Late Cretaceous Antarctic fish diversity

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Abstract: New material from the Santa Marta Formation (late Coniacian–?early Maastrichtian) of James Ross Island contributes significantly to the current knowledge of Late Cretaceous Antarctic fish diversity. The taxon list for the Santa Marta Formation is extended, and new records of neoselachians and teleosts are reported. The stratigraphic ranges of some previously known taxa are enlarged, and the palaeobiogeography and palaeoecology of Late Cretaceous Antarctic fishes are discussed. Top predators that occupied the higher levels in the food chain along with marine tetrapods dominate the marine faunas from the Santa Marta and López de Bertodano formations. The only fish adapted to crushing hard-shelled invertebrates were the chimeroids. Rays, an important component of marine fish associations, as well as fish from lower trophic levels, remain unknown from the Late Cretaceous of Antarctica.

Fossil fish remains have long been known from the extensive Cretaceous marine deposits of the James Ross Basin on the NE flank of the Antarctic Peninsula (Fig. 1a). The first fish fossils were collected during the 1901–1903 Swedish South Polar Expedition and were subsequently described by Woodward (1908). The James Ross Basin is one of a series of largely back-arc basins that formed in the southernmost South American–Antarctic Peninsula region during the Late Mesozoic–Cenozoic (Riding & Crame 2002), and their origin is closely related to the early stages of Gondwana break-up (Hathway 2000). The islands forming the James Ross Island Group comprise an extensive and remarkably fossiliferous Cretaceous–Palaeogene sedimentary succession, including a well-preserved Cretaceous–Tertiary (K/T) boundary section on Seymour Island (Zinsmeister *et al.* 1989; Zinsmeister 1998; Crame *et al.* 1991). Consequently, the James Ross Island Group is important in reconstructing global Cretaceous and Palaeogene palaeoclimatic and palaeobiological changes (Ditchfield *et al.* 1994; Crame *et al.* 1996; Huber 1998; Riding & Crame 2002).

The regressive Cretaceous megasequence of the James Ross Basin is divided into three principal lithostratigraphic groups: the basal Gustav (Aptian–Coniacian); the Marambio (Coniacian–Danian); and the Seymour Island (Palaeogene) groups (e.g. Crame *et al.* 1991; Riding & Crame 2002). Late Cretaceous fish remains comprising chimeroids, selachians and bony fish have been reported from the Marambio Group of James Ross and Seymour islands (Woodward 1908; Grande & Eastman 1986; Cione & Medina 1987; Grande & Chatterjee 1987; Richter & Ward 1990; Stahl & Chatterjee 1999, 2002). These few published studies indicate that our knowledge of Cretaceous fish faunas in the high southern latitudes, compared to other regions, is still very incomplete. Recent fieldwork by two of the authors (J. M. Lirio, H. J. Nuñez) yielded new fish material from the Late Cretaceous Santa Marta Formation of James Ross Island. Additional unpublished material collected by M. Richter (Rio Grande do Sul, Brazil) and J. J. Hooker (Natural History Museum, London, UK) during the 'James Ross Island Scientific Cruise' of the British Antarctic Survey in 1989, and housed in the Natural History Museum, London, was also examined.

It is the purpose of this paper to review the current state of knowledge of Antarctic Cretaceous fish fossils and to present new material. In addition, this study provides new insights into Antarctic fossil fish communities and biogeography as a basis for future investigations.

Geological and stratigraphic framework

The Marambio Group is exposed in both northern James Ross, Vega and Humps islands in the north and southern James Ross, Snow

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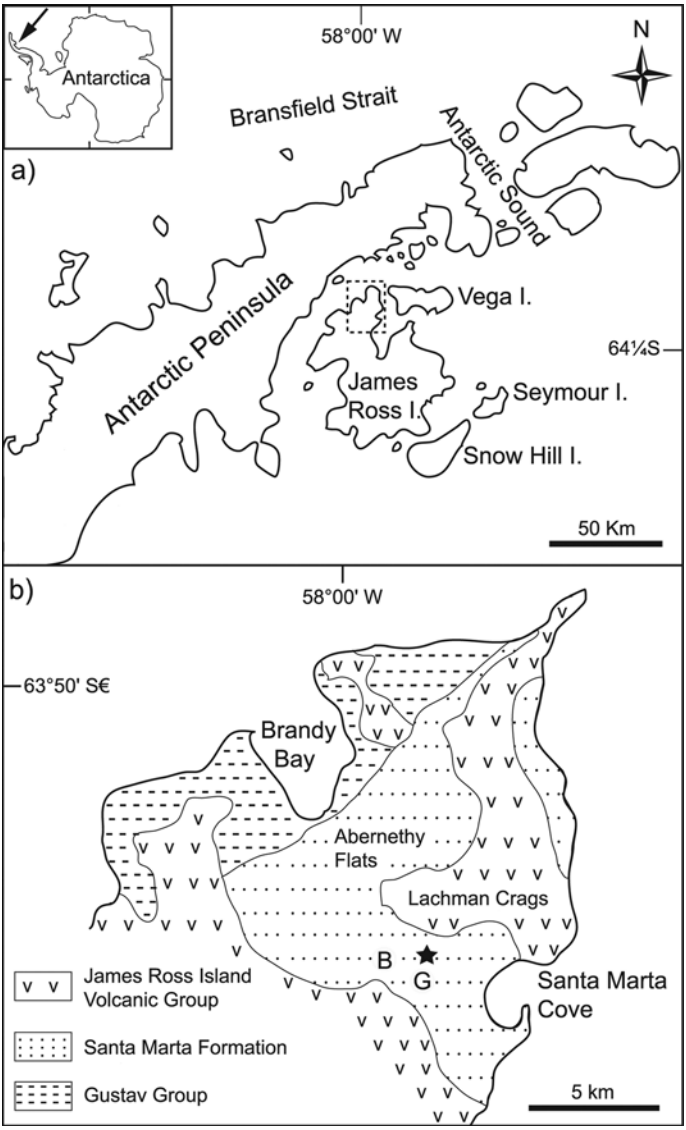


Fig. 1. Sketch maps showing the location of the Antarctic Peninsula (inset: arrow) and study area. (**a**) Location of James Ross Island east of the Antarctic Peninsula. The rectangle indicates the study area. (**b**) Collecting sites in the Santa Marta Formation on northern James Ross Island. B specifies the Argentinean collecting site of Lachman Crags specimens and G the one of Herbert Sound specimens. The asterisk shows the collecting site of the British Antarctic Survey expedition.

Hill, Seymour and Cockburn islands in the south (Olivero *et al.* 1986, 1992; Lirio *et al.* 1989; Pirrie *et al.* 1991, 1997). Both areas are separated by a major fault causing extensive repetition of the stratigraphical sequences. Four formations are included in the Marambio Group (in stratigraphical order): Santa Marta, Snow Hill Island, López de Bertodano and Sobral formations (Pirrie *et al.* 1997). The Santa Marta Formation that crops out on northern James Ross Island between Brandy Bay and Santa Marta Cove (Fig. 1b) represents volcaniclastic, shallow-marine fan and shelf sediments that were deposited adjacent to an active volcanic arc (Fig. 1a). This is the type area for the Santa Marta Formation, as defined by Olivero *et al.* (1986), and the base of the Santa Marta Formation is late Coniacian in age (McArthur *et al.* 2000).

The lower part (*c.* 500 m), which consists of mudstones, siltstones and sandstones together with rare conglomerates, was named the Alpha Member by Olivero *et al.* (1986). The following approximately 350 m-thick Beta Member is characterized by an increased proportion of conglomeratic interbeds; these are up to 4 m thick and poorly sorted. Because of their very similar lithostratigraphic appearance, Crame *et al.* (1991) united the Alpha and Beta members within the Lachman Crags Member. The topmost 250 m-thick Gamma Member of Olivero *et al.* (1986), comprising mainly fine-grained cross-bedded sandstones and shell coquinas, was named the Herbert Sound Member by Crame *et al.* (1991). The lower part of the Lachman Crags Member (Alpha member) is late Coniacian–early Campanian in age, and the upper part (Beta Member) is probably early–late Campanian. A late Campanian–?early Maastrichtian age is assigned to the Herbert Sound (Gamma) Member, based on ammonites, other fossils and strontium isotope dating (Crame *et al.* 1991, 1999; Olivero *et al.* 1992; Olivero & Medina 2000).

Lirio *et al.* (1989) established the 435 m-thick Rabot Formation, which is characterized by less prominent coarse-grained beds and by the absence of coquinas and carbonaceous plant material in the Rabot Point–Hamilton Point area of SE James Ross Island. However, Crame *et al.* (1991) assigned member status to this unit and Pirrie *et al.* (1997) transferred part of it to the Hamilton Point Member. Precise correlation of these members to those of the northern part of the island is difficult, but it would appear that the Rabot Member is the lateral equivalent of both the upper Lachman Crags and lower Herbert Sound members, and probably ranges in age from the early to the late Campanian. The Hamilton Point Member is ?mid–late Campanian in age (Pirrie *et al.* 1997).

Material and methods

The material presented here was collected from siltstones and conglomerates in the uppermost part (Beta Member) of the Lachman Crags Member and from conglomerates in the middle part of the Herbert Sound Member in the northern part of James Ross Island by Argentinean and British field parties (Fig. 1b). The Herbert Sound Member conglomerate that yielded most of the material has an erosive base and increases in thickness southwards up to about 60 cm. It is mainly composed of reworked concretionary sandstones, mudstones, intraclasts and bivalve shells, and is interpreted as a submarine reworked horizon comprising amalgamated beds (Scasso *et al.* 1991). Further published records from the Santa Marta and López de Bertodano formations were scrutinized and used to reconstruct the diversity changes of Antarctic fish in the Late Cretaceous.

As the exact stratigraphic age of the sampled horizons is still unresolved, the faunas were divided into those coming from the (Beta Member) upper part of the Lachman Crags Member and those from the Herbert Sound Member. It is assumed that all this material is Campanian in age. The terminology for sharks used herein follows that of Cappetta (1987); the systematic scheme for sharks is based on Carvalho (1996) and that for teleosts follows Nelson (1994).

Abbreviations: BMNH, Natural History Museum, London. The prefix BAS indicates material collected by the British Antarctic Survey. IAA-IRJ2000-1–IAA-IRJ2001-27 – material housed in the collection of the Instituto Antartico Argentino.

Previous research

The majority of previous studies on Late Cretaceous Antarctic fish concentrated on records from the López de Bertodano Formation of Seymour Island (e.g. Woodward 1908; Grande & Eastman 1986; Grande & Chatterjee 1987). The only account of Late Cretaceous fish from James Ross Island is that of Richter & Ward (1990), who described material from the 'Beta' (Lachman Crags) and 'Gamma' (Herbert Sound) members of the Santa Marta Formation, in the northern part of James Ross Island. The fish association of the Lachman Crags Member is extremely low in taxonomic diversity. Richter & Ward (1990) reported the presence of hexanchiforms (*Chlamydoselachus thomsoni*, *Notidanodon dentatus*) and synechodontiforms (*Sphenodus* sp.), based on three isolated teeth and additional unidentified selachian vertebrae derived from conglomerates and coquinas. The Herbert Sound Member yielded a more diverse fauna of selachians, including *Notidanodon pectinatus* (= *N. dentatus*), *Sphenodus* sp., *Squatina* sp., and undetermined lamniforms, as well as actinopterygians such as *Enchodus* sp. and ?*Sphaeronodus* sp.

Fish from the Santa Marta Formation

Holocephalians

Stahl & Chatterjee (1999, 2002) described the callorhynchid *Ischyodus dolloi* and the chimaerid *Chimaera zangerli* from the Maastrichtian López de Bertodano Formation of

Table. 1. *Occurrence of Late Cretaceous Antarctic neoselachians and teleosts. Asterisks indicate first records. Numbers in brackets denote the number of specimens used in this study*

Santa Marta Formation		López de Bertodano Formation
Lachman Crags Member	Herbert Sound Member	Undifferentiated
Neoselachii		
Chlamydoselachus thomsoni (1) *Notidanodon dentatus* (3) *Lamniformes indet.* (3) *Sphenodus* sp. (1) *Paraorthacodus* sp.* (1)	*Chimaera zangerli** (12) *Chlamydoselachus thomsoni** *Notidanodon dentatus* (8) *Squatina* sp. (11) *Scapanorhynchus* sp.* Lamniformes indet. (75) *Sphenodus* sp. (4) *Paraorthacodus* sp.* (2)	*Chimaera zangerli* (4) *Ischyodus dolloi* (1) *Notidanodon dentatus* (3) Lamniformes indet. (1) *Sphenodus* sp. (1)
Teleostei		
Albuliformes indet.* (2) Ichthyodectiformes indet.* (5) Teleostei indet. (<10)	Albuliformes indet.* (1) Ichthyodectiformes* (21) *Enchodus* sp. (3) *Apateodus?* sp.* (1) Teleostei indet. (>10)	*Antarctiberyx seymouri* (1) *Enchodus cf. ferox** (1) Teleostei indet. (>10)

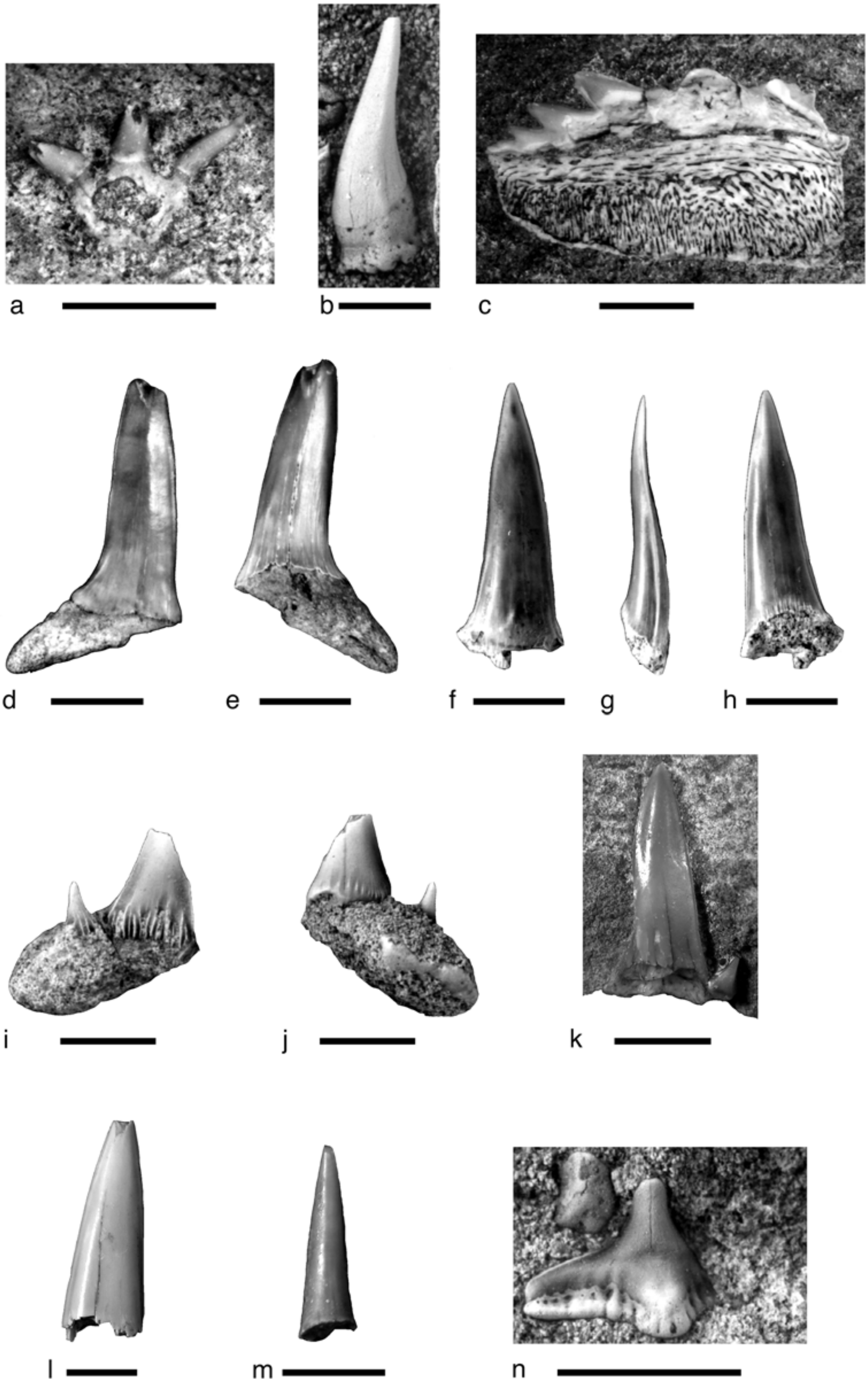
Seymour Island. Additional specimens assignable to *Chimaera zangerli* are now recorded in the Herbert Sound Member of James Ross Island. The material consists of two tooth plates that are still embedded in sandy matrix and several tritor fragments. The material will form the focus of a forthcoming taxonomic publication.

Neoselachians

Selachian remains are the main component of the marine vertebrate fauna, and are known from several sites in the Lachman Crags and Herbert Sound members. So far, only neoselachian remains have been discovered. Remains of hybodontoids and rays have not yet been reported from Antarctica. This is almost certainly due to the mode of collection; all material was surface collected and there has been no systematic chemical treatment or screen washing. Sharks include at least 11 species of Hexanchiformes, Lamniformes, Squatiniformes and Synechodontiformes (Table 1).

Hexanchiformes. Hexanchiform sharks are represented by only two species, *Chlamydoselachus thomsoni* Richter & Ward, 1990 (Chlamydoselachoidei) and *Notidanodon dentatus* (Agassiz, 1843) (Hexanchoidei) (see Agassiz, 1833–1844). *Chlamydoselachus thomsoni* is restricted to Antarctica and was based on a single tooth from the 'Beta Member' (= Lachman Crags Member) (Richter & Ward 1990). An additional, smaller specimen (IAA-IRJ2000-1) was recovered from the Herbert Sound Member (Fig. 2a). It is still embedded in an indurate sandy concretion and only the lingual side was prepared due to the very fragile condition of the specimen. The root is slightly shorter than in the specimen described by Richter & Ward (1990); 3.2 mm wide compared to 4.9 mm. The lingual root surface is slightly damaged, and the crown lacks the tips of the mesial and central cusps; all cusps are massive and the apex of the distal cusp is slightly twisted (Fig. 2a). No additional intercalated cusplets between cusps, as in the type-species, are

Fig. 2. Neoselachians from the Herbert Sound Member. (**a**) Tooth of *Chlamydoselachus thomsoni* (IAA-IRJ2000-1) in occlusal view embedded in sandy matrix. The scale bar is 0.5 cm. (**b**) Isolated tooth crown tentatively assigned to *Chlamydoselachus thomsoni* (BAS DJ.172.28) in lateral view. The scale bar is 0.25 cm. (**c**) Split tooth of *Notidanodon dentatus* (IAA-IRJ2000-2) in lateral view exposing modified anaulacorhize root vascularisation pattern. The scale bar is 0.5 cm. (d)–(h) Teeth of *Scapanorhynchus* sp. Scale bars are 1.0 cm. (**d**) Specimen 1 (IAA-IRJ2000-9), labial view. (**e**) Specimen 1 (IAA-IRJ2000–9), labial view. (**f**) Specimen 2 (IAA-IRJ2000-10), labial view. (**g**) Specimen 2 (IAA-IRJ2000-10), mesial view. (**h**) Specimen 2 (IAA-IRJ2000-10), lingual view. (i)–(j) Fragmentary tooth of cf. *Scapanorhynchus* sp. (BAS DJ.172.11). The scale bars are 0.5 cm. (**i**) Labial view. (**j**) Lingual view. (**k**) Tooth of Lamniformes indet. (IAA-IRJ2000-12) in matrix. The scale bar is 0.5 cm. (**l**) Isolated tooth crown of Lamniformes indet. (IAA-IRJ2000-13). The scale bar is 0.5 cm. (**m**) Isolated tooth crown of Lamniformes indet. (IAA-IRJ2000-14). The scale bar is 0.5 cm. (**n**) *Squatina* sp., lingual view. (BAS DJ.172.39). The scale bar is 0.5 cm.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preserved. The ornamentation is less developed, consisting of fewer and shorter vertical folds than in the Lachman Crags Member specimen and is restricted to basal parts of the cusps. The root is labio-lingually shorter and is less bifid; the crown–root junction is not constricted.

A very fragmentary tooth (BAS DJ.172.28), from the Herbert Sound Member with the central cusp and root remains preserved, displays the general morphology of *Chlamydoselachus* teeth (Fig. 2b). However, this single specimen is about three times larger than the other Herbert Sound Member specimen (IAA-IRJ2000-1), and about twice as large as the Lachman Crags Member specimen described by Richter & Ward (1990).

The differences in the ornamentation and size of the specimens might be related to different positions within the jaws rather than representing different species. Although the attribution of isolated teeth to a definite jaw position is very difficult, general trends might apply to fossil sharks (Welton 1979). The tooth figured by Richter & Ward (1990, fig. 5) was interpreted as coming from an anterior file based on file position reconstructions by Welton (1979) for the extant *C. anguineus*. The morphology of the root, with a smaller median cusp angle in specimen IAA-IRJ2000-1, indicates a lateral to latero-posterior jaw position.

Despite the size of teeth, hexanchoids are relatively uncommon in the Lachman Crags and Herbert Sound members. A single species, *Notidanodon dentatus*, occurs in the Lachman Crags and Herbert Sound members. (NB. The validity of this species is dubious; for a detailed discussion see Cione 1996.) Here, we follow Cione (1996) in regarding *N. pectinatus* as a *nomen dubium* and *N. dentatus* as valid. The presence of *N. dentatus* in the Lachman Crags and Herbert Sound members was indicated by Richter & Ward (1990, fig. 6d) on the basis of a single tooth from each unit (Table 1). Additional new material includes two fragments from the Lachman Crags Member and seven mostly fragmentary teeth from the Herbert Sound Member (IAA-IRJ2000-2–IAA-IRJ2000-8) (Fig. 2c). *N. dentatus* also occurs in the López de Bertodano Formation (Maastrichtian) of Seymour Island (Cione & Medina 1987; Grande & Chatterjee 1987 (as *N. antarcticus*)).

Lamniformes. Lamniform sharks are rare in the Lachman Crags Member (Table 1). Conversely, in the Herbert Sound Member, lamniform teeth are the major component of the selachian association, although most specimens are too fragmentary to be identified below ordinal level. Richter & Ward (1990, fig. 6j, k) figured two tooth crowns that display vertical, slightly flexuous folds on the lingual side. The third specimen assigned to lamniforms by these authors reveals a morphology similar to that of the new material of *Sphenodus* (see below).

At least three additional lamniform teeth (IAA-IRJ2000-9 to IAA-IRJ2000-10, BAS DJ.172.11) of the taxon figured by Richter & Ward (1990, fig. 6j–l) have been recovered (Fig. 2d–k). All these specimens are fragmentary. Specimen IAA-IRJ2000-9 has an awl-shaped, pointed and sigmoidal curved central cusp with a smooth labial face (Fig. 2d), but with numerous weak and parallel vertical folds on the lingual face extending from the crown base to the middle of the crown (Fig. 2e). The labial crown face is flat, lacking a basal labial ledge (Fig. 2d), whereas the lingual one is convex with a faint basal bulge but without a basal crown band (Fig. 2e). The preserved root lobe is slender with pointed terminations and diverges from the crown (Fig. 2d). Lateral cusplets are not present, but this might be due to secondary loss since the tooth is abraded. The central cusp of specimen IAA-IRJ2000-10 is also sigmoidal in profile view (Fig. 2g) and the ornamentation consists of very short lingual folds that are restricted to the crown base (Fig. 2f, h). Specimen BAS DJ.172.11 from the Herbert Sound Member is heavily broken; however, it displays a mesio-distally expanded but short and rounded root lobe (Fig. 2i, j), and a very acute and delicate lateral cusplet that is well separated from the main cusp (Fig. 2i). No basal labial ledge uniting the lateral cusplet with the base of the main cusp is developed (Fig. 2i). Basally, there are numerous short vertical ridges on the labial face (Fig. 2i); the lingual folds are also very short and feeble (Fig. 2j).

The three teeth are more or less damaged and it is not always possible to assign specimens to a specific lamniform; teeth of Cretaceous odontaspidids and mitsukurinids can easily be confused when incomplete. Most specimens share character combinations that occur in several species of *Carcharias* and *Scapanorhynchus*, e.g. cutting edges complete or almost reaching the crown base, acute lateral cusplets and conspicuous ornamentation pattern (specimen IAA-IRJ2000-11). However, the awl-shaped main cusps, absence of a labial basal edge that unites the main cusp and lateral cusplets, and the morphology of the root (pointed and slender root lobes in anterior (Fig. 2d–h) and more spatulate lobes with rounded extremities (Fig. 2i–k) in lateral teeth) are characteristic for teeth of *Scapanorhynchus* rather than odontaspidids. As far as can be ascertained, there is no distinct nutritive groove separating the two root lobes (Fig. 2e) and the protuberance is not shelf-like as it is in most *Carcharias* species. However, the nutritive groove is rather deep and distinct in several specimens of *Scapanorhynchus* and the generally massive lingual protuberance might also be shelf-like in some species (cf. Case & Cappetta 1997). The ornamentation, consisting of rather short and more flexuous lingual folds, is more typical for teeth of odontaspidids. Specimen BAS DJ.172.11 (Fig. 2i) resembles teeth of *Carcharias* in the labial ornamentation and the presence of a labial basal central ridge (Siverson 1996). Labial folds are present in *S.* aff. *praeraphiodon* from the late Cenomanian of Texas (Cappetta & Case 1999) and in *Scapanorhynchus* sp. (= *S. minimus*) from the Cenomanian of France (Landemain 1991). In addition, teeth of *Carcharias* generally have a basal labial ledge that unites the lateral cusplets with the main cusp, which is absent in teeth of *Scapanorhynchus*. Nevertheless, better material is needed to establish the exact systematic position of the Antarctic lamniforms.

Other fragmentary teeth of lamniforms (IAA-IRJ2000-12–IAA-IRJ2000-14) are rather abundant in the Herbert Sound Member (Fig. 2k–m), but are too incomplete for any specific identification. Specimen IAA-IRJ2000-13 (Fig. 2l) is very similar to specimen IAA-IRJ2000-10 (Fig. 2h) and may also belong to *Scapanorhynchus*.

Squatiniformes. Richter & Ward (1990, fig. 6a–c) indicated the presence of *Squatina* in the Herbert Sound Member, with a species similar to *S. hassei* from the Campanian and Maastrichtian of Europe. This identification was based on a single vertebra and two fragmentary teeth. Here we record seven more specimens from the Argentinean collection (IAA-IRJ2000-10–IAA-IRJ2000-16) and two additional specimens from the BAS collections in the Natural History Museum, London. Specimen BAS DJ.172.39 is embedded in matrix and the lingual side is exposed (Fig. 2n); this tooth displays an erect, central cusp and an oblique lateral blade with continuous cutting edge.

The fossil record of *Squatina* extends back to the Middle Jurassic, and the morphology of the tooth crown and root is supposed to be the unifying character of all extant and fossil species. However, a *Squatina*-like morphology is also found in teeth of several extant and fossil orectolobiforms such as *Orectolobus*, *Cretorectolobus* and *Cretascyllium* (Case 1978; Müller & Diedrich 1991; Herman *et al.* 1992; Siverson 1997). In fact, teeth of extant *Orectolobus*, *Eucrossorhinus* and *Squatina* species share some important morphological features such as a root base having a large outer depression and a large inner central protuberance, tooth crown with mesial and distal heels, and a small but well-developed apron and large but narrow uvula (Herman *et al.* 1992). The main feature to distinguish *Squatina* teeth from similar orectolobiform teeth is the root-supported apron. In addition, the lateral blades have denticles or are enlarged at their distal ends in most orectoloboids (D. Long pers. comm. 2004). A single specimen from the Herbert Sound Member (IAA-IRJ2000-10) displays a root-supported apron, and the lateral blades are low, oblique and without denticles or distal enlargements in most Antarctic specimens (e.g. BAS DJ.172.39) (Fig. 2n). Consequently, the Herbert Sound specimen is assigned to *Squatina* without specific identification here.

Synechodontiformes. Antarctic synechodontiform sharks include at least two species. Richter & Ward (1990, fig. 6h, i) indicated the presence of *Sphenodus* sp. (Orthacodontidae) in the Lachman Crags Member on the basis of an isolated and large tooth root, and in the Herbert Sound Member on the basis of an isolated crown with tooth remnants. They stated that these remains belong to a new species resembling *Sphenodus lundgreni* from the Danian of Scandinavia. However, the material was too fragmentary to define this species.

Two additional specimens recovered by the Argentinean expedition (IAA-IRJ2000-17 and IAA-IRJ2000-18) (Fig. 3a–e) and a fragmentary specimen collected by a British Antarctic Survey expedition (BMNH/BAS uncatalogued (uncat.)) provide further morphological information, although both specimens are damaged. The slightly lingually bent tooth crowns (Fig. 3b) are rather broad, almost triangular in labial view, and elongated with pointed apices (Fig. 3a). The cutting edges are well developed and prominent, reaching the base of the crown (Fig. 3b). The labial face is convex in the middle, especially in its central part near the base, with several very short and weak folds along the crown base (Fig. 3a), but does not jut out over the root (Fig. 3b). The lingual face is very convex with numerous stronger vertical folds at the crown base (Fig. 3c). The root is rather narrow and slightly mesio-distally expanded with a horizontal root base and numerous randomly arranged foramina

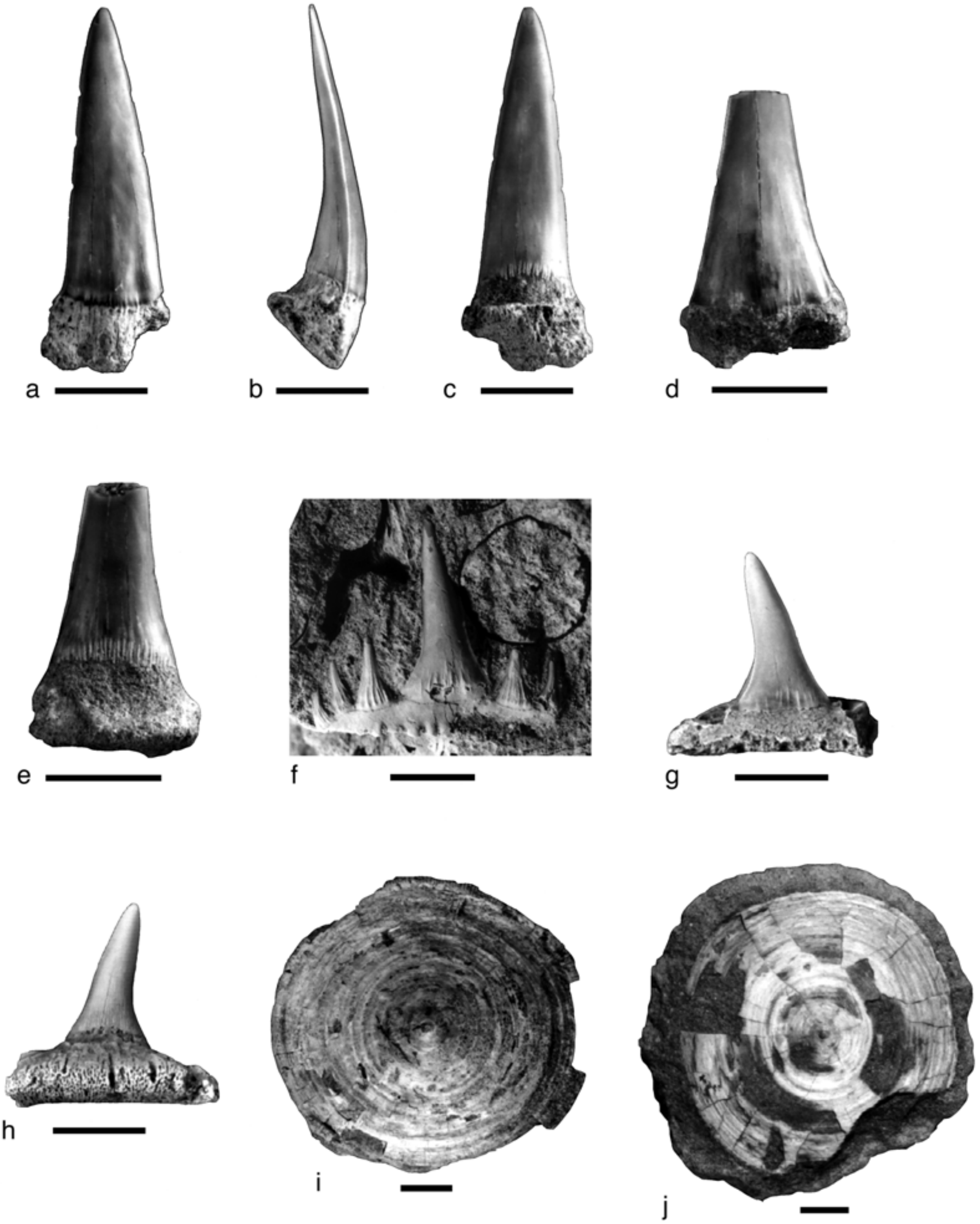


Fig. 3. Neoselachians from the Lachman Crags and Herbert Sound members. (a)–(e) *Sphenodus* sp., Herbert Sound Member. The scale bars are 1.0 cm. (**a**) Specimen 1 (IAA-IRJ2000-17), labial view. (**b**) Specimen 1 (IAA-IRJ2000-17), mesial view. (**c**) Specimen 1 (IAA-IRJ2000-17), lingual view. (**d**) Specimen 2 (IAA-IRJ2000-18), labial view. (**e**) Specimen 2 (IAA-IRJ2000-18), lingual view. (**f**) *Paraorthacodus* sp. (IAA-IRJ2000-19), Lachman Crags Member, labial view. The scale bar is 0.5 cm. (g)–(h) *Paraorthacodus* sp. (BAS DJ.136.2), Herbert Sound Member, lacking lateral cusplets. The scale bars are 0.5 cm. (**g**) Labial view. (**h**) Lingual view. (**i**) Lamniformes indet. (IAA-IRJ2000-20), isolated vertebra, Herbert Sound Member. The scale bar is 1.0 cm. (**j**) Lamniformes indet. (IAA-IRJ2000-21), isolated vertebra, Herbert Sound Member. The scale bar is 1.0 cm.

piercing the surface (Fig. 3a, b, e). The fragmentary crown figured by Richter & Ward (1990, fig. 6l) as Lamniformes indet. displays a very similar morphology and ornamentation to the Argentinean specimens, and is consequently referred to *Sphenodus*.

The fossil record of *Sphenodus* ranges from the Early Jurassic to the Danian (Beaumont 1960). However, the validity of most if not all Late Cretaceous species (e.g. Pictet & Campiche 1858; Priem 1912) is dubious because the material consists mainly of isolated tooth crowns. The Antarctic specimens resemble those from the late Campanian of Angola, especially in the ornamentation (Antunes & Cappetta 2002). Teeth of *S. lundgreni* from the Danian of Scandinavia differ in the higher degree of labial wrinkles that reach far up the crown, and in the more pronounced basal folds.

The specimen identified as *Isurus* sp. from the Maastrichtian López de Bertodano Formation by Grande & Eastman (1986, fig. 3H, I) in fact represents another specimen of this *Sphenodus* species and extends its range from the Campanian to the Maastrichtian in Antarctica. The specimen identified as *Sphenodus*? sp. from the same formation by Grande & Chatterjee (1987, fig. 2F, G) certainly does not belong to a neoselachian shark (see below).

The second synechodontiform species represents the first record of *Paraorthacodus* (Palaeospinacidae) in Antarctica. Two specimens were recovered by the Argentinean (IAA-IRJ2000–19) and BAS expeditions (BAS DJ.136.2), respectively (Fig. 3f–h). Specimen IAA-IRJ2000-19 comes from the Lachman Crags Member and is still embedded in silty matrix that also contains abundant plant remains and a few bivalves (Fig. 3f). The other specimen (BAS DJ.136.2) was recovered from the Herbert Sound Member. The central cusp and the root are well preserved, but the specimen lacks the lateral cusplets (Fig. 3g, h). The teeth are up to 12 mm wide and 11 mm high. The main cusp in both specimens is slender in its upper part with the cutting edges being almost parallel; basally the cusp widens rapidly in its basal third (Fig. 3f–h). The labial face of the central cusp is flat, does not overhang the root, and has folds that differ in length but are restricted to the base (Fig. 3f, g). Conversely, the lingual face is strongly convex so that the margins of the basal part are visible in labial view (Fig. 3g), and has more and tenuous folds ascending halfway up from the base of the cusp (Fig. 3h). There are three pairs of distal and two pairs of mesial cusplets with numerous folds that also ascend half way up in specimen IAA-IRJ2000–19 (Fig. 3f). The root is rather low and displays the typical vascularization pattern of palaeospinacids (Fig. 3f, g). Comparison of the Antarctic specimens with contemporaneous taxa is difficult because of the still insufficient knowledge of Late Cretaceous *Paraorthacodus* species. Six species are regarded as being valid (Siverson 1992): *P. andersoni* (Case 1978) from the ?Cenomanian–Campanian of the USA, France and Sweden; *P. conicus* (Davis 1890) from the Coniacian–Campanian of Kazakhstan, Germany, Belgium and Sweden; *P. patagonicus* (Ameghino 1893) from the Coniacian of Argentina; *P. recurvus* (Trautschold 1877) from the Albian–Cenomanian of Lithuania and Russia; *P. sulcatus* (Davis 1888) from the ?Campanian of New Zealand; and *P. validus* (Chapman 1918) from the Late Cretaceous of New Zealand. The following character combination distinguishes the Antarctic specimens from all other *Paraorthacodus* species: cusp and lateral cusplets labio-lingually compressed; labial crown face very flat; very high, acute and slender main cusp and lateral cusplets; comparably fine and short labial folds; and the basal part of the lingual face of the cusp visible in labial view. This character combination indicates that the Antarctic *Paraorthacodus* represents a hitherto unknown species.

Other remains. Isolated vertebral centra of neoselachians occur sporadically in different horizons of both the Lachman Crags and Herbert Sound members. For example, Richter & Ward (1990, fig. 6a) figured a centrum of typical squatinid appearance from the Herbert Sound Member (cf. Hasse 1882). Some vertebral centra or imprints of centra studied here are of tectospondylic type and can be assigned to squatinids. A few other, more or less circular, vertebral centra and imprints of asterospondylic-type with regular concentric laminae (e.g. IAA-IRJ-2000-20 and IAA-IRJ2000-21) are characteristic of orectolobiforms and lamniforms (Fig. 3i, j). Because no orectolobiform remains have been recovered so far, and because of the size of the centra, these remains are assigned to lamniforms without further identification.

Actinopterygii

The teleostean fauna of the Santa Marta Formation is rather low in diversity compared to contemporaneous fish faunas, and comprises mostly disarticulated fragments. The Lachman Crags Member yielded only isolated scales, and the Herbert Sound Member assemblage is represented by isolated teeth, vertebrae, skull and caudal fin elements.

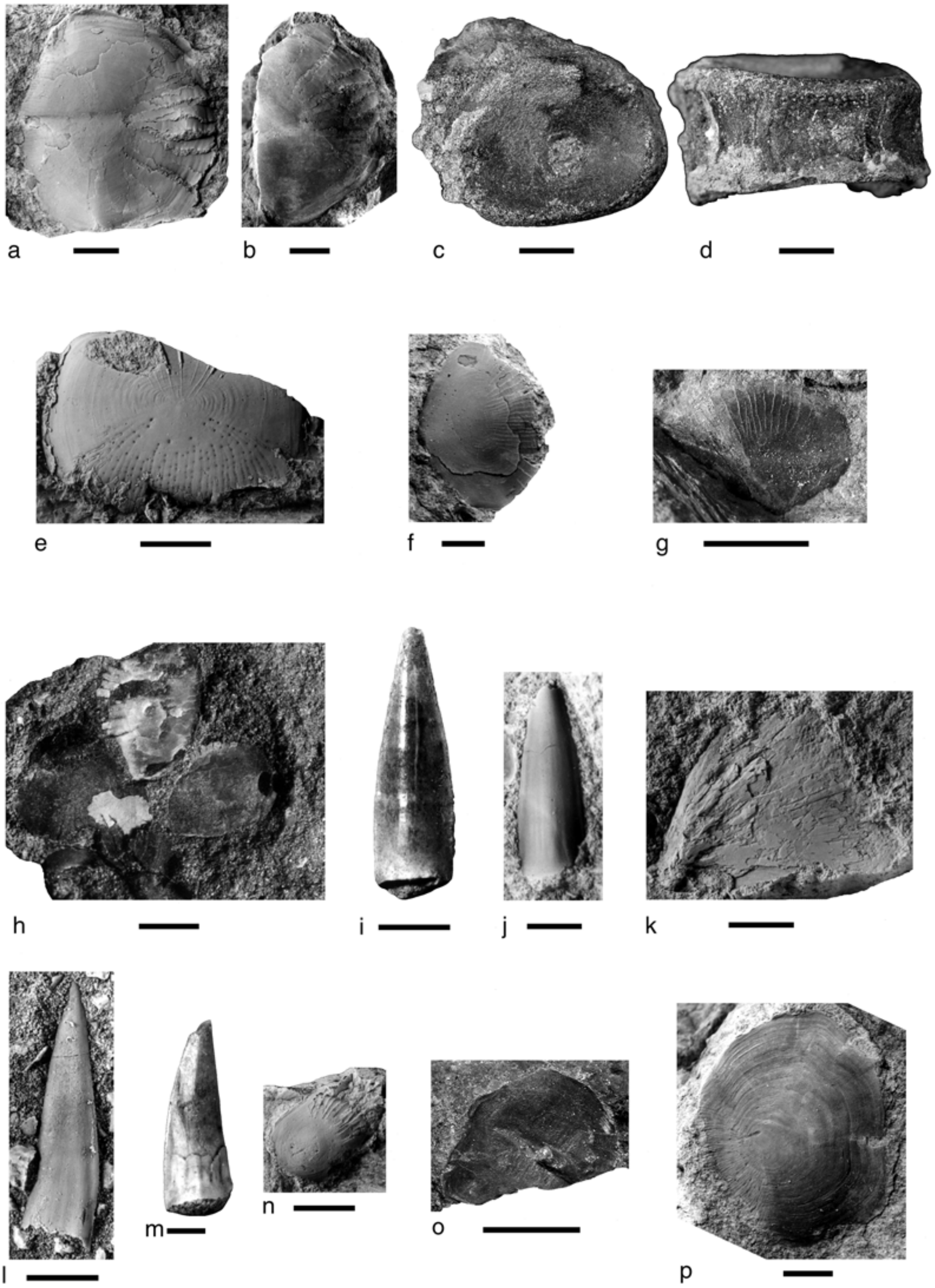
Elopomorpha. Two single scales from the Lachman Crags Member are assigned to albuliforms, which closely resemble scales of *Osmeroides* (Fig. 4a, b). The better-preserved specimen (IAA-IRJ2000-22) is roughly subrectangular in outline, being only slightly higher than long. There are some deep, slightly convergent anterior radii directed toward the centre of the scale but not actually reaching it (Fig. 4a). The posterior field is marked by faint, subparallel, short grooves obscured by very small granulations. The focus is more or less in the middle of the scale. The posterior margin of the scale is slightly triangular, almost straight (Fig. 4a). Fine circuli occupy the lateral and posterior areas. The second specimen (IAA-IRJ2000-23), although lacking the posterior part, is almost identical to the former (Fig. 4b). The morphology of these scales is very similar to that of *Osmeroides lewesiensis* (BMNH P.10220 and BMNH P.49893) from the Turonian of England, and *Osmeroides* sp. from the late Cenomanian of Germany (BMNH P.306). They also slightly resemble scales assigned to *Osmeroides* from the Turonian of Canada (Fielitz 1996; Wilson & Chalifa 1989). Scales of extant elopomorphs, such as *Megalops atlanticus*, display the same morphology, although they generally have more anterior radii (Roberts 1993, fig. 4B).

Identification of isolated fossil scales is difficult due to poor preservation and insufficient knowledge of scale morphologies in fossil taxa. However, based on comparisons with numerous articulated fish skeletons from the Cretaceous of Europe and North and South America, these Antarctic scales are allocated here to Albuliformes. This is the first record of albuliforms in Antarctica, although positive identification must await the acquisition of better-preserved material. A single, relatively large vertebral centrum from the Herbert Sound Member (IAA-IRJ2000-24) is rostro-caudally compressed and ventrally flattened (Fig. 4c, d). It resembles those described and figured for *Osmeroides* by Loomis (1900).

Ichthyodectiformes. Ichthyodectiform teleosts are represented by numerous scales in the Lachman Crags Member (Fig. 4e–g). The scales are rounded–subtriangular in outline and are wider than long. All have numerous (more than 20) rather deep anterior radii that are directed towards the centre of the scales (Fig. 4f, g). The focus is suboval–oval and is located in the centre of the scales (Fig. 4e). Fine circuli are closely arranged following the outer edge of the scale (Fig. 4e). In addition, punctae decorate the inner parts in a triangular area and randomly around the focus area of the scales (Fig. 4e, f). Bigger scales (e.g. IAA-IRJ2000-25) are more rounded, with the anterior radii being shorter compared to those in the smaller scales and restricted to a small area (Fig. 4e). A few damaged scales from the Herbert Sound Member display the same morphology and are also assigned to ichthyodectiforms (e.g. IAA-IRJ2000-28, Fig. 4h).

The presence of numerous anterior radii, the outer form of the scales and the punctuated inner parts are characteristic of ichthyodectiform scales. Most of these scales resemble closely those of *Ichthyodectes* and *Gillicus* spp. from the Campanian of North America, and might thus be referred to one of these genera. The scales of *Cladocyclus* from the Early Cretaceous of Brazil differ in the general appearance and shorter anterior radii.

Fig. 4. Teleostean remains from the Lachman Crags and Herbert Sound members. (**a**) Isolated scale of Albuliformes indet. (IAA-IRJ2000-22), Lachman Crags Member. The scale bars are 0.5 cm. (**b**) Isolated scale of Albuliformes indet. (IAA-IRJ2000-22, IAA-IRJ2000-23), Lachman Crags Member. The scale bars are 0.5 cm. (c) & (d) Isolated vertebra (IAA-IRJ2000-24), Herbert Sound Member, assigned to Albuliformes. The scale bars are 0.5 cm. (**c**) Anterior view. (**d**) Lateral view. (**e**) Isolated scale of Ichthyodectiformes indet. (IAA-IRJ2000-25), Lachman Crags Member. The scale bar is 0.5 cm. (**f**) Isolated scale of Ichthyodectiformes indet. (IAA-IRJ2000-26), Lachman Crags Member. The scale bar is 0.5 cm. (**g**) Isolated scale of Ichthyodectiformes indet. (IAA-IRJ2000-27), Lachman Crags Member. The scale bar is 0.5 cm. (**h**) Associated scales of Ichthyodectiformes indet. (IAA-IRJ2000-28), Herbert Sound Member. The scale bar is 0.5 cm. (**i**) Isolated tooth of Ichthyodectiformes (IAA-IRJ2000-29), Herbert Sound Member. The scale bar is 0.5 cm. (**j**) Isolated tooth of Ichthyodectiformes (IAA-IRJ2000-30), Herbert Sound Member. The scale bar is 0.25 cm. (**k**) Isolated caudal hypural bone of Ichthyodectiformes indet. (IAA-IRJ2000-31), lateral view, Herbert Sound Member. The scale bar is 0.5 cm. (**l**) Isolated tooth of *Enchodus* sp. (IAA-IRJ2000-32), Herbert Sound Member. The scale bar is 0.5 cm. (**m**) Isolated tooth of *Enchodus* sp. (IAA-IRJ2000-33), Herbert Sound Member. The scale bar is 0.25 cm. (**n**) Isolated scale, Lachman Crags Member tentatively assigned to Ichthyodectiformes indet. (IAA-IRJ2000-34). The scale bar is 0.5 cm. (**o**) Isolated scale of uncertain affinities (IAA-IRJ2000-35), Lachman Crags Member. The scale bar is 0.5 cm. (**p**) Isolated scale of uncertain affinities (?Ichthyodectiformes) (IAA-IRJ2000-36), Lachman Crags Member. The scale bar is 0.5 cm.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Isolated ichthyodectiform teeth are quite common in the Herbert Sound Member. Most teeth are tall, rather slender, laterally compressed and sometimes slightly posteriorly curved but never sigmoidal in lateral view (e.g. IAA-IRJ2000-29 and IAA-IRJ2000-30, Fig. 4i, j). The apices are pointed, the cutting edges distinct and continuous from the tip to the base (Fig. 4i, j). The lateral sides are more or less convex especially in the middle part of the crowns; the base is subcircular–oval. Most teeth are completely smooth; only a few display faint vertical striations along the lateral edge (Fig. 4j), a character that also might be found in larger teeth of some enchodontids. In their general appearance these teeth resemble those of *Enchodus* spp. However, these differ in the sigmoidal curvature of the crown in lateral view, more needle-like appearance, absence of posterior continuous cutting edges, post-apical barb and/or distinct elliptic cross-sections. Some of these characters might be present in ichthyodectiform teeth, but never all together. The most reliable character to distinguish large teeth of enchodontoids and ichthyodectiforms seems to be the sigmoidal curve of the crown in the former group. Because of the apparent differences, these teeth are referred to ichthyodectiforms. However, it is possible that comparable enchodontid teeth have been included with those of ichthyodectiforms. The tooth figured by Richter & Ward (1990, fig. 6e) and referred to as ?*Enchodus* sp. more closely resembles those of ichthyodectiforms. Teeth of *Gillicus* are very similar and most if not all teeth of this type from Antarctica might belong to the same taxon as the scales described above. Whereas teeth of the ichthyodectiform *Cladocyclus* from Brazil differ in having a folded base, those of North American *Xiphactinus* species are more massive, stouter and exhibit striations on the lateral surfaces (cf. Schwimmer *et al.* 1997).

An isolated hypural bone (IAA-IRJ2000-31) that is very high and slightly inclined ventrally is tentatively also assigned to ichthyodectiforms (Fig. 4k). Hypural bones of enchodontids are sometimes also enlarged, but still narrower than the Antarctic specimen. In addition, the enlarged hypurals of enchodontids often bear basal openings that are absent in this specimen.

Alepisauriformes. Alepisauriform remains are extremely rare. Richter & Ward (1990, fig. 6g) assigned an isolated and damaged tooth to *Enchodus* that displays the typical morphology of enchodontid palatine teeth. Two isolated teeth (IAA-IRJ2000-32 and IAA-IRJ2000-33) that are referred here to *Enchodus* were recovered from the Herbert Sound Member (Fig. 4l, m). Both specimens display the typical sigmoidal curvature in lateral view.

A single specimen was erroneously identified as ?*Sphaeronodus* by Richter & Ward (1990, fig. 6f). This specimen resembles teeth of the alepisauriform *Apateodus*. An isolated, rather small scale from the Lachman Crags Member (IAA-IRJ2000-34) displays the general morphology found in several extant alepisauriforms (Fig. 4n). It is roughly rectangular in outline and crenate with a rounded focus and closely arranged, fine circuli.

Teleostei indet. A number of isolated teeth and scales from both members cannot be assigned to any teleostean group because they are too fragmentary or to unspecific (e.g. IAA-IRJ2000-35 and IAA-IRJ2000-36, Fig. 4o, p). A moderately large scale (IAA-IRJ2000-36) with rounded outline and almost straight anterior margin from the Lachman Crags Member is characterized by very fine circuli and short, narrow, posterior radii (Fig. 4p). A very similar scale was figured by Wilson & Chalifa (1989, fig. 7M) from the Turonian of Canada without any taxonomic allocation. This scale resembles those of *Cladocyclus mawsoni* from the Late Cretaceous of Brazil (e.g. BMNH P.3872a and BMNH P.9615) and thus might also represent an ichthyodectiform. Additional isolated bones and small vertebral centra indicate the likely presence of further unidentified bony fishes.

Maastrichtian teleosts

Maastrichtian Antarctic fish are exclusively known from the López de Bertodano Formation of Seymour Island (Table 1). Grande & Chatterjee (1987) described *Antarctiberyx seymouri* and indicated the presence of *Orthacodus* (= *Sphenodus*) sp. in the same formation (Grande & Chatterjee 1987, fig. 2F, G). However, the single specimen of *Orthacodus* differs significantly from teeth of *Sphenodus* (see above). It displays some striations on the lateral sides and a posterior groove that almost reaches the apex. In this respect, the tooth resembles closely those of *Enchodus ferox* from the Campanian and Maastrichtian of the Western Interior Seaway of North America and the Maastrichtian of Morocco. Additional teleostean material includes about 100 isolated bones and vertebral centra, indicating that a probably diverse teleostean fauna waits to be described.

Palaeobiogeographical and palaeoecological implications

The James Ross Basin was a back-arc basin with rather unstable margins; sediment was intermittently transported into it from an active magmatic arc to the NW (Crame *et al.* 1991). After a period of deep-marine sedimentation (Gustav Group) sediments of the Marambio Group were deposited at shelf depth, with the Lachman Crags Member representing a mid–outer shelf setting and the overlying Herbert Sound Member an inner shelf environment with significant shallowing of the basin (Pirrie 1990; Crame *et al.* 1991; McArthur *et al.* 2000).

Oxygen isotope analyses of planktonic foraminifera from the Falkland Plateau (high-latitude South Atlantic) suggest that warm surface waters may have endured in this region from the Turonian through to the early Campanian, before the beginning of a long-term cooling in the late Campanian through to the end of the Maastrichtian (Huber *et al.* 1995). Direct surface and midwater access for South Atlantic equatorial waters into the Weddell Basin was initiated in the Turonian, shortly after the transpolar shallow seaway linking the southern Weddell Sea to the Tasman and eastern Australian margins had been closed (Dingle 1999; Dingle & Lavelle 2000). The mid-Campanian witnessed an enlargement of the trans-equatorial Tethyan seaway, which was at its largest in the mid-Campanian–Maastrichtian. This may well have been a time of enhanced faunal exchanges between the James Ross Basin and lower latitudes, with large predatory fish having cosmopolitan or widespread distributions entering Antarctic waters.

Hexanchiformes

The hexanchoid *Notidanodon* displays a bipolar distribution with most records being from the Northern Hemisphere Late Cretaceous and Palaeogene (Cappetta 1987). The species *N. dentatus* is a typical Southern Hemisphere hexanchoid that is known from Angola (Antunes & Cappetta 2002), New Zealand (Davis 1890) and Antarctica. The stratigraphically youngest records come from the Palaeocene of Seymour Island and possibly the Danian of New Zealand. According to Cione (1996), *N. dentatus* preferred warm temperate to temperate waters.

The feeding behaviour of fossil hexanchoids is still not fully understood. Extant hexanchoids feed on a wide range of marine organisms, including other sharks, rays, chimaeras, bony fish, squids, crabs, shrimps, carrion and even seals (e.g. Bigelow & Schroeder 1984). Fossil hexanchoid teeth are also often associated with plesiosaur or cetacean bones (e.g. Welles 1943) and it is usually assumed that hexanchoids were scavenging on carcasses. The co-occurrence of *N. dentatus* teeth and plesiosaur remains in the López de Bertodano Formation (Maastrichtian) of Seymour Island (Cione & Medina 1987) and in the Herbert Sound Member (Richter & Ward 1990; this study) supports this interpretation.

The Cretaceous and Cenozoic distribution of *Chlamydoselachus* is rather patchy and thus similar to the distribution of the single extant species. Cretaceous species are relatively rare and most records come from the Campanian. Antunes & Cappetta (2002) described *C. goliath* from the late Campanian, and *C. gracilis* and *Chlamydoselachus* sp. from the late Campanian–early Maastrichtian of Angola, respectively. In addition, *Chlamydoselachus* occurs in the Santonian and Maastrichtian of Japan (M. Goto pers. comm. 2001), indicating a distribution of *Chlamydoselachus* in both hemispheres early in its evolutionary history. It displays its greatest diversity in the Cenozoic with all species being restricted to the Northern Hemisphere (Pfeil 1983). The extant *C. anguineus* is bathydemersal, ranging from surface waters to more than 1200 m depth on outer continental and insular shelves, and upper slopes. *C. thomsoni* represents an endemic faunal element in the Santa Marta Formation, and its occurrence in mid–outer (Lachman Crags Member) and inner shelf settings (Herbert Sound Member) is in accordance with the bathymetric distribution of other *Chlamydoselachus* species.

The dentition of fossil and extant species is of clutching type with generally very slender, needle-like cusps, and similar prey is assumed for fossil and extant species (e.g. cephalopods, fish). However, *C. thomsoni* is characterized by more robust cusps than other Campanian–Maastrichtian species; this supports the interpretation by Richter & Ward (1990) of prey with harder skeletal structures such as belemnites and ammonites. Other prey includes heavier bodied fish, such as a variety of bony fish, and also sharks (e.g. Cox & Francis 1997).

Lamniformes

Lamniforms include large predaceous sharks of demersal and mesopelagic forms occurring from surface waters to the deep sea (e.g. Last & Stevens 1994). Cretaceous lamniforms are among the largest known selachians (Siverson 1999). The only undoubtedly identifiable lamniform teeth from the Late Cretaceous of Antarctica belong to the exclusively Late Cretaceous mitsukurinid *Scapanorhynchus*. At least seven species of *Scapanorhynchus* have been described that are widely distributed in the Northern Hemisphere, and range from the Albian to the Maastrichtian. The oldest record (without specific identification) comes from the Aptian of Japan (Goto *et al.* 1993). Southern Hemisphere occurrences are extremely rare: they include the Turonian and Campanian–Maastrichtian of Angola and Maastrichtian of Brazil (Cappetta 1987; Antunes & Cappetta 2002). *Scapanorhynchus* is an epibenthic–eurybathic predator with a cosmopolitan distribution and it is interpreted here as a casual inhabitant of Antarctic waters, probably related to seasonal feeding migrations. The dental morphology implies small fish and soft-bodied invertebrates as prey. The Herbert Sound Member records expand the range of *Scapanorhynchus* to Antarctica.

Squatiniformes

Modern and fossil species of *Squatina* are widely distributed from cold northern boreal waters to the tropics, and occur at intertidal–upper continental slope depths (e.g. Compagno 1984). They are bottom dwellers that ambush their prey from buried positions in mud or sand. Modern angel sharks display rather pronounced patterns of endemism. The wide distribution of several fossil species might be explained by the rather conservative dental morphology that renders the identification of species difficult. Cretaceous Southern Hemisphere occurrences of *Squatina* are extremely rare (e.g. Maastrichtian of Chile; M. Suarez pers. com. 2001). Many *Squatina*-like specimens might belong either to *Cretorectolobus* or other orectolobiforms (e.g. Siverson 1997).

Synechodontiformes

Cretaceous occurrences of *Sphenodus* (Orthacodontidae) are extremely rare compared to its Jurassic distribution. Only two species from the Early Cretaceous (*S. salandianus* and *S. subaudianus*) and two from the Late Cretaceous (*S. planus* (Cenomanian) and *S. sennessi* (Santonian)) have been described so far (Duffin & Ward 1993). Additional unidentified specimens were reported from the Campanian of Angola (Antunes & Cappetta 2002). The Antarctic and Angola specimens represent a third, still unnamed, Late Cretaceous species. Apart from the Antarctic and Angola specimens, which are the youngest Late Cretaceous records, all other material is from the Northern Hemisphere. However, *Sphenodus* had already displayed a Northern and Southern Hemisphere distribution in the Late Jurassic (Arratia *et al.* 2002). It represents a typical pelagic predator that might have followed its prey during seasonal feeding migrations, in a way similar to that of the lamniforms reported from Antarctica.

The distribution of palaeospinacids, especially that of *Paraorthacodus*, is very similar to that of the hexanchoid *Notidanodon*. Although the species diversity of *Paraorthacodus* is rather low in the Cretaceous, it displays a wide, bipolar distribution in warm–cool temperate areas. The occurrence of *Paraorthacodus* from the Late Cretaceous of Antarctica supports this interpretation. Species of *Paraorthacodus* are interpreted as small, slow-swimming predators in shallow-marine environments with a diet similar to extant orectolobiforms of fish and soft-bodied invertebrates (Thies & Reif 1985).

Elopomorpha

Elopomorph teleosts are a highly diversified group with a rich fossil record. Southern Hemisphere records are, for example, from the Early Cretaceous of Brazil (e.g. Maisey 1991), and from the Late Cretaceous of Brazil (*Brannerion*) and Australia (*Istieus*) (Nelson 1994). The Antarctic specimens assigned to albuliforms expand the range of this group into Antarctic waters during the Late Cretaceous.

Ichthyodectiformes

The fossil history of ichthyodectiforms ranges back to the Middle Jurassic and, as early as the Late Jurassic, ichthyodectiforms are known from Antarctica (Arratia *et al.* 2004). In the Cretaceous ichthyodectiforms are widespread, but are most abundant in the Late Cretaceous of the Northern Hemisphere and include some very large taxa (e.g. *Xiphactinus*). Southern Hemisphere occurrences are mainly of Early Cretaceous age, and include *Cooyoo* from Australia and *Cladocyclus* from freshwater and marine deposits of Brazil (Lees & Bartholomai 1987; Maisey 1991). The large ichthyodectiform *Xiphactinus* has also been reported from the Late Cretaceous of Australia (Bardack 1965).

The rare Cretaceous Southern Hemisphere records of ichthyodectiforms might be related to collecting and/or identification biases.

Alepisauriformes

Alepisauriforms display rather wide distribution patterns in the Late Cretaceous (Kriwet 2003*a*). For example, the enchodontid *Enchodus* is reported from 18 Late Cretaceous localities (Chalifa 1996). The only other positive Southern Hemisphere occurrence of *Enchodus* comes from the Late Cretaceous (?Campanian) of Brazil. *Enchodus* is interpreted as an open-water pelagic predator that also ventured into near-shore areas from the open ocean (Goody 1976). *Apateodus* is very rare and most records are confined to the Late Cretaceous of Europe and North Africa. Alepisauriforms preyed on fish and probably soft-bodied cephalopods, but were in turn preyed on by marine tetrapods, such as plesiosaurs (Cicimurri & Everhart 2001).

Diversity and abundance

Unfortunately, patterns of diversity and abundance in the Early Cretaceous fish of Antarctica are still poorly known (Kriwet 2003*b*). The Herbert Sound Member yielded the highest number of taxa in this study with at least seven chondrichthyans (eight if lamniforms are considered) and four teleosts, compared to four (five if lamniforms are considered) chondrichthyans and two teleosts from the Lachman Crags Member, and four (five if lamniforms are considered) chondrichthyans and at least two teleosts from the López de Bertodano Formation (Table 1).

Most common are unidentified lamniform remains including isolated and fragmentary teeth and vertebrae. Teeth and bones assigned to ichthyodectiforms are the second most common group of fish remains. *Enchodus*, which is quite common in the Late Cretaceous of the Northern Hemisphere, is here reported from both the Santa Marta and López de Bertodano formations: remains such as tooth plates and isolated dental tritors of *Chimaera zangerli* are also rather abundant in the Herbert Sound Member and López de Bertodano Formation.

Reviewing all available information it is apparent that the collections of Late Cretaceous Antarctic fish are still extremely incomplete (if compared to contemporaneous collections form the Western Interior of North America, NW Europe, etc.). This is especially so for both the latest Cretaceous and the Palaeogene, and further intensive taxonomic investigations of these intervals are required.

Conclusions

- The main localities that have yielded Late Cretaceous Antarctic fish to date are situated in the northern part of James Ross Island and on Seymour Island. Three faunas in stratigraphic order can be distinguished that differ slightly in taxonomic composition. The fish fauna from the late Campanian part of the Lachman Crags Member comprises eight taxa, five of which are sharks and three are teleosts. The slightly younger Herbert Sound association comprises at least 11 taxa plus some still unidentified lamniforms. The lamniform *Scapanorhynchus*, the synechodontiform *Paraorthacodus*, as well as an elopomorph, ichthyodectiforms and an alepisauriform close to *Apateodus*, are reported from the Campanian of Antarctica for the first time.
- The stratigraphic ranges of *Chlamydoselachus thomsoni*, *Paraorthacodus* sp. and ichthyodectiforms include both members of the Santa Marta Formation. The stratigraphic range of the chimeroid *Chimaera zangerli*, which was previously only known from the Maastrichtian López de Bertodano Formation, is extended back into the Herbert Sound Member. *Enchodus* cf. *ferox*, previously identified as *Sphenodus* sp., is reported from the López de Bertodano Formation for the first time.
- Medium- to large-sized top predators that occupied the higher levels in the food chain, along with marine tetrapods, dominate the Late Cretaceous Antarctic marine vertebrate faunas. Fish occupying lower levels in the trophic chain are extremely rare in the fossil record. The only fish adapted to crushing hard-shelled prey was a chimeroid. Rays, which are quite common in other Late Cretaceous fish associations (e.g., Maastrichtian of Morocco), are still not known from the Late Cretaceous of Antarctica.
- Many fish above species level, and especially the teleosts, belong to cosmopolitan groups or had wide geographical distributions during the Late Cretaceous. The migration of Northern Hemisphere fish was facilitated and supported by wide open-marine seaways between the Weddell Basin and the Tethyan realm.
- Late Cretaceous Antarctic fish diversity seems highest in the Campanian, with a decrease in the Maastrichtian, and might be

assumed to be related to long-term Late Cretaceous climatic trends. However, the collections are too imperfect for reconstructing any diversity patterns at the moment.
- The Lachman Crags and Herbert Sound members are characterized by several species endemic to Antarctica (e.g. *Chlamydoselachus thomsoni* and *Chimaera zangerli*). In addition, *Notidanodon dentatus*, both synechodontiforms, and probably *Squatina* sp. may be species typical of the high latitudes. Consequently, the Late Cretaceous Antarctic fish fauna is assumed to consist of two groups. One is indicative of the Weddellian Province (Antarctica–Patagonia–New Zealand), and is characterized by high-latitude species, while the second (including probably most of the lamniforms, ichthyodectiforms and alepisauriforms) is widespread to cosmopolitan.

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References

AGASSIZ, L. 1833–1844. *Recherches sur les Poissons Fossiles,* 5 volumes. Petitpierre, Neuchâtel et Soleure (with supplements).

AMEGHINO, F. 1893. Sobre la presencia de vertebrados de aspecto Mesozóico, en la formación Santacruceña de la Patagonia austral. *Revista del Jardín Zoológico de Buenos Aires*, **1**, 76–84.

ANTUNES, M.T. & CAPPETTA, H. 2002. Sélaciens du Crétacé (Albien–Maastrichtien) d'Angola. *Palaeontographica A*, **264**, 85–146.

ARRATIA, G., KRIWET, J. & HEINRICH, W.-D. 2002. Selachians and actinopterygians from the Upper Jurassic of Tendaguru, Tanzania. *Mitteilungen aus dem Museum für Naturkunde zu Berlin, Geowissenschaftliche Reihe*, **5**, 207–230.

ARRATIA, G., SCASSO, R. & KIESSLING, W. 2004. Late Jurassic fishes from Longing Gap, Antarctic Peninsula. *Journal of Vertebrate Paleontology*, **24**, 41–55.

BARDACK, D. 1965. Anatomy and evolution of chirocentrid fishes. *University of Kansas Paleontological Contributions*, **10**, 1–88.

BEAUMONT, G., DE. 1960. Contribution à l'étude des genres *Orthacodus* Woodw. et *Notidanus* Cuv. (Selachii). *Mémoires Suisses de Paléontologie*, **77**, 1–46.

BIGELOW, H. & SCHROEDER, W. 1948. *Fishes of the Western Atlantic*, Volume 1. Memoirs of the Sears Foundation for Marine Research, Yale, 59–546.

CAPPETTA, H. 1987. Mesozoic and Cenozoic Elasmobranchii, Chondrichthyes II. *In:* SCHULTZE, H.-P. (ed.) *Handbook of Paleoichthyology 3B.* Gustav Fischer, Stuttgart.

CAPPETTA, H. & CASE, G.R. 1999. Additions aux faunes de sélaciens du Crétacé du Texas (Albien supérieur–Campanian). *Palaeo Ichthyologica*, **9**, 5–111.

CARVALHO, M., DE 1996. Higher-level elasmobranch phylogeny, basal squaleans, and paraphyly. *In:* STIASSNY, M.L., PARENTI, L.R. & JOHNSON, G.D. (eds) *Interrelationships of Fishes.* Academic Press, San Diego, CA, 35–62.

CASE, G.R. 1978. A new selachian fauna from the Judith River Formation (Campanian) of Montana. *Palaeontographica A*, **160**, 176–205.

CASE, G.R. & CAPPETTA, H. 1997. A new selachian fauna from the Late Maastrichtian of Texas (Upper Cretaceus/Navarroan); Kemp Formation. *Münchner Geowissenschaftliche Abhandlungen A*, **34**, 131–189.

CHALIFA, Y. 1996. A new species of *Enchodus* (Aulopiformes: Enchodontidae) from the Northern Negev, Israel with comments on evolutionary trends in the Enchodontoidei. *In:* ARRATIA, G. & VIOHL, G. (eds) *Mesozoic Fishes – Systematics and Paleoecology.* Dr Friedrich Pfeil, Munich, 349–367.

CHAPMAN, F. 1918. Description and revision of the Cretaceous and Tertiary fish remains of New Zealand. *Palaeontological Bulletin*, **7**, 1–46.

CICIMURRI, D.J. & EVERHART, M.J. 2001. An elasmosaur with stomach contents and gastroliths from the Pierre Shale (late Cretaceous) of Kansas. *Transactions of the Kansas Academy of Science*, **104**, 129–143.

CIONE, A.L. 1996. The extinct genus *Notidanodon* (Neoselachii, Hexanchiformes). *In:* ARRATIA, G. & VIOHL, G. (eds) *Mesozoic Fishes – Systematics and Paleoecology.* Dr Friedrich Pfeil, Munich, 63–72.

CIONE, A.L. & MEDINA, F.A. 1987. A record of *Notidanodon pectinatus* (Chondrichthyes, Hexanchiformes) in the Upper Cretaceous of the Antarctic Peninsula. *Mesozoic Research,* **1**, 79–88.

COMPAGNO, L.J.V. 1984. *FAO Species Catalogue. Volume 4. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 1. Hexanchiformes to Lamniformes.* FAO Fisheries Synopses, **125**, 1–249.

COX, G. & FRANCIS, M. 1997. *Sharks and Rays of New Zealand.* Canterbury University Press, Canterbury.

CRAME, J.A., LOMAS, S.A., PIRRIE, D. & LUTHER, A.

1996. Late Cretaceous extinction patterns in Antarctica. *Journal of the Geological Society, London*, **153**, 503–506.

Crame, J.A., McArthur, J.M., Pirrie, D. & Riding, J.B. 1999. Strontium isotope correlation of the basal Maastrichtian stage in Antarctica to the European and US biostratigraphic schemes. *Journal of the Geological Society, London*, **156**, 957–964.

Crame, J.A., Pirrie, D., Riding, J.B. & Thomson, M.R.A. 1991. Campanian–Maastrichtian (Cretaceous) stratigraphy of the James Ross Island area, Antarctica. *Journal of the Geological Society, London*, **148**, 1125–1140.

Davis, J.W. 1888. On the fossil fish-remains from the Tertiary and Cretaceous–Tertiary formations of New Zealand. *Scientific Transactions of the Royal Dublin Society*, **4**, 1–62.

Davis, J.W. 1890. On the fossil fish of the Cretaceous formations of Scandinavia. *Scientific Transactions of the Royal Dublin Society*, **4**, 363–434.

Dingle, R.V. 1999. Walvis Ridge barrier: its influence on palaeoenvironments and source rock generation deduced from ostracod distribution in the early South Atlantic Ocean. *In:* Cameron, N., Bate, R.H. & Clure, R. (eds) *Hydrocarbon Habitats of the South Atlantic.* Geological Society, London, Special Publications, **153**, 293–302.

Dingle, R.V. & Lavelle, M. 2000. Antarctic Peninsula Late Cretaceous–Early Cenozoic palaeoenvironments and Gondwana palaeogeographies. *Journal of African Earth Sciences*, **31**, 91–105.

Ditchfield, P.W., Marshall, J.D. & Pirrie, D. 1994. High latitude palaeotemperature variations: New data from the Tithonian to Eocene of James Ross Island, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **107**, 79–101.

Duffin, C.J. & Ward, D.J. 1993. The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. *Belgian Geological Survey, Professional Papers*, **264**, 53–102.

Fielitz, C. 1996. A Late Cretaceous (Turonian) ichthyofauna from Lac de Bois, Northwest Territories, Canada, with palaeobiogeographic comparisons with Turonian ichthyofaunas of the Western Interior Seaway. *Canadian Journal of Earth Sciences*, **33**, 1375–1389.

Goody, P.C. 1976. *Enchodus* (Teleostei: Enchodontidae) from the Upper Cretaceous Pierre Shale of Wyoming and South Dakota with an evaluation of the North American enchodontid species. *Palaeontographica A*, **152**, 91–112.

Goto, M., Uyeno, T. & Yabumoto, Y. 1993. Summary of Mesozoic elasmobranch remains from Japan. *In*: Arratia, G. & Viohl, G. (eds) *Mesozoic Fishes – Systematics and Paleoecology.* Dr Friedrich Pfeil, Munich, 71–85.

Grande, L. & Eastman, J.T. 1986. A review of Antarctic ichthyofaunas in the light of new fossil discoveries. *Palaeontology*, **29**, 113–137.

Grande, L. & Chatterjee, S. 1987. New Cretaceous fish fossils from Seymour Island, Antarctic Peninsula. *Palaeontology*, **30**, 829–837.

Hasse, C. 1882. *Das natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule. Eine morphologische und paläontologische Studie. Besonderer Theil.* von Gustav Fischer, Jena, 97–179.

Hathway, B. 2000. Continental rift to back-arc basin: Jurassic–Cretaceous stratigraphical and structural evolution of the Larsen Basin, Antarctic Peninsula. *Journal of the Geological Society, London*, **157**, 417–432.

Herman, J., Hovestadt-Euler, M. & Hovestadt, D.C. 1992. Part A: Selachii. No. 4: Order Orectolobiformes – Families: Brachaeluridae, Ginglymostomidae, Hemiscylliidae, Orectolobidae, Parascylliidae, Rhiniodontidae, Stegostomidae. Order Pristiphoriformes – Family: Pristiophoridae. Order Squatiniformes – Family: Squatinidae. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique*, **65**, 193–254.

Huber, B.T. 1998. Tropical paradise at the Cretaceous poles? *Science*, **282**, 2199–2200.

Huber, B.T., Hodell, D.A. & Hamilton, C.P. 1995. Middle-Late Cretaceous climate of the southern high latitudes: stable isotope evidence for minimal equator-to-pole thermal gradients. *Bulletin of the Geological Society of America*, **107**, 1164–1191.

Kriwet, J. 2003*a*. Lancetfish teeth (Neoteleostei, Alepisauroidei) from the Early Cretaceous of Alcaine, NE Spain. *Lethaia*, **12**, 323–332.

Kriwet, J. 2003*b*. First record of Early Cretaceous shark (Chondrichthyes, Neoselachii) from Antarctica. *Antarctic Science*, **15**, 519–523.

Landemain, O. 1991. Sélaciens nouveaux du Crétacé supérieur du sud-ouest de la France. Quelques apports à la systématique des elasmobranches. *Saga Information, Société Amicale des Géologues Amateurs*, **1**, 1–45.

Last, P.R. & Stevens, J.D. 1994. *Sharks and Rays of Australia*. CSIRO, Australia.

Lees, T. & Bartholomai, A. 1987. Study of Lower Cretaceous actinopterygian (class Pisces) *Cooyoo australis* from Queensland, Australia. *Memoirs of the Queensland Museum*, **25**, 177–192.

Lirio, J.M., Marenssi, S.A., Santillana, S.N., Marshall, P.A. & Rinaldi, C.A. 1989. Marambio Group at the southeastern part of James Ross Island, Antarctica. *Contribución del Instituto Antártico Argentino*, **371**, 1–45.

Loomis, F.B. 1900. Die Anatomie und die Verwandtschaft der Ganoid- und Knochenfische aus der Kreide Formation von Kansas. *Palaeontographica*, **46**, 213–283.

Maisey, J.G. 1991. *Santana Fossils: An Illustrated Atlas.* Tropical Fish Hobbyist, T.F.H. Publications, NJ.

McArthur, J.M., Crame, J.A. & Thirlwall, M.F. 2000. Definition of Late Cretaceous stage boundaries in Antarctica using Strontium Isotope Stratigraphy. *Journal of Geology*, **108**, 623–640.

Müller, A. & Diedrich, C. 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Ascheloh am Teutoburger Wald (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **20**, 1–105.

Nelson, J.S. 1994. *Fishes of the World.* Wiley, New York.

Olivero, E.B. & Medina, F.A. 2000. Patterns of Late Cretaceous ammonite biogeography in southern high latitudes: the family Kossmaticeratidae in Antarctica. *Cretaceous Research*, **21**, 269–279.

Olivero, E.B., Martinioni, D.R. & Mussel, F.J. 1992. Upper Cretaceous sedimentology and biostratigraphy of Western Cape Lamb (Vega Island, Antarctica). Implications on sedimentary cycles and evolution of the basin. *In:* Rinaldi, C.A. (ed.) *Geología de la Isla James Ross*. Instituto Antártico Argentino, Buenos Aires, 147–166.

Olivero, E.B., Scasso, R.A. & Rinaldi, C.A. 1986. Revision of the Marambio Group, James Ross Island, Antarctica. *Contribución del Instituto Antártico Argentino*, **331**, 1–28.

Pfeil, F.H. 1983. Zahnmorphologische Untersuchungen an rezenten und fossilen Haien der Ordnungen Chlamydoselachiformes und Echinorhiniformes. *Palaeo Ichthyologica*, **1**, 1–315.

Pictet, F.J. & Campiche, G. 1858. Description des fossiles du terrain Crétacé des environs de Sante-Croix. *Matériaux pour la Paléontologie Suisse*, **2**, 1–380.

Pirrie, D. 1990. A new sedimentological interpretation of the Santa Marta Formation, James Ross Island. *Antarctic Science*, **2**, 77–78.

Pirrie, D., Crame, J.A., Lomas, S.A. & Riding, J.B. 1997. Late Cretaceous stratigraphy of the Admiralty Sound Region, James Ross Basin, Antarctica. *Cretaceous Research*, **17**, 109–137.

Pirrie, D., Crame, J.A. & Riding, J.B. 1991. Late Cretaceous stratigraphy and sedimentology of Cape Lamb, Vega Island, Antarctica. *Cretaceous Research*, **12**, 227–258.

Priem, F. 1912. Sur les poissons fossiles des terrains Tertiaires du sud de la France. *Bulletin de la Société Géologique de France, 4 série*, **12**, 213–245.

Richter, M.A. & Ward, D.J. 1990. Fish remains from the Santa Marta Formation (Late Cretaceous) of James Ross Island, Antarctica. *Antarctic Science*, **2**, 67–76.

Riding, J.B. & Crame, J.A. 2002. Aptian to Coniacian (Early–Late Cretaceous) palynostratigraphy of the Gustav Group, James Ross Basin, Antarctica. *Cretaceous Research*, **23**, 739–760.

Roberts, C.D. 1993. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. *Bulletin of Marine Science*, **52**, 60–113.

Scasso, R.A., Olivero, E.B. & Buatois, L. 1991. Lithofacies, biofacies and ichnoassemblage evolution of a shallow submarine volcanoclastic fan-shelf depositional system (Upper Cretaceous – James Ross Island, Antarctica. *Journal of South American Earth Sciences*, **4**, 239–260.

Schwimmer, D.R., Stewart, J.D. & Williams, G.D. 1997. *Xiphactinus vetus* and the distribution of *Xiphactinus* species in the eastern United States. *Journal of Vertebrate Paleontology*, **66**, 994–1001.

Siverson, M. 1992. Late Cretaceous Paraorthacodus (Palaeospinacidae, Neoselachii) from Sweden. *Journal of Paleontology*, **35**, 519–554.

Siverson, M. 1996. Lamniform sharks from the mid-Cretaceous Alinga Formation and Beedagong Claystone, Western Australia. *Palaeontology*, **39**, 813–849.

Siverson, M. 1997. Sharks from the Mid-Cretaceous Gearle Siltstone, southern Carnarvon Basin, Western Australia. *Journal of Vertebrate Paleontology*, **17**, 543–465.

Siverson, M. 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **90**, 49–66.

Stahl, B.J. & Chatterjee, S. 1999. A Late Cretaceous chimaerid (Chondrichthyes, Holocephali) from Seymour Island, Antarctica. *Palaeontology*, **42**, 979–989.

Stahl, B.J. & Chatterjee, S. 2002. A Late Cretaceous callorhynchid (Chondrichthyes, Holocephali) from Seymour Island, Antarctica. *Journal of Vertebrate Paleontology*, **22**, 848–850.

Thies, D. & Reif, W.-E. 1985. Phylogeny and evolutionary ecology of Mesozoic Neoselachii. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **169**, 333–361.

Trautschold, H. 1877. Über Kreidefossilien Russlands. *Bulletin de la Société de Moscou*, **11**, 332–349.

Welles, S.P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. *Memoirs of the University of California*, **13**, 125–254.

Welton, B.J. 1979. *Late Cretaceous and Cenozoic Squalomorphii of the Northwest Pacific region.* PhD thesis, University of California, Berkeley, CA.

Wilson, M.V.H. & Chalifa, Y. 1989. Fossil marine actinopterygian fishes from the Kaskapau Formation (Upper Cretaceous: Turonian) near Watino, Alberta. *Canadian Journal of Earth Sciences*, **26**, 2604–2620.

Woodward, A.S. 1908. On fossil fish-remains from Snow Hill and Seymour Islands. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903*, **3**, 1–4.

Zinsmeister, W.J. 1998. Discovery of fish mortality horizon at the K–T boundary on Seymour Island: re-evaluation of events at the end of the Cretaceous. *Journal of Paleontology*, **72**, 556–571.

Zinsmeister, W.J., Feldmann, R.M., Woodburne, M.O. & Elliot, D.H. 1989. Late Cretaceous/Earliest Tertiary transition on Seymour Island, Antarctica. *Journal of Paleontology*, **63**, 731–738.