmonizes well with the

#### EXPLANATION OF PLATE 3

Figs 1-9 - *Scymnodalatias* aff. *garricki* Kukuev & Konovalenko, 1988. Lower Pliocene, S. Andrea Bagni, Parma, Northern Apennines.

- 1) MPP, n. 120-2, FCF Coll. - left upper anterior tooth (possibly the 1st);
- 2) MPP, n. 120-11, FCF Coll. - lower symphyseal tooth;
- 3) MPP, n. 120-5, FCF Coll. - left lower anterior tooth;
- 4) MPP, n. 120-13, FCF Coll. - left lower anterior tooth;
- 5) MPP, n. 120-4, FCF Coll. - right lower antero-lateral tooth;
- 6) MPP, n. 120-14, FCF Coll. - left lower antero-lateral tooth;
- 7) MPP, n. 120-24, FCF Coll. - right lower anterior tooth;
- 8) MPP, n. 120-15, FCF Coll. - left lower lateral tooth;
- 9) MPP, n. 120-6, FCF Coll. - left lower antero-lateral tooth;
- a) labial and b) lingual views; scale bar = 1 mm.



corresponding lower latero-posterior of the holotype (Pl. 1, figs 8a, b).

MPP, n. 120-26, FCF Coll. (Pl. 4, figs 6a, b). Right lower latero-posterior tooth. Very small tooth (almost 1.5 mm high) with a relatively high root and large distal blade of the crown. The cusp is slightly beaked and the vascularization style (herring-bone patterned foramina around the apron) matches that of the teeth described above. This tooth may be interpreted as an expression of ontogenetic heterodonty (juvenile specimen).

*Comments* – The differences regarding the more or less bell-shaped profile of the cusp base may be an expression either of individual variation, but more probably of sexual dimorphism. The apron appears narrower than that of the holotype teeth. If, when checked on a sufficient number of living specimens, this difference were to prove recurrent, it might provide the basis on which to justify a separate *taxon*. Slight differences in the style of root foramina at the side of the apron in teeth showing the same kind of bell-shaped cusp base (e.g. Pl. 3, figs 3a, 4a) strengthen the hypothesis that it is a question of intraspecific variation. The size of the largest fossil teeth (e.g. Pl. 3, figs 5, 9; Pl. 5, figs 1, 6), checked on a sufficient group of specimens, similar to that of the *S. garricki* holotype (e.g. Pl. 1, figs 2, 7, 8) and consistently less than that met with in *S. sherwoodi* (Garrick, 1956, text-figs 1, K, L) and *S. albicauda* (e.g. the holotype and the specimen figured by Herman, Hovestadt-Euler & Hovestadt, 1989, pl. 17, lower teeth) might mean that *S. garricki* does not reach the size of the other two species of the same genus. This might provide further evidence that *S. garricki* is a valid species and confirm the likening of the fossil teeth to this *taxon*.

Genus ZAMEUS Jordan & Fowler, 1903  
ZAMEUS SQUAMULOSUS (Günther, 1877)  
[= *Scymnodon obscurus* (Vaillant, 1888)]  
Pl. 5, fig. 8; Pl. 6, figs 1-5

*Material and description* – MPP, n. 120-29, FCF Coll. (Pl. 6, figs 1a, b). Right lower anterior tooth. The tooth is blade-like and the root anaulacorhizid. Its height is about 3.5 mm. The root is straight, subrectangular with its basal ends slightly rounded. The cusp is inclined towards the commissure. The height of the crown, measured on the lingual face from the base of the enameloid near the longitudinal ridge, is about the same as that of the root. The enameloid at the base of the crown is worn away. The cusp is slightly convex both on the lingual and labial face. The longitudinal ridge on the lingual face of the root has a central and a mesial aperture. A long central sulcus is present basally on the root. The uvula is absent. On the labial face the apron is relatively long and axially slightly convex but not overhanging the root. At the sides of the apron, on the root, there are from one to two small round foramina. The distal and mesial depressions, as a result of the interlocking of the tooth rows, are small.

MPP, n. 120-30, FCF Coll. (Pl. 6, figs 2a, b). Left lower lateral tooth. Characters conforming to those typical of the species. The tooth differs from the preceding one in the larger openings at the sides of the apron, and for the more inclined cusp and root, due to a more lateral position along the tooth file. It is about 3 mm in height.

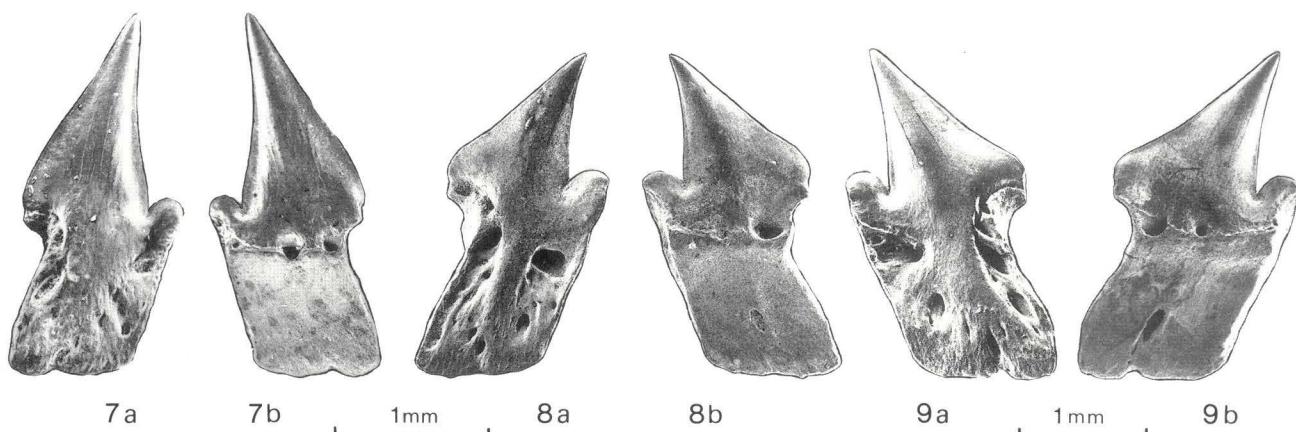
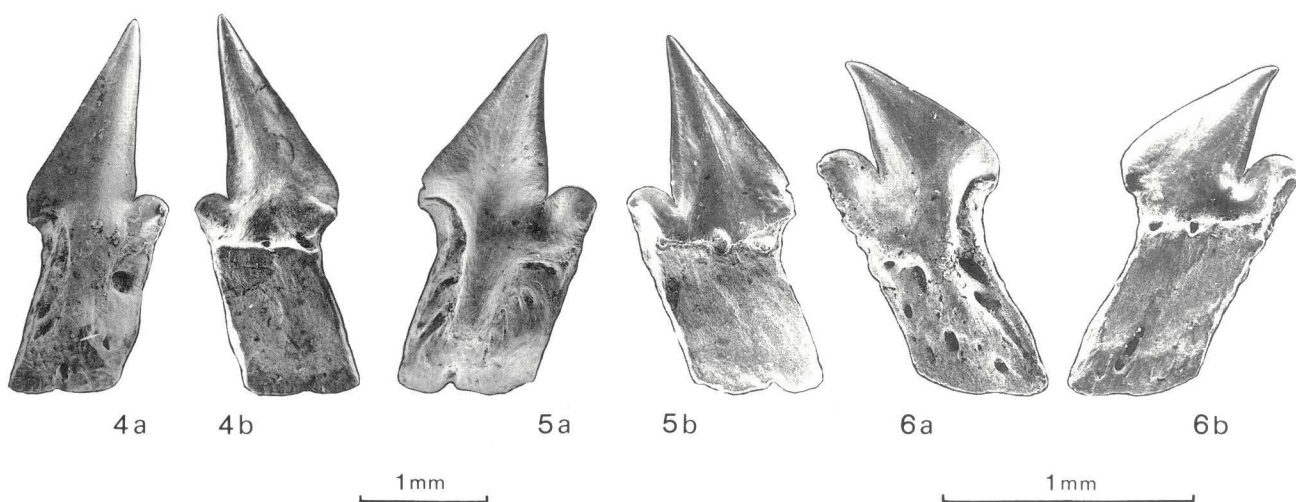
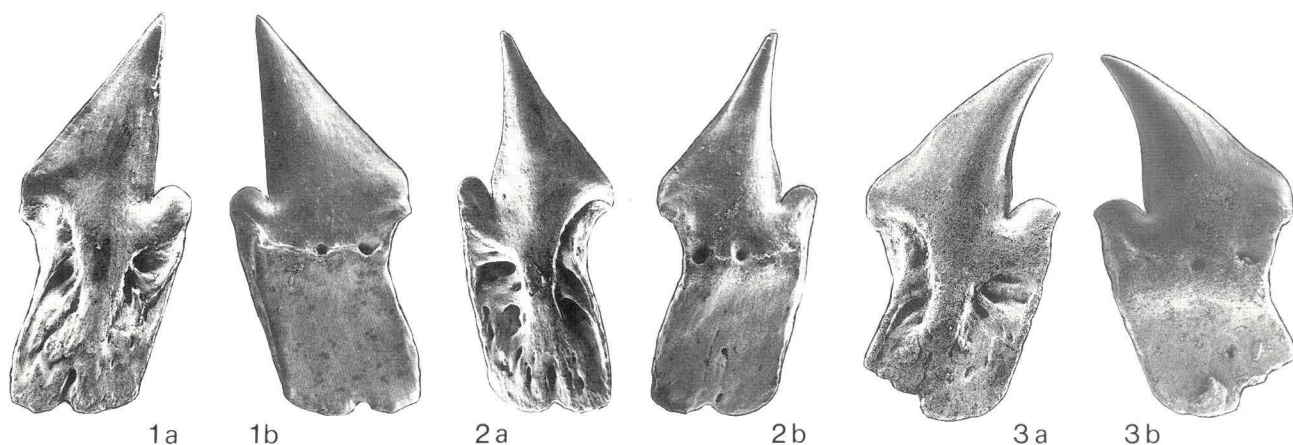
MPP, n. 120-31, FCF Coll. (Pl. 6, figs 3a, b). Left lower latero-posterior tooth. Apart from the apron which is slightly wider, the tooth differs only in the sense that it is more inclined towards the commissure.

MPP, n. 120-32, FCF Coll. (Pl. 6, figs 4a, b). Left lower lateral tooth. This small tooth (little more than 1 mm in height) is more slender than the preceding ones and the mesial and distal cutting edges of the cusp are slightly more convex. The distal blade of the crown appears larger. This morphology characterizes the juvenile stages (ontogenetic heterodonty).

MPP, n. 120-33, FCF Coll. (Pl. 6, figs 5a, b). Left

#### EXPLANATION OF PLATE 4

- Figs 1-9 - *Scymnodontias* aff. *garricki* Kukuev & Konovalenko, 1988. Lower Pliocene, S. Andrea Bagni, Parma, Northern Apennines.
- 1) MPP, n. 120-12, FCF Coll. - left lower lateral tooth;
  - 2) MPP, n. 120-7, FCF Coll. - right lower lateral tooth;
  - 3) MPP, n. 120-10, FCF Coll. - left lower latero-posterior tooth;
  - 4) MPP, n. 120-16, FCF Coll. - left lower lateral tooth;
  - 5) MPP, n. 120-17, FCF Coll. - left lower lateral tooth;
  - 6) MPP, n. 120-26, FCF Coll. - right lower latero-posterior tooth (juvenile);
  - 7) MPP, n. 120-18, FCF Coll. - left lower lateral tooth;
  - 8) MPP, n. 120-9, FCF Coll. - left lower lateral tooth;
  - 9) MPP, n. 120-8, FCF Coll. - right lower latero-posterior tooth;
- a) labial and b) lingual views; scale bar = 1 mm.



upper anterior tooth. The tooth has an elongated crown devoid of lateral cusps. The labial face of the crown is relatively flat, and the lingual face strongly convex. The labial face of the crown is arched basally, forming two short processes of enameloid that rest on the root lobes, these also being slightly arched. Basally, a short sulcus and a central aperture are present. On the labial face of the root and on each side of the sulcus, there is at least one foramen. A relatively large foramen can be found on the depressed mesial and distal side of the root. The cusp is narrow at the base and slightly curved at the top towards the commissure matching the anterior tooth cusps of the living specimen from Senegal (Pl. 2, figs 2a, b). There seems, however, to be a remarkable degree of variability in this species since in another living specimen from Senegal (Herman, Hovestadt-Euler & Hovestadt, 1993, pl. 50, tooth ps and a) the cusps are sigmoid. The mesial and distal cutting edges are interrupted at the cusp base, but they re-appear as crests at the sides of the enameloid surface in light relief with regards to the crown base. One foramen is present on the lingual bulge of the root. The crown base does not show any ornamentation.

MPP, n. 120-34, FCF Coll. (Pl. 5, figs 8a, b). Right lower anterior tooth near the symphysis. Relatively small tooth (about 2.4 mm in height) with angular root basal ends. The characters are those typical of the juvenile stages: slenderness, strongly convex mesial and distal cutting edges of the cusp strongly convex and relatively wide distal blade of the crown. A long and open groove occurs on the basal face of the root.

*Comments* – The morphology of the fossil teeth (Pl. 5, fig. 8, Pl. 6, figs 1-5) well matches that of the teeth of the specimen from Senegal of «*Scymnodon obscurus*» *sensu stricto* (Pl. 2, figs 1-11). A certain

degree of variability can be noted in the form of the lower teeth cusp if we consider the Japanese specimen (Herman, Hovestadt-Euler & Hovestadt, 1993, pl. 49) of *Zameus squamulosus* where it appears to be slightly straightened at the apex.

The strong resemblance between the latero-posterior teeth with *Centrosymnus crepidater* (Bocage & Capello, 1864) causes some confusion (see Ledoux, 1970, text-fig. 17, Ba). The distinction may be based on the style of the crown cutting edges after having located the tooth along the file. In *C. crepidater* the cusp is remarkably straighter in the males, and in the females, the crown mesial cutting edge is from slightly concave to subrectilinear, while in the Atlantic specimens of *S. obscurus* it appears to be consistently slightly convex. Furthermore, the apron in *C. crepidater* appears to be slightly shorter.

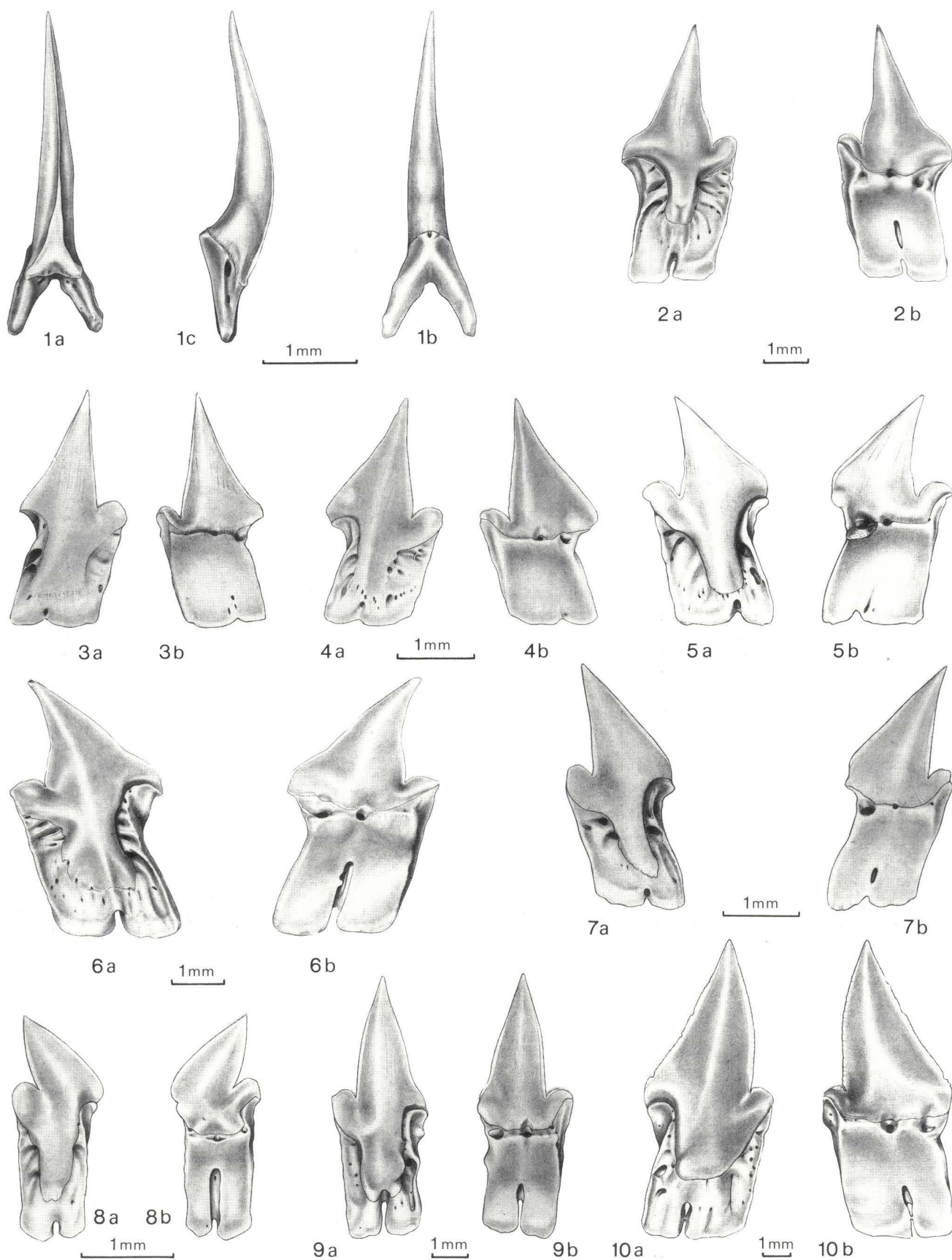
Genus SCYMNODON Bocage & Capello, 1864  
SCYMNODON RINGENS Bocage & Capello, 1864  
Pl. 5, figs 9, 10; Pl. 6, fig. 6

*Material and description* – MPP, n. 120-27, FCF Coll. (Pl. 5, figs 9a, b). Right lower anterior tooth. The tooth is narrower than the preceding one ( $h/w = 2.7$ ) and the crown height/root height ratio similar. The cusp is subvertical with the distal cutting edge convex and the mesial one flexuous. If magnified, these show a faintly visible discontinuous serration. The apron slightly overhanging the root is relatively longer than that of the preceding tooth and its distal and mesial cutting edges subparallel and vertical. The arrangement of the foramina is similar. The central basal sulcus is deep.

MPP, n. 120-28, FCF Coll. (Pl. 5, figs 10a, b). Left lower lateral tooth. The blade-like tooth is relatively large (about 10 mm high) and wide ( $h/w$

#### EXPLANATION OF PLATE 5

- Figs 1-7 - *Scymnodalatias* aff. *garricki* Kukuev & Konovalenko, 1988. Lower Pliocene, S. Andrea Bagni, Parma, Northern Apennines.  
1) MPP, n. 120-3, FCF Coll. - left upper anterior tooth;  
2) MPP, n. 120-23, FCF Coll. - left lower anterior tooth;  
3) MPP, n. 120-19, FCF Coll. - left lower antero-lateral tooth;  
4) MPP, n. 120-20, FCF Coll. - left lower lateral tooth;  
5) MPP, n. 120-21, FCF Coll. - right lower lateral tooth;  
6) MPP, n. 120-25, FCF Coll. - right lower latero-posterior tooth;  
7) MPP, n. 120-22, FCF Coll. - right lower lateral tooth;  
Fig. 8 - *Scymnodon obscurus* (Vaillant, 1888) synonymized with *Zameus squamulosus* (Günther, 1877). Lower Pliocene, S. Andrea Bagni, Parma, Northern Apennines.  
8) MPP, n. 120-34, FCF Coll. - right lower anterior tooth (possibly the first) (juvenile).  
Figs 9, 10 - *Scymnodon ringens* Bocage & Capello, 1864. Lower Pliocene, S. Andrea Bagni, Parma, Northern Apennines.  
9) MPP, n. 120-27, FCF Coll. - right lower anterior tooth;  
10) MPP, n. 120-28, FCF Coll. - left lower antero-lateral tooth;  
a) labial, b) lingual and c) lateral views; scale bar = 1 mm.



= 2.28). The crown, measured on the lingual face is higher than the root. The tooth is slightly inclined towards the commissure, while the apex of the cusp tends to straighten in such a way that the mesial cutting edge is slightly concave while the distal edge is convex and subvertical; both show a very fine serration. Both the lingual and labial faces of the cusp are convex. The apron is wide and relatively short, slightly overhanging the root. The foramina around the apron are small and vertically arranged on the mesial and distal parts of the root. Basally a deep sulcus occurs. The distal blade of the crown is relatively small as well as the mesial and distal facets of interlocking.

MPP, n. 120-35, FCF Coll. (Pl. 6, figs 6a, b). Right upper latero-posterior tooth. The tooth, which is 3mm high, has a crown with an acute cusp inclined toward the commissure. The lingual face of the crown more convex than the labial. The distal and mesial cutting edges do not reach the crown base; the mesial cutting edge is longer. The labial face of the crown brings numerous crests of enameloid at the base and a thick distal blade is present, disjunct from the distal cutting edge. The subrectangular root is longitudinally expanded. On its labial face, there is a longitudinal alignment of small foramina. Other foramina are very close to the base of the enameloid. A central aperture is present at the base of the labial face of the root. On the lingual face of the root, near the enameloid-root junction (not visible in figure 6b) there are two foramina on the mesial and distal side. A central foramen is present at the top, likewise an elongated central aperture or sulcus basally.

*Comments* – There is a certain amount of variation in the cusp height/root height and tooth height/width ratios both in the fossil teeth and in those of the living species, which can be considered as due to size and possibly sex. To confirm this, the jaw from a large living specimen (Cadenat & Blache, 1981, p. 89, text-fig. 66b) shows very wide and relatively short teeth, which recall some fossil specimens (e.g. specimen in Pl. 5, figs 10a, b).

#### TAPHONOMY, PALEOECOLOGY AND PALEOBIOGEOGRAPHY

*Taphonomy* – Due to the method of recovering the material (the sieving of surface wash probably at least in part from small concentrations), we must take into account the fact that we are not dealing with a paleocommunity *sensu stricto*, but with a mixture of heterochronous populations; even though they appear to characterize a relatively short time interval, which may make the variability range wider.

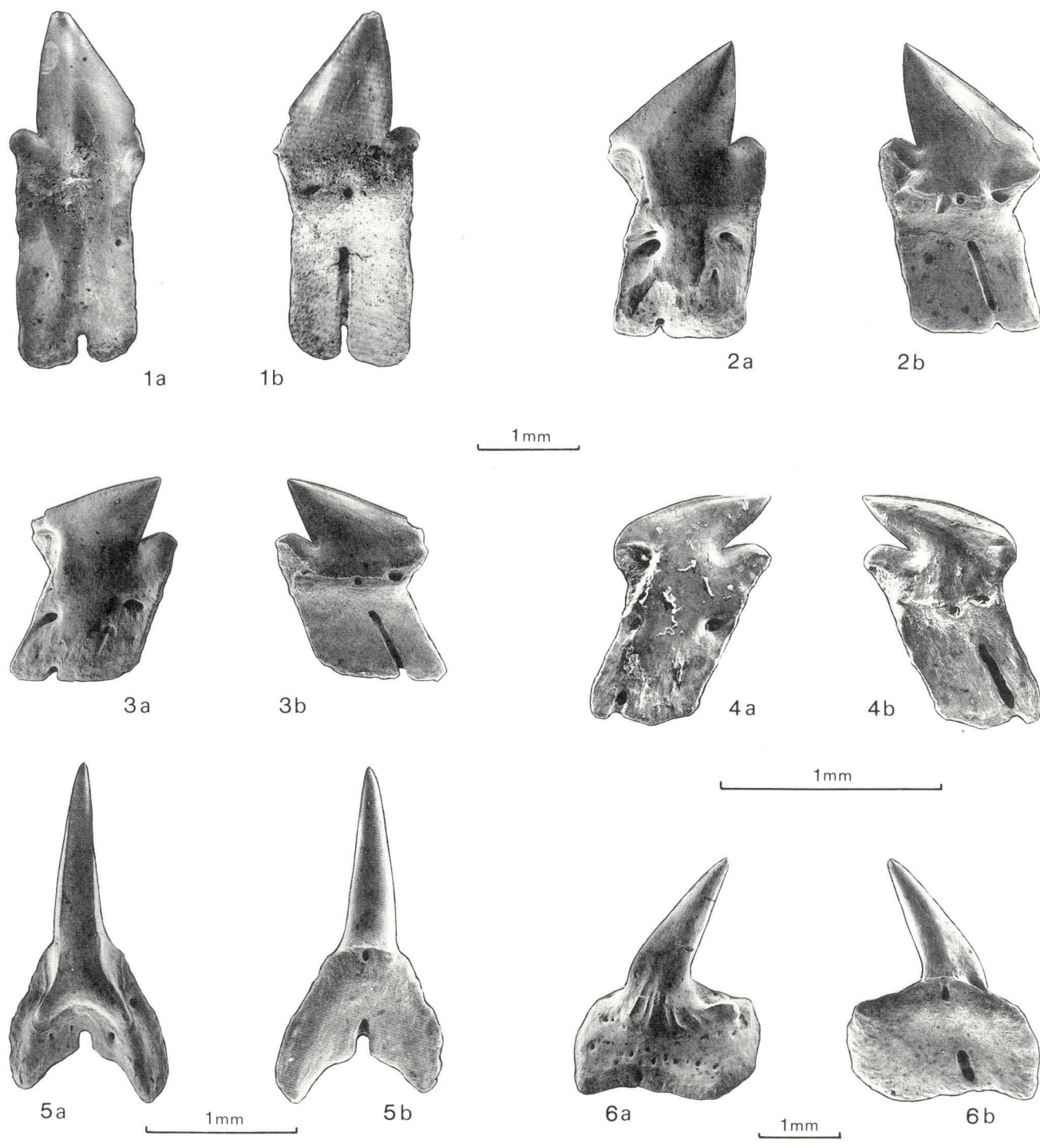
Detailed considerations relating to the complex biostratigraphic processes and to fossilization, as indicated by Ledoux (1972, par. III), are difficult, even involving the fauna as a whole.

The possible inferences are abstract on these grounds.

These concentrations, which are difficult to detect, and washed away, appear on the ground like surfaces rich in coarser material, can be due to winnowing by weak bottom currents during periods of basin starvation or, less probably, represent the lag deposit of bypassing turbidity currents. Some very rare pebbles have been found in the sediment. The first model may match the formation of a succession of substrata that are sufficiently compact to accommodate deep water invertebrate shoals (small deposit feeder bivalves, deep water isolated corals etc.).

Of the three species considered, *Scymnodalatias* aff. *garricki* is the most frequent (probably more frequent than in the present Atlantic), *Zameus squamulosus* is relatively rare, *Scymnodon ringens* is slightly rarer. The relative rareness of the latter species might also be explained by the fact that it lives on or near the bottom while *Scymnodalatias* aff. *garricki* (probably epi-mesopelagic) lives in a larger thickness of the water column thus depositing a larger amount of remains on a given area of the bottom. However, they must still be considered as speculations that have partly been invalidated by a more complex and at present undetectable phenomenology: species-specific movements, sex, size, breeding and depth segregation, as recently observed in some squaloid sharks (e.g. Yano & Tanaka, 1983) and sorting-winnowing action by bottom and upper currents.

The teeth do not show wear from transport, they are well mineralized and, albeit relatively small, sometimes slightly robust. Rootless hollow cusps of the inner files are not infrequent, suggesting in-life shedding rather than disaggregated corpses. Albeit generally attributable to other species, scales have also been found. The dimensions of the teeth are equivalent to or slightly smaller than the average size of the living species. In particular, apart from some specimens, most of the teeth of *S.* aff. *garricki* are smaller in size with regards to those of the holotype, possibly in relation to the restricting environmental factors of a marginal basin, which are responsible both for light endemisms and a young mortality rate. On the other hand, one might hypothesize a more or less consistent supply of individuals (possible for nectonic organisms) from the ocean. The latter would have ended their existence in the marginal regions of the basin (e.g. Adriatic paleo-area) in far from optimal conditions.



EXPLANATION OF PLATE 6

Figs 1-5 - *Scymnodon obscurus* (Vaillant, 1888) synonymized with *Zameus squamulosus* (Günther, 1877). Lower Pliocene, S. Andrea Bagni, Parma, Northern Apennines.

1) MPP, n. 120-29, FCF Coll. - right lower anterior tooth; 2) MPP, n. 120-30, FCF Coll. - left lower lateral tooth; 3) MPP, n. 120-31, FCF Coll. - left lower latero-posterior tooth; 4) MPP, n. 120-32, FCF Coll. - left lower latero-posterior tooth (juvenile); 5) MPP, n. 120-33, FCF Coll. - left upper anterior tooth;

Fig. 6 - *Scymnodon ringens* Bocage & Capello, 1864. Lower Pliocene, S. Andrea Bagni, Parma, Northern Apennines.

6) MPP, n. 120-35, FCF Coll. - right upper latero-posterior tooth;  
a) labial and b) lingual views; scale bar = 1 mm.

*Paleoecology and Paleobiogeography* – In the first account (Cigala Fulgosi, 1986) on the S. Andrea Bagni Lower Pliocene, I initially inferred a bathymetric evaluation, by directly transferring the present day data to the past situation. The bathymetry of the area might, however, be more modest if we were to consider the possibility of cold psychrospheric waters, usually deeper in the ocean, but more superficial in the paleo-Mediterranean during the stage of maximum «oceanization».

*Present-day data: Scymnodon obscurus* and/or = *Zameus squamulosus*. As reported by Compagno (1984, Part 1) this species is «usually found on or near the bottom at depths of 550 to 1450 metres; Western Atlantic: Northern Gulf of Mexico, Surinam, Southern Brazil. Eastern Atlantic: Iceland and Faeroe Ridge to Madeira, Morocco, Cape Verde Islands and Senegal. Western Indian ocean: South Africa». If synonymized with *Zameus squamulosus* also Western Pacific: Japan (Southeastern Honshu), probably Kyushu-Palau Ridge, South China Sea, New South Wales and New Zealand (Compagno, 1984, Part 1). Sometimes epipelagic and oceanic at depths of 550 m in water 2000 m deep (off Brazil). It predates on bottom fishes and invertebrates. Absent in the Mediterranean.

*Scymnodon ringens*. «Deep water species, temperate to subtropical, that is essentially confined to the eastern Atlantic continental slope, on or near the bottoms at depths of 200 to 1600 m». Because of its relatively high and sharp cutting teeth, it may be regarded as a formidable predator among similar sharks. Absent from the Mediterranean.

*Scymnodalatias garricki*. This species, known only by the holotype (Kukuev & Konovalenko, 1988), was fished at a depth of 300 m on the North Atlantic Ridge a little higher than Gibraltar. Since we lack more precise information, we must presume that is an oceanic meso-epipelagic species, capable of widespread bathymetric excursions.

These species, which are absent in the present Mediterranean, are now confined to the deep waters of the continental slopes or of the oceanic outer shelves. *Zameus squamulosus*, in particular, follows a diel pattern of movement through the water mass, and can be found in the epipelagic kingdom. There is little data regarding *S. garricki*. Apparently it seems to be represented by isolated populations distributed at the centre of the Atlantic over the North Atlantic Ridge. If we consider only the Recent situation, we might hypothesize that the species prefers chimico-physical or typical physiographical conditions of the ocean ridges. Yet its widespread diffusion during the early Pliocene (lower part of the MPL 2) leads us to think of a

species of psychrospheric oceanic waters (central water masses) which underwent a strong regression of its preceding area of distribution due to biological factors as well, surrounding the area in the Atlantic too. The scenario hypothesized from the extensive paleoceanographic and biostratigraphic literature for the early Pliocene of the Mediterranean paleo-area is substantially confirmed and enriched. The overall fish fauna demonstrates deep water oceanic conditions (psychrospheric waters, Benson, 1972; 1975) also in the northern Adriatic paleo-area. Even when taking a partial bathymetric limitation into account, imposed by psychrospheric locally more superficial waters (intense estuarine circulation connected also to a sufficient depth of the gateway in the Gibraltar paleo-area), it is possible to hypothesize a range of local depth of at least 400-900 m. Apart from deep water species (benthonic and mesopelagic species), including also *Hexanchus griseus* (Bonnaterre, 1788), sporadic remains of epipelagic, offshore-coastal sharks [e.g. *Isurus oxyrinchus* Rafinesque, 1810, *Cetorhinus maximus* (Gunnerus, 1765), represented by frequent gill-rakers, *Prionace glauca* (Linnaeus, 1758) and *Carcharhinus* species] together with a species of kogiinae (Cetacea: Odontoceti) and sea turtle, indicate that the water column was normally populated. On this basis an apparently stabilized complex ecosystem, implying also bottom oxygenated conditions, was present. It is an unquestionable piece of evidence of the already occurred establishment of a fully open marine connection (lower part of the biozone MPL 2) with the Atlantic ocean (McKenzie, Sprovieri & Channel, 1990, p. 1) after the Messinian salinity crisis.

The penetration of cold bottom waters during the MPL 2 in the Eastern Mediterranean was inferred by psychrospheric ostracods found even recently in sediments of Crete (Van Harten, 1984 in McKenzie, Sprovieri & Channel, 1990, p. 87). The fish fauna allows us to exclude from the outcropping section the MPL 1 biozone span, the length of which (300000 years) was claimed to be necessary (McKenzie & Channel, 1990) for the gradual infilling of the Mediterranean after the Messinian terminal flood and the restoration of open marine conditions (possibly open deep-sea normal biological conditions) around the MPL 1/MPL 2 boundary.

The possible route followed by the deep water fauna, including the fish fauna to populate the Eastern Mediterranean and in particular the Northern Adriatic paleo-area, must be sought in Southern Italy around the Sicily and the Sicily Channel paleo-area [see the considerations regarding the depth of sedimentation of the Trubi Formation cropping out in Sicily (Cita, 1972; Sprovieri, 1974)].

Another possible sufficiently deep water way in the surrounding area may even be glimpsed in the deep Paleostrait of Monte Torre which crossed Calabria in the Plio-Pleistocene (Colella & D'Alessandro, 1988) in which sediments with bathyal organisms were described; it connected the trough of the Tyrrhenian basin with the Ionian paleo-area.

#### CONCLUSIONS

Of the three species considered, *Zameus squamulosus* and *Scymnodon ringens* appear to be well defined taxonomically and the range of variation found in the Recent teeth is wider than in fossil ones. Apart from some differences that still cannot be checked in the living populations and its relation to congeneric species, *Scymnodalatias* aff. *garricki* also seems to be easily identified. Furthermore, the relative geographical proximity of the holotype of *S. garricki* confirms this. One possibly discriminating difference found in the fossil teeth is a recurrent smaller width of the apron in the lower teeth. Some fossil teeth show a different profile of the crown cutting edges, which are subrectilinear and do not present the marked widening at the cusp base. However, it should be noted that some intermediate forms can be observed. This difference may be due either to an individual and ontogenetic variation, but more probably to sexual dimorphism.

The ecology of the living representatives further demonstrates a deep water oceanic environment in the Adriatic paleo-area during the early Pliocene (lower part of the MPL 2).

As a whole, the fauna gives evidence of the establishment in the Mediterranean basin of a deep environment that stabilized after the Messinian salinity crisis.

If found elsewhere in the Mediterranean Lower Pliocene, this association with deep water squaloid sharks (including some of the other species of the fauna) might become a biostratigraphic marker for the lower part of the MPL 2 Zone. Indeed, it would be worthwhile carrying out a high resolution stratigraphic check on the squaloid shark fauna described by Cappetta and Nolf (1991) from the Lower Pliocene (*G. margaritae* B Zone of Spaak, 1983) of South-eastern France where the taxa treated here were not found.

The diffusion and persistence for such a brief period (lower part of the MPL 2 Zone) (it has still to be checked whether it is a question only of a local phenomenon) of these species in the Lower Pliocene of the Paleo-Mediterranean may lead us to presume that their disappearance from the basin may not be due to subsequent climatic deteriorations (e.g. final

Pliocene, Quaternary glaciations) as hypothesized by Cappetta and Nolf (1991) also on the basis of other species that are absent today in the Mediterranean and noted by the author (Cigala Fulgosi, 1986) [e.g. *Centrophorus squamosus* (Bonaterre, 1788), *Deania*], but rather to the early failing of a sufficiently open and deep Atlantic-Mediterranean connection in the paleo-area of Gibraltar, and therefore of the conditions of maximum «oceanization» in the basin.

#### APPENDIX

Observations on *Mollisquama parini* Dolganov, 1984 and *Scymnodalatias oligodon* Kukuev & Konovalenko, 1988.

##### MOLLISQUAMA PARINI Dolganov, 1984

*Odontology* – The holotype dentition (Text-fig. 4) appears damaged by formalin and there has been great difficulty in isolating and cleaning the teeth. The description is, therefore, partial - the upper teeth have not been figured.

The dentition shows a strong dignathic heterodonty together with a weak gradient monognathic heterodonty. The root is anaula-corhizid and the largest teeth are about 6 millimetres. Dolganov (1984, p. 1589) gives the following formula for this species  $\frac{12-1-12}{15-1-15}$ .

*Mollisquama parini* has a relatively low number of teeth like *Euprotomicroides zantedeschia* Hulley & Penrith, 1966 (Stehmann & Krefft, 1988, p. 5; Herman, Hovestadt-Euler & Hovestadt, 1989, p. 103). Not having checked the number of teeth, and judging from the figure of Dolganov (1984, text-figs B, B, p. 1590), the author may, however, have neglected at least two upper teeth (the last posterior and the commissural) and a lower one.

*Upper teeth*: parasymphysial tooth slightly shorter than the anteriors which have a straight crown. The cusps have convex lingual and labial faces. On the labial face of the crown the cutting edge is central and ends steeply lower down in lateral view (see also the drawing of Dolganov, 1984, p. 1590, text-fig. D). Due to this feature, the teeth are easily distinguished from the upper ones of *Scymnodalatias*. The root lobes are shorter than in *S. garricki* and more open as the root is arched. A large central foramen is present where the two root lobes join. A small foramen is present on the lingual bulge of the root (below the crown-root junction) and some foramina are found on the slightly hollowed sides of the root lobes. Substantially the type of

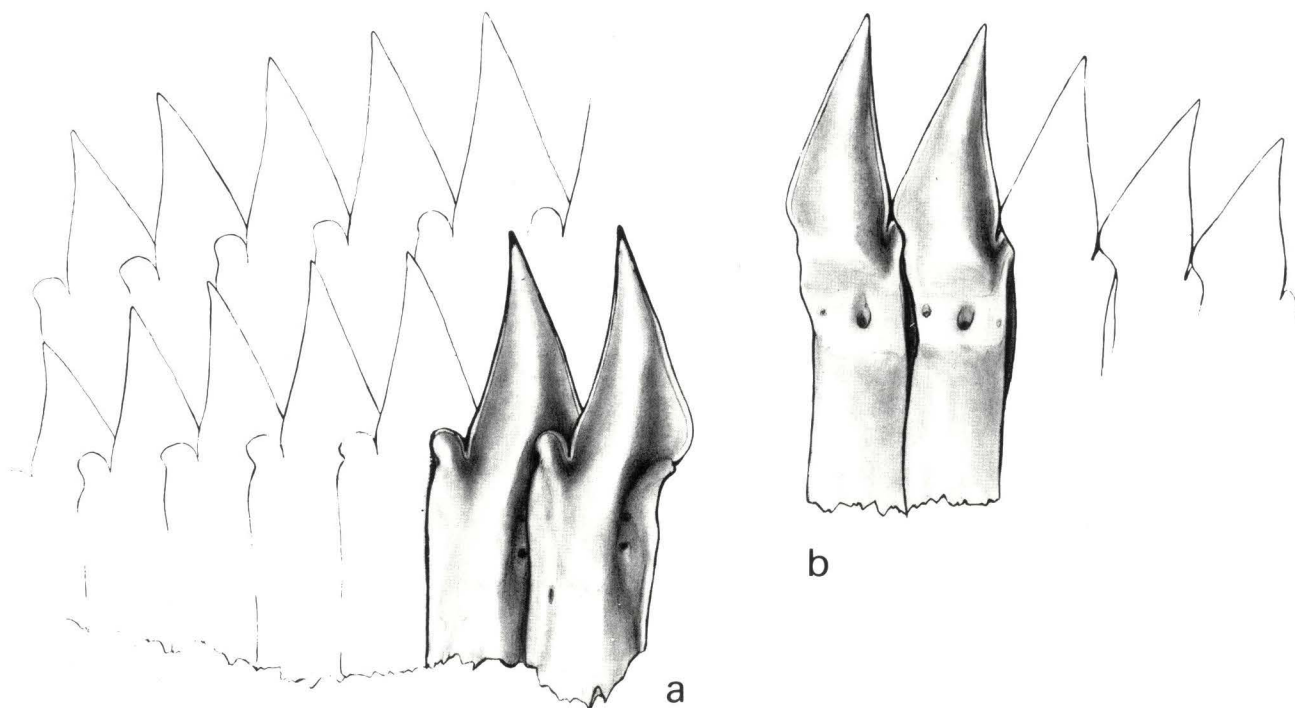
vascularization is the same as *Scymnodalatias* and *Euprotomicroides zantedeschia*, although the morphology is more similar to that of *Euprotomicroides*.

**Lower teeth:** the teeth (Text-fig. 4) are blade-like and strongly compressed. In the anteriors the cusp is slightly inclined towards the commissure and the inclination increases regularly along the tooth file. The cusps are sharp and tapered at the top; the profile of the distal and mesial cutting edges is bell-shaped at the cusp base and narrows in correspondence to the notch where the distal cutting edge joins the distal blade. The worn root base does not allow us to evaluate precisely the ratio crown/root height, but in any case, the root appears to be remarkably longer and the teeth are narrow and high with similar proportions to those of *Euprotomicroides zantedeschia*. The crowns are medially convex both on the labial and lingual faces. On the labial face of the tooth (Text-fig. 4a) the convexity proceeds into a long apron overhanging the long and deep distal depression of the root. The mesial part of the cusp base is depressed too. Only one or two subrounded foramina occur in the deep distal depression of the root and on the mesial side of the labial face of the root. The root is rectangular with a basal sulcus (see Dolganov, 1984, p. 1590, fig. B). The uvula is absent (Text-fig. 4b), but the crown shows a strong median convexity in the lingual face which continues almost up to the enameloid base.

On the root surface between the lower limit of the crown and the longitudinal ridge of the root, there is a central foramen and a latero-mesial one too. In this region around the central foramen there is a slight depression that may in part concern the median part of the longitudinal ridge. In transmitted light, the root shows numerous canals.

**Comments** - The teeth of this species are similar to those of *E. zantedeschia*. The lateral body scales are of the type with a hollowed surface and are covered by dense muscus or epidermis; they recall those of *E. zantedeschia* (Stehmann & Krefft, 1988, text-fig. 9a, b). The putatively luminous villous tissue which characterizes the abdominal pouch of *E. zantedeschia* (see Munk & Jørgensen, 1988) is present in *Mollisquama* in an axillary pouch of the pectorals (Dolganov, 1984, fig. A). Even if only topographical, such a difference might not be of a heavy systematic significance.

The pectoral fins are also strongly rounded at the apex as in *E. zantedeschia* and not more or less sharp as in *Scymnodalatias*. An obvious difference concerns the position of the first dorsal fin which in *Mollisquama* is much nearer the ventrals than in *Euprotomicroides*. The superficial examination of the holotype of *M. parini* does not allow me to make any systematic considerations, even though a certain relationship with *Euprotomicroides* seems sure, which might justify inclusion in a common subfamily at least.



Text-fig. 4 - *Mollisquama parini* Dolganov, 1984; holotype, female, 400 mm TL; lower teeth file; a) labial view, b) lingual view. x 11.8.

## SCYMNODALATIAS OLIGODON Kukuev &amp; Konovalenko, 1988

*Comments* – The holotype is an immature male, about 260 mm TL. This specimen shows a small white area devoid of scales on the anterior edge of the dorsals, marking a probable spine in course of growth. Small dorsal fin spines or spines not emerging from the skin of the dorsals characterize all the known species of *Centroscymnus*. An analysis of the teeth also convinced me that the specimen does not belong to *Scymnodalatias* but presumably to a young specimen of *Centroscymnus*.

## ACKNOWLEDGEMENTS

I would like to thank Prof. G. Pelosio, Institute of Geology, Parma University and Mr D. Ward, Orpington, Kent for their critical comments on the manuscript, Mrs E. Masini, Institute of Geology, Parma University for the elegant drawings (Plate 5 and Text-fig. 4) Mr Luca Barchi, Petrography Institute, Parma University who kindly took the SEM photographs.

Thanks also go to B. Seret, formerly ORSTOM, Dakar and J. Herman, Service Géologique de Belgique, Bruxelles for providing some specimens for this study; Prof. T. Taniuchi, Department of Fisheries, Faculty of Agriculture, Tokyo and Dr. A. Neyelov, Zoological Institute, Academy of Sciences, St. Petersburg for allowing me to examine the collections in Tokyo and St. Petersburg; Ms G. Mansfield for translating the original script.

The SEM photographs were printed by the author.

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(manuscript received October 24, 1995  
accepted February 5, 1996)

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