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Fish remains from the Santa Marta Formation (Late Cretaceous) of James Ross Island, Antarctica

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Abstract: Isolated fish remains including a tooth of the oldest described frilled shark, *Chlamydoselachus thomsoni* sp. nov. are described and figured from the Santa Marta Formation (Santonian–Campanian, Late Cretaceous) of James Ross Island, Antarctic Peninsula. Their geological and palaeoecological context is considered in the light of recent geological studies.

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Key words: *Chlamydoselachus*, frilled shark.

Introduction

The 'James Ross Island Scientific Cruise' organized by the British Antarctic Survey provided the opportunity for one of us (M.R.) to visit many fossiliferous localities in some islands of the Antarctic Peninsula during January and February of 1989. Eight days were spent on James Ross Island prospecting for fossil fishes in the Santa Marta Formation, a Santonian–Campanian marine unit within the Marambio Group (Figs 1, 2). Fish remains were not common but a small collection of sharks' teeth was made. The chlamydoselachid tooth described in this paper and one of the hexanchid teeth were found by Dr M.R.A. Thomson during the field season. Other shark teeth remains referred to here were collected by one of us (M.R.) and by Dr J Hooker during the same expedition. The fish remains figured in this paper come from strata ascribed to the Beta and Gamma members of the Santa Marta Formation. They have been deposited in the Natural History Museum, London and have registration numbers prefixed by 'BAS P.'.

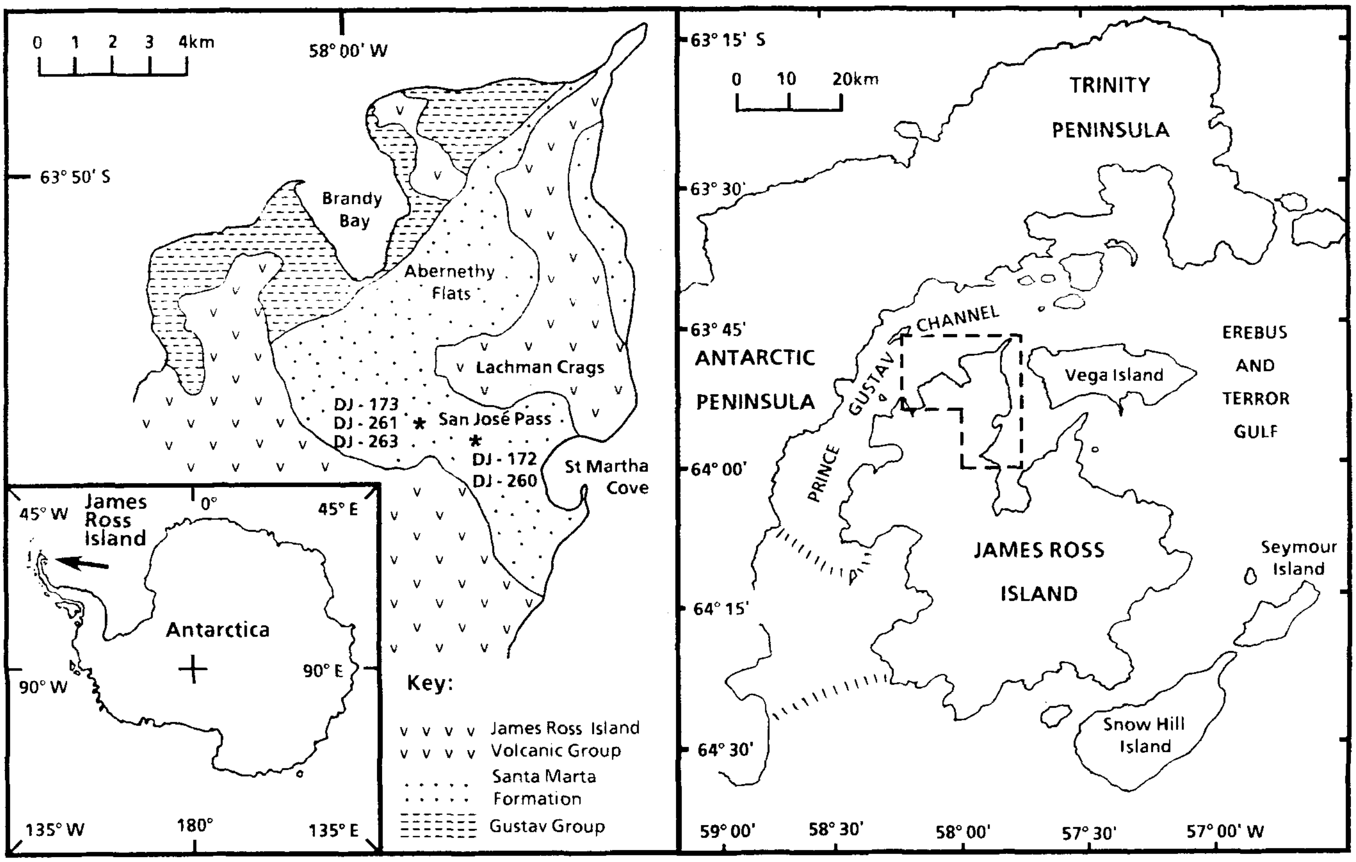

Fig. 1. Sketch maps to show the location of James Ross Island, the outcrop of the Santa Marta Formation and the location of the collecting sites.

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Localities

Most of the fish remains (Table I) were collected from surface debris on conglomeratic beds of two adjacent slopes (British Antarctic Survey field localities DJ-173, DJ-261 and DJ-263), between Abernethy Flats and San José Pass (Fig. 1). A few teeth were chiselled out of a shell coquina (DJ-260 and DJ-172) situated between San José Pass and St Martha Cove (Fig. 1). It is difficult to be more precise about the location of the collecting sites in the absence of a detailed map of the area. During the time of the field work the only available map was at 1:250 000 scale, published by the British Antarctic Survey in 1974.

Previous work on Mesozoic fish from the Antarctic Peninsula

There are few references to fossil fish remains from James Ross Island, most of the previous work having been concentrated on the more accessible slopes of Seymour (Vicecomodoro Marambio) Island. The earliest record is that by Woodward (1908) who described large selachian vertebral centra from the Cretaceous of Seymour Island. He attributed these to *Ptychodus* on the basis of their similarity to supposed *Ptychodus* teeth from the English Chalk, although Welton & Zinsmeister (1980) suggested that they would better be regarded as indeterminate. The fossil fish literature from Antarctica was reviewed by Grande & Eastman 1986, who also figured some new material. This includes a specimen of *Sphenodus* (determined as *Isurus* sp.) from the Cretaceous/Tertiary boundary at Seymour Island. Cione & Medina (1987) described three specimens of *Notidanodon dentatus* as *N. pectinatus*. The validity of *N. pectinatus* was discussed by Ward (1979, p. 122) and Ward & Thies (1987, p. 96), from the López de Bertodano Formation of Seymour Island. Three further teeth of *Notidanodon dentatus* from the same formation on Seymour Island were described by Grande & Chatterjee (1987). The tooth they figured as *Sphenodus*? sp. (Grande & Chatterjee 1987, text-fig. 2f–g) is not selachian, probably from a teleost fish.

This is the first paper describing fossil fishes from the Santa Marta Formation of James Ross Island, although Bibby (1966) and Olivero *et al.* (1986, p.15) both mentioned the presence of fish remains.

Geological features of the Santa Marta Formation

The Santa Marta Formation, as defined by Olivero *et al.* (1986) is older than the López de Bertodano Formation on Seymour Island from which it was separated. The Santa Marta Formation outcrops on James Ross Island in an area stretching from St Martha Cove to the south-east of Brandy Bay and also on the western side of Lachman Crags (Olivero *et al.* 1986, fig. 2) and comprises about 1100 m of sedimentary rocks. It is characterized by the presence of conglomeratic

Age		Lithostratigraphy		Environmental interpretation
TERTIARY	Mio-Pliocene	JAMES ROSS ISLAND VOLCANIC GROUP		Ensialic Alkaline Volcanism
TERTIARY	Late Eocene	SEYMOUR ISLAND GROUP	La Meseta Fm.	Delta slope.
TERTIARY	Late Palaeocene	SEYMOUR ISLAND GROUP	Cross Valley Fm.	Delta top.
TERTIARY	Early Palaecene	MARAMBIO GROUP	Sobral	Delta complex.
LATE CRETACEOUS	Maastrichtian	MARAMBIO GROUP	Lopez de Bertodano Fm.	Outer shelf, inner shelf, ? deltaic.
LATE CRETACEOUS	Campanian	MARAMBIO GROUP	Santa Marta Fm.	Tectonically active inner - outer marine shelf.
LATE CRETACEOUS	Santonian	GUSTAV GROUP	Hidden Lake Fm.	Tidal shelf / fan delta.
LATE CRETACEOUS	Coniacian	GUSTAV GROUP	Hidden Lake Fm.	Tidal shelf / fan delta.
LATE CRETACEOUS	Turonian	GUSTAV GROUP	Whisky Bay Fm.	Deep marine submarine fan / slope apron complex.
LATE CRETACEOUS	Cenomanian	GUSTAV GROUP	Whisky Bay Fm.	
EARLY CRET.	Albian	GUSTAV GROUP	Kotick Point Fm.	
EARLY CRET.	Aptian	GUSTAV GROUP	Kotick Point Fm.	
EARLY CRET.	Barremian	GUSTAV GROUP	Lagrelius Pt Fm.	

Fig. 2. Lithostratigraphic and environmental interpretation of the Mesozoic and Cenozoic rocks of the James Ross Island area after Macdonald *et al.* (1988).

horizons and coquinas and well-defined carbonaceous levels with abundant plant remains.

A review of the geological work done on the northern part of the James Ross Island was given by Pirrie (1989), who described, in detail, the lithologies occurring in that area as well as interpreting the palaeoenvironmental settings which produced the different facies (for a synthesis see Pirrie 1989, fig. 16).

Olivero *et al.* (1986, p. 16) stated that the Santa Marta Formation bears resemblance to the overlying López de Bertodano Formation in the grey and brown colour, the friable character of the rocks, the abundance of massive fine-grained epiclastic sediments, the presence of calcareous concretions, the rich fauna and marine nature. According to their original description, it passes transitionally from the underlying Hidden Lake Formation (Coniacian–Santonian) which, on James Ross Island, crops out in the Brandy Bay area. They recognized three units with transitional contacts within the Santa Marta Formation, termed the Alpha, Beta and Gamma

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members. The Alpha Member comprises friable muddy sandstones with concretions and intercalated conglomeratic sandstones (the latter interpreted by Pirrie, 1989 as accretionary lapilli); The Beta Member, rhythmic sequence of sandstones, pelites as well as intercalated conglomerates. The Gamma Member is mainly fine- and medium-grained sandstone; there is also a decrease of conglomerates in comparison to the Beta Member and the inclusion of supposed turbiditic deposits.

Macdonald *et al.* (1988) interpreted the Santa Marta Formation as having been deposited in a tectonically active shallow marine shelf and/or deltaic environment.

Pirrie (1989) has recently reassessed the sedimentology and palaeoenvironmental interpretations of the Santa Marta Formation. He studied 15 stratigraphical sections mostly between San José Pass and Brandy Bay (Pirrie 1989, fig. 1). He did not attempt to relate his sections to those of Olivero (1984) but recognized 12 different lithological facies lettered AL, which he groups into 'Facies Associations 1 and 2'. He concluded that Facies Association 2 represented a shallower depositional setting than Facies Association 1.

Olivero *et al.* (1986) and Macdonald *et al.* (1988) agree that most of the Santa Marta Formation was deposited during the Campanian but that the basal part of the sequence may be of Santonian age. The age was estimated on the basis of the ammonite assemblage (Olivero 1981, 1984 and Olivero *et al.* 1986) and also dinoflagellates (Dettmann & Thomson 1987).

The geographical and stratigraphical context of the fish remains

During field work, the stratigraphical subdivisions of the Santa Marta Formation (Alpha to Gamma members) proved to be difficult to identify. This was due to the lithological similarities of each member and a lack of precise information about their area of outcrop. The only available stratigraphic guide was the lithological section in Olivero *et al.* (1986, figs 2, 3). This makes no allowance for small scale facies variation at outcrops outside the straight line of the published sections. Pirrie (1989) considered the Alpha and Beta members to be lithologically similar and included them within his facies Association 1, whereas he thought the Gamma Member was lithologically distinct and equivalent to Facies Association 2.

Conglomerates and shell coquinas were the main lithology prospected for fossil vertebrates. Conglomerates form prominent relief features, often capping small hills. They are ubiquitous throughout the Abernethy Flats area (Fig. 1) and the local stratigraphic context is frequently obscured by scree, it was difficult to localize the collecting sites within the section. Those conglomerates at the transitional borders between the members (e.g. localities DJ-261 and DJ-263) can therefore, only arbitrarily be considered part of one particular member.

The fish remains described in this paper come from localities and strata attributable to Pirrie's (1989) Facies A and K. Facies A ('sheet conglomerates') were described as comprising matrix supported pebble to boulder conglomerates, while Facies K (shell coquina) is characterized by a thick bed of fragmented shelly debris with sandstones above and below. The first, (Facies A), was interpreted by Pirrie (1989) as debris flow deposits resulting from syn-sedimentary slumps or slides originating on gentle palaeoslopes in a shallow marine setting. The shell coquina (facies K) was interpreted as a high energy storm deposit.

Systematic palaeontology

The terminology and classification is based on Compagno (1973), Welton (1979) and Cappetta (1987).

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Cohort EUSELACHII
Superorder SQUALOMORPHII Compagno 1973
Order HEXANCHIFORMES Buen 1926
Suborder CHLAMYDOSELACHOIDEI Berg 1958
Family CHLAMYDOSELACHIDAE Garman 1884

Diagnosis (based on isolated teeth): Teeth with three prominent lingually recurved conical cusps; root basally flat and lingually bilobate. Dignathic heterodonty absent, disjunct monognathic heterodonty weekly developed, enameloid, triple-layered; root vascularization, anaulacorhize.

Referred genera: *Chlamydoselachus* Garman 1884
Thrinax Pfeil 1983

Discussion. Pfeil (1983, p. 112) based the genus *Thrinax*, type species: *T. baumgartneri*, on two relatively complete teeth and two isolated crowns. They are separated from *Chlamydoselachus* by their upright unornamented crowns, labio-lingually short root and the absence of intermediate cusplets. In the same deposit Pfeil described *Chlamydoselachus fiedleri*, based on 50 tooth fragments Among his paratypes is a tooth, FHP 1982-D-107, intermediate in morphology between *Chlamydoselachus* and *Thrinax*. This tooth has a relatively small root, reduced ornamentation and no intermediate cusplets. Teeth of the Recent species *Chlamydoselachus anguineus* Garman 1884 may also lack intermediate cusplets and have considerable variation in the degree of coronal ornamentation (Pfeil 1983, pls 13–31; Welton 1979)

We feel that the case for the existence of a separate chlamydoselachiid genus cannot be made on such limited material. It would appear that the criteria upon which *Thrinax* is separated from *Chlamydoselachus* are within the normal variation of *Chlamydoselachus*. We therefore regard *Thrinax* as a junior synonym of *Chlamydoselachus* and the type species, *T. baumgartneri*, is a junior synonym of *Chlamydoselachus fiedleri*.

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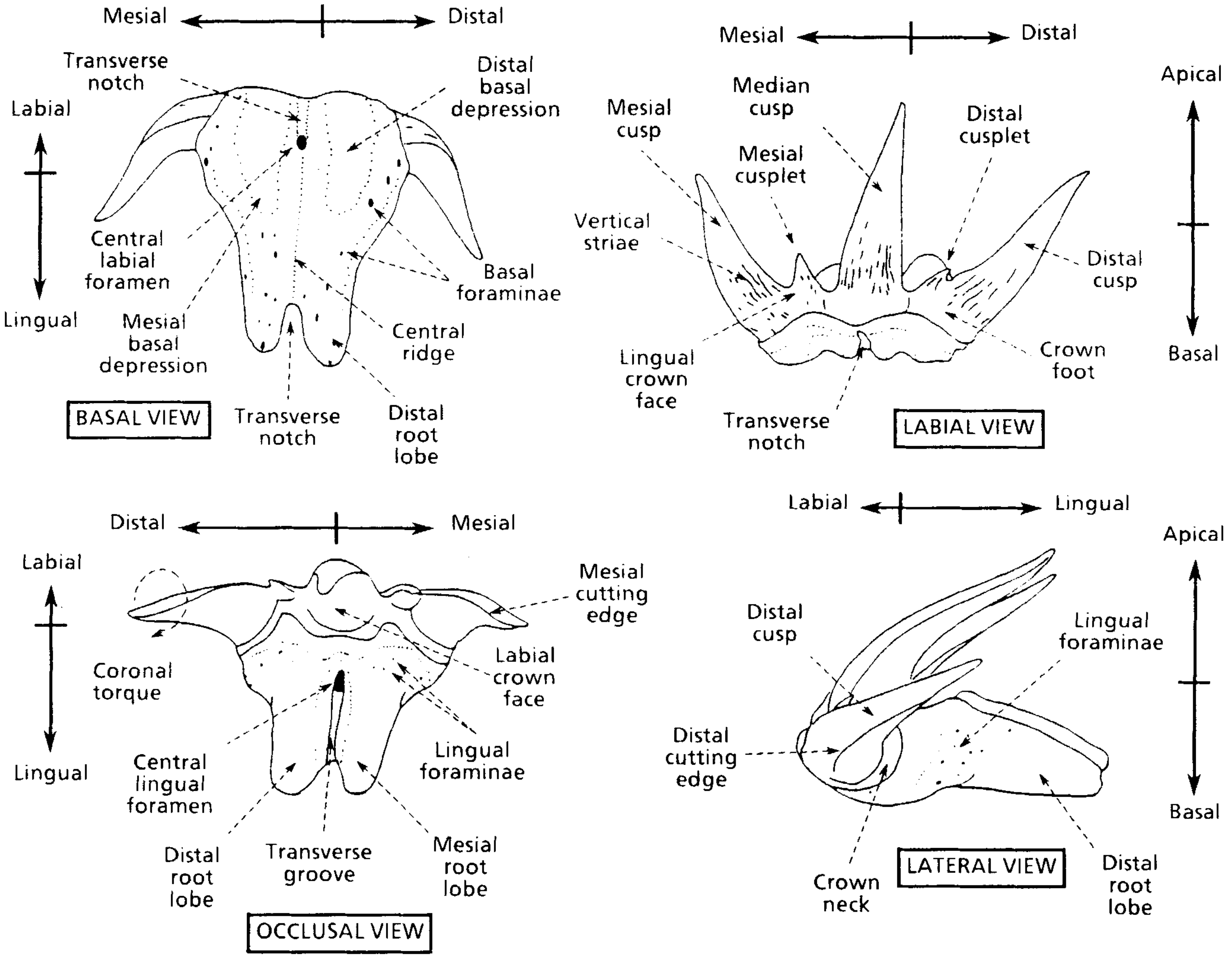

Fig. 3. Terminology applied to *Chlamydoselachus* teeth, after Pfeil (1983).

Chlamydoselachus Garman 1884

Type species: Chlamydoselachus anguineus Garman 1884.

Generic diagnosis: as family.

Referred species: Other than the Recent species, *Chlamydoselachus anguineus*, there are five named fossil species (Pfeil 1983, p. 271; Cappetta 1987, p. 44).

These are:

C. fiedleri Pfeil 1983 from the Middle Eocene of St Pankraz, Austria.

C. brachleri Pfeil 1983 from the Early Miocene of Offenhausen, Austria.

C. lawleyi Davis 1887 from the Pliocene of Orciano, Tuscany, Italy.

C. tobleri Leriche 1929 from the Oligocene or Miocene of Trinidad.

C. garmani Welton (in Pfeil 1983) from the Early Miocene of Schooner Gulch, California, USA.

Discussion: The frilled shark *Chlamydoselachus* is a strange fish, arguably one of the most primitive of the living sharks (Compagno 1973). It was discovered in the early 1880's amongst a miscellaneous lot of alcohol-pickled specimens obtained by Prof. H. Ward from Japan. Although partially decomposed and eviscerated, its description by Garman in 1884 caused considerable scientific debate. It was immediately hailed as being a living cladodont shark, a group that ranges from the Devonian to the Permian. Cope (1884) took the matter further and synonomized it with the Carboniferous genus *Didymodus* Cope = (in part) *Diplodus* Agassiz. Garman (1885, p. 22) disagreed with this and argued that, if it was to be referred to a Palaeozoic genus, then *Cladodus* was a more appropriate choice. Compagno (1973), however, saw far greater affinities between the skeletons of *Chlamydoselachus* and those of the Recent hexanchoid and squaloid sharks. He regarded the cladodont-like teeth as a case of parallelism, which remains the prevailing opinion.

Teeth of the Frilled Shark *Chlamydoselachus* are rare in the fossil record and are restricted to outer shelf and bathyal

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facies (Welton 1979, p. 140). Apart from the rarity of suitable facies preserved in the geological record, the fragility of the teeth make them less likely to be recovered than other genera. The first illustration of fossil *Chlamydoselachus* teeth is in Lawley (1876, pl. 1, fig. 1a–c). Lawley was unable to place them within a known genus, a task that fell to Davis (1887) who described them as *Chlamydoselachus lawleyi*. Previously the oldest documented occurrence of *Chlamydoselachus* is an unnamed species from the Palaeocene of California (Welton 1979, p. 214) although (Cappetta 1987, p. 44) recorded it from the Campanian (Late Cretaceous) of Angola.

Dental formulae

Welton (1979) gives the dental formula of *Chlamydoselachus anguineus* as:

$$P\frac{4}{4}-AL\frac{7-9}{7}-M\frac{0}{1}-AL\frac{7-9}{7}-P\frac{4}{4}$$

where M = Median tooth, AL = Anterolateral teeth, P = Posterior teeth.

Chlamydoselachus thomsoni sp. nov.
Fig. 5a–f

Derivation of name: named in honour of Dr Michael R.A. Thomson of the British Antarctic Survey.

Type series:
Holotype: Isolated tooth BAS P. 1009
Locality: western side of San José Pass, James Ross Island, locality DJ-261.
Collector: M.R.A. Thomson.
Stratigraphic unit: Sheet conglomerates (within ?Beta Member), Santa Marta Formation.
Age: Late Cretaceous, Campanian.
Depository: The Natural History Museum, London.

Diagnosis: Chlamydoselachus thomsoni can be separated from all other species of *Chlamydoselachus* by the combination of the following characters: Stout upright median cusp with coarse continuous anastomosing vertical striae on the labial crown face, very wide cutting edges; fine discontinuous striae on the lingual crown surface; root apically high and labio-lingually short with poorly differentiated root lobes.

Description: The unique specimen is a large tooth lacking its distal cusp and with a damaged mesial cusp. The two intact cusps are upright, somewhat stout and basally inflated. Both are lingually recurved becoming very slightly sigmoid close to their apices with little coronal torque. The cutting edge, where preserved, is wide, almost forming a narrow blade on the mesial and distal sides of the cusps. The labial surface of the median cusp is ornamented with seven continuous coarse raised striae which anastomose apically. The labial surface of the mesial cusp is less coarsely ornamented with five discontinuous striae. There is a single, small, irregularly shaped mesial cusplet, closely applied to the median cusp. Both cusps are constricted at their base and at their widest about 15% of the way up, giving them an inflated appearance. The root-crown junction is indistinct and lies in a shallow depression that parallels the root base. The labial root surface is convex and studded with numerous small foraminae. There is a centrally placed transverse notch. The lingual faces of the median and mesial cusps bear a dozen or so discontinuous raised vertical striae, some of which anastomose

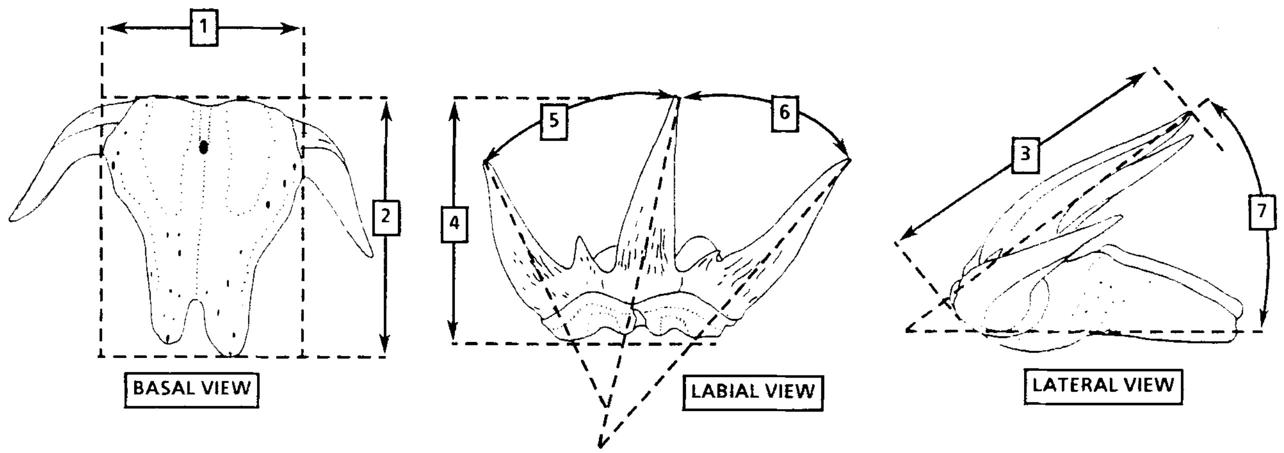

Fig. 4. Measurements applied to *Chlamydoselachus* teeth, after Welton (1979). 1. Root width; greatest mesial distal root width. 2. Root length; greatest labio-lingual root length. 3. Median cusp length; length of median cusp from the apex to the root base. 4 Tooth height; vertical distance from the apex of the median cusp to the root base. 5. Mesial–median cusp angle; Angle between the mesial and median cusps projected through the long axis of the cusps. 6. Mesial distal cusp angle; Angle between the distal and median cusps projected through the long axis of the cusps. 7. Median cusp angle; angle formed between the root base and a line from the cusp apex intersecting the centre of labial root border of the crown foot.

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Table I. Measurements of the holotype of *Chlamydoselachus thomsoni* (see Fig. 3). Measurements 1, 2 and 7 are based on Welton (1979, fig. 8).

1. Root Width	2. Root Length	3. Median Cusp Length	4. Tooth Height	5. Mesial–Median Angle	6. Distal–Median Angle	7. Median Cusp Angle
4.9 mm	6.33 mm	8.53 mm	8.18 mm	37°	34°	62°

apically. Below this, lacking enameloid, is a wide lingual crown neck.

An impression of the mesial cusp is preserved in the indurated sandstone block from which the tooth was extracted.

The apical surface of the root is divided into two lobes that are separated lingually by a transverse groove which terminates labially behind the median cusp. A central lingual foramen lies slightly mesially, midway along the groove. The distal root lobe is further divided by a second transverse groove which lacks any discernible foraminae. The root base has mesial and distal depressions and a median ridge. There is no evidence of a transverse groove, nor a central labial foramen. All aspects of the root are pitted with numerous small foraminae.

Position in the dentition: Welton (1979) discussed the problem of locating teeth within a dentition. He determined that reference to the root length/width ratio and median cusp angle of an isolated tooth of *Chlamydoselachus anguineus* could, with reasonable accuracy, determine which row it came from. Welton noted that with an increasing lateral position:

a. the teeth become relatively wider,
b. the median cusp angle increased,
c. there were more and longer transverse grooves, and
d. the root becomes labio-lingually relatively shorter and less bifid.

The data obtained from jaws of *Chlamydoselachus anguineus*, however, did not directly apply to other fossil species, although the general trends probably did (Welton 1979, p. 212). If one applies Welton's criteria to the single tooth of *C. thomsoni*, the high median cusp angle (62°) and root shape suggest a position of AL 6 or 7 (Welton 1979, table 7). The high number of transverse grooves, however, are more characteristic of posterior teeth, although ontogeny may also play a role in increasing rugosity; Welton's Recent *Chlamydoselachus* teeth were much smaller. This is a problem that only further fossil material can fully resolve.

Comparison with other fossil species

C. fiedleri Pfeil 1983, is known from a number of complete, relatively large teeth (up to 10 mm in height) with a variable degree of vertical coronal striae. It differs from *C. thomsoni* in having finer striae in the labial and lingual crown and greater degree of coronal torque.

C. brachleri Pfeil 1983 is also known from a number of complete, teeth. The crown is less robust, more lanceolate, and has a higher degree of coronal torque than *C. thomsoni.*

C. lawleyi Davis 1887. As the holotype of this species was destroyed by Allied bombing during World War II, direct comparison is not possible. Lawley's original plates show a gracile species, lacking intermediate cusplets. As Lawley was unaware of their presence (*C. anguineus* was not described until eight years later), he might have omitted them Welton (1979, p. 197).

C. tobleri Leriche 1929. Both the stratigraphic origin and the depositary of this species are in doubt. It is known from a single specimen which was collected from a tuff, ejected from a mud volcano in Trinidad. Unfortunately the location of the holotype is unknown (Welton 1979) and Leriche's type figure lacks sufficient detail, other than to confirm the genus.

C. garmani Welton (in Pfeil 1983) is of a similar size as *C. thomsoni* and has as coarse, but fewer striae on the crown. It is less basally inflated and has more labio-lingually sigmoid cusps than *C. thomsoni.*

The Oligo-Miocene species, *C. brachleri, C. tobleri* and possibly *C. garmani* may well represent a single species. Similarly *C. lawleyi* from the Italian Pliocene may be conspecific with *Chlamydoselachus anguineus.*

Discussion: Time and morphology separate *C. thomsoni* from the other described species. Compagno (1984, p. 14) suggests that *Chlamydoselachus anguineus* feeds on deep-water cephalopods, for which the needle-sharp, lanceolate teeth must be well suited. Considerable change has occurred in the abundance of shelled cephalopods since the late Mesozoic, so it is understandable that this is also reflected in *Chlamydoselachus* tooth morphology. The large and robust tooth of *C. thomsoni* would be more suited to a fish feeding on a prey with harder skeletal structures such as belemnites or even ammonites.

The associated biota

Olivero *et al.* (1986) gave a brief account of the faunal associations of each of the three members of the Santa Marta Formation:

Invertebrates

The Alpha Member. The lower part of this member contains scanty remains of brachiopods, gastropods, bivalves and

Fig. 5. *Chlamydoselachus thomsoni* sp. nov. holotype, BAS P.1009, sheet conglomerates, ?Beta Member, Santa Marta Formation, Late Cretaceous, James Ross Island; **a.** labial view ×8, **b.** distal view ×10, **c.** mesial view ×10, **d.** lingual view ×10, **e.** occlusal view ×10, **f.** basal view ×10.

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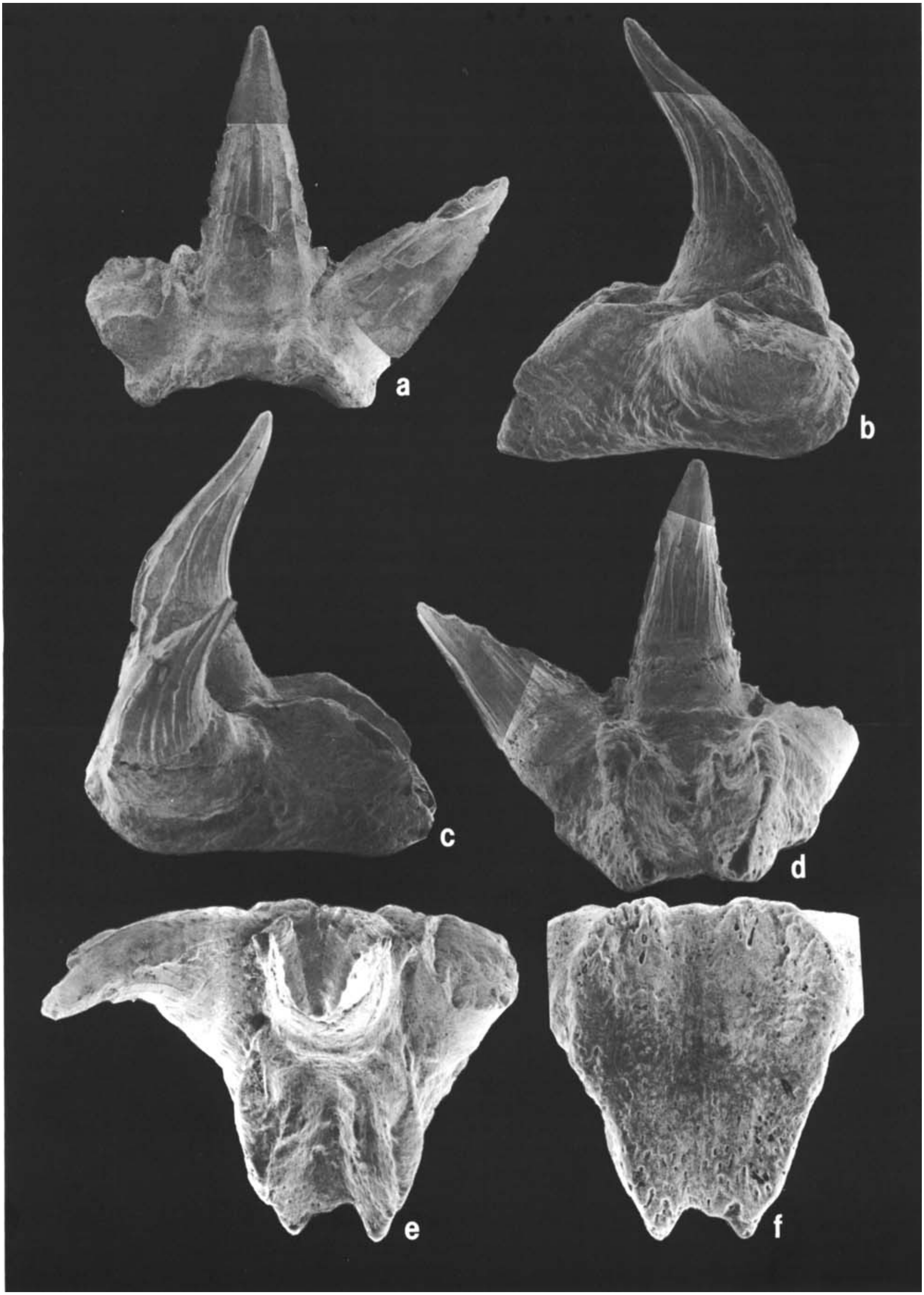

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Table II. Summary of data relating to the figured specimens.

	BAS (field) no.	Taxon	Material	Fig. no.	BM(NH) reg. no.	Collector
Association 1, facies A of Pirrie 1989	DJ.173.1	*Notidanodon dentatus*	Tooth	6d	BAS P.1008	M.R.A. Thomson
Environment: Mid–outer shelf	DJ.261.1	*Chlamydoselachus thomsoni*	Tooth	5a–f	BAS P.1009	M.R.A. Thomson
Lithology: Sheet conglomerate	DJ.263.3	Selachii undetermined	Vertebra	6 m	BAS P.1010	M. Richter
Locality: Abernethy Flats area	DJ.261.4	*Sphenodus* sp.	Tooth	6 h	BAS P.1011	M. Richter
	DJ.172.7	*Sphenodus* sp.	Tooth	6i	BAS P.1007	J. Hooker
	DJ.172.8	*Enchodus* sp.	Tooth	6g	BAS P.1006	J. Hooker
	DJ.172.1	*Enchodus* sp.	Tooth	6e	BAS P.1012	J. Hooker
Association 2, facies K of Pirrie 1989	DJ.172.2	Lamnoid undetermined	Tooth	6j	BAS P.1013	J. Hooker
Environment: Inner shelf	DJ.172.3	Lamnoid undetermined	Tooth	6k	BAS P.1014	J. Hooker
Lithology: Shell coquina	DJ.172.4	Lamnoid undetermined	Tooth	6l	BAS P.1015	J. Hooker
Locality: Between St Martha Cove	DJ.172.5	*Squatina* sp.	Tooth	6b	BAS P.1016	J. Hooker
and San José Pass	DJ.172.6	*Squatina* sp.	Tooth	6c	BAS P.1017	J. Hooker
	DJ.260.1	*Squatina* sp.	Vertebra	6a	BAS P.1018	M. Richter
	DJ.172.10	*?Sphaeronodus* sp.	Tooth	6f	BAS P.1019	J. Hooker
	DJ.172.9	*Notidanodon dentatus*	Tooth	unfig'd	BAS P.1020	J. Hooker

ammonites (*Bacculites* sp.). Higher up, the marls and calcareous sandstones of the Alpha Member, contain a rich fauna of ammonites (Scaphitidae, *Baculites* sp., Nostoceratidae, Diplomoceratidae and Pachydiscidae) and bivalves (especially large *Inoceramus* sp. up to 20 cm across). (Pirrie (1989) interpreted the Alpha Member marls as amalgamated concretions.)

The Beta Member. This unit contains a variety of ammonites (Olivero 1984) and also trigonid bivalves, echinoderms (Echinoidea), gastropods and serpulids. Well-preserved fossil wood is common in this member especially in the Abernethy Flats area.

The Gamma Member. Gastropods and bivalves dominate the lower section of the Gamma Member while serpulids (*Rotularia* sp.) are very common in the upper part. Ammonites include specimens of the *Gunnarites antarcticus* group and large pachydiscids (Olivero *et al.* 1986). Fossil wood is abundant at many levels.

Vertebrates

Sharks' teeth from the Late Cretaceous of James Ross Island are not as abundant as they are in Eocene–Oligocene sediments (La Meseta Formation) of the adjacent Seymour Island. Table II lists those figured with their field localities and registration numbers.

The ?Beta Member sheet conglomerates yielded *Chlamydoselachus*, a specimen of *Notidanodon dentatus* and the root of an extremely large *Sphenodus* tooth. Both the latter species were previously recorded from the Late Cretaceous of Seymour Island but are new to James Ross Island.

The Gamma Member contains the richest vertebrate assemblage within the Formation. Plesiosaur bones are abundant in places, and this member yielded the first dinosaur known from Antarctica (Ornithischia – Olivero *et al.*, in press). Many isolated actinopterygian teeth and vertebrae, sharks' teeth including *Notidanodon dentatus*, *Sphenodus*, *Squatina* and large vertebral centra of unidentified sharks were collected from the shell coquinas (Figs 5, 6a–m).

Despite their large size, teeth of *Notidanodon* are usually relatively uncommon. Those described by Cione & Medina (1987) were found associated with a plesiosaur skeleton which it was presumed to have predated, as were similar teeth described by Applegate (1965) from California, USA. It seems, therefore, likely that the apparent abundance of *Notidanodon* in the Santa Marta Formation is related to the number of plesiosaurs, or predatable plesiosaur carcasses.

The teeth of *Sphenodus* (= *Orthacodus*) belong to an undescribed species, but unfortunately the remains collected so far are too poorly preserved to allow its formal description. In root morphology and stature it most closely resembles *Sphenodus lundgreni* from the Danian (Palaeocene) of Denmark and Sweden.

The teeth and vertebra of *Squatina* are considered indeterminate. During its fossil history (Jurassic–Recent) teeth of *Squatina* show little variation. Of those recorded from the Late Cretaceous, those from the La Meseta Formation most closely resemble *S. hassei* Leriche 1929 as figured by Herman (1977, pl. 5, fig. 3)

Fig. 6. Associated fish fauna from Beta and Gamma members of Santa Marta Formation, Late Cretaceous, James Ross Island, Antarctic Peninsula. **a–c.** *Squatina* sp. **a.** vertebra ×1.5, **b, c.** fragmentary teeth ×5. **d.** tooth of *Notidanodon dentatus* Woodward 1886 ×1.5. **e.** ?*Enchodus* sp., tooth, ×3. **f.** *Sphaeronodus* sp., tooth, ×1.5. **g.** *Enchodus* sp., tooth, ×1.5. **h, i.** *Sphenodus* sp., **h.** tooth root cast, ×1.5; **i.** fragmentary tooth, × 1.5. **j–m.** Lamnoid undetermined, **j, k, l.** teeth ×4; **m.** vertebra, × 1.5.

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Palaeoenvironmental significance of the fossil fish remains

The fossil fish listed here were found in facies A of Facies Association 1 and facies K of Facies Association 2 (Pirrie 1989). Of those from facies A, certainly the presence of *Chlamydoselachus* is consistent with the interpretation of Association 1 as being a mid-outer shelf deposit (Welton 1979, p.140). Similarly the presence of *Squatina* with small lamnid sharks' teeth found in facies K is more typical of shallow inner shelf environment. Recent species of the angelshark *Squatina* can be found in water up to 1300 m deep but are rarely recorded in depths exceeding 200 m (Compagno 1984). This is also in accord with Pirrie's interpretation of Association 2 as being an inner shelf deposit.

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