

An Early Miocene elasmobranch fauna from the Navidad Formation, Central Chile, South America

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A rich elasmobranch assemblage is reported from the Early Neogene marine sediments of the lower member of the Navidad Formation, Central Chile. The fauna comprise *Squalus* sp., *Pristiophorus* sp., *Heterodontus* sp., *Megascyliorhinus trelewensis*, *Carcharias cuspidata*, *Odontaspis ferox*, *Isurus oxyrinchus*, *Isurus hastalis*, *Cosmopolitodus hastalis*, *Carcharoides totuserratus*, *Myliobatis* sp. and *Callohrinchus* sp., all of which are reported for the first time in the Early Miocene of Chile. The presence of *Carcharoides totuserratus* supports the Early Miocene age for the lower part of the basal Navidad Formation. The Chilean fossil elasmobranch fauna is represented by deep water and shallow water taxa, which probably were mixed in a submarine fan. Certain taxa suggest warm-temperate waters. The Early Miocene fauna from the Navidad Formation show affinities with other faunas previously reported from the Late Paleogene and Neogene of Argentina and New Zealand.

Se describe una rica asociación de elasmobranquios fósiles proveniente de los sedimentos marinos del Neógeno Inferior de la Formación Navidad, Chile central. La fauna comprende *Squalus* sp., *Pristiophorus* sp., *Heterodontus* spp., *Megascyliorhinus trelewensis*, *Carcharias cuspidata*, *Odontaspis ferox*, *Isurus oxirinchus*, *Cosmopolitodus hastalis*, *Carcharoides totuserratus*, *Myliobatis* sp. and *Callohrinchus* sp., todos los cuales son reportados por primera vez para el Mioceno Temprano de Chile. La presencia de *Carcharoides totuserratus* permite proponer una edad miocena temprana para la parte basal del miembro inferior de la Formación Navidad. Los componentes de la fauna de elasmobranquios fósiles incluyen formas de agua profunda y somera que habrían sido mezcladas al depositarse en un abanico submarino. Algunos taxones sugieren la presencia de aguas templadas-cálidas. La fauna de la Formación Navidad presenta afinidades faunísticas con otras faunas de elasmobranquios previamente reportadas para el Paleógeno tardío y Neógeno de Argentina y Nueva Zelanda.

KEY WORDS: Miocene, Elasmobranch, Teeth, Chile Navidad Formation.

Introduction

First described by Darwin (1900), the Navidad Formation is one of the largest onshore exposures of Tertiary sedimentary successions in western South America. These fossiliferous outcrops have been known since the last century through the work of a number of authors: Phillipi (1887), Darwin (1900), Tavera (1942, 1968), Osorio (1976), Tavera (1979), Martínez & Valenzuela (1979), Covacevic & Frassinetti (1980), Martínez-Pardo (1990), Troncoso (1991), Troncoso & Romero (1993), who described the presence of bivalves, gastropods, scaphopods, brachiopods, echinoids, Bryozoa, barnacles, cephalopods, corals, foraminifera, discoasters, ostracods, leaves, tree trunks and plant pollen. Fossil vertebrates such as fish are, however, scarce or absent judging from the major part of the literature cited. Phillipi (1887) provided the first description of

shark remains from this formation, commenting briefly on a large tooth, which had been recovered from the Matanzas locality. That tooth was described as *Carcharias giganteus* Phillipi and also compared with a similar one from La Heradura locality (Coquimbo Formation). Both teeth were illustrated in Phillipi's classic work (Phillipi, 1887) "*Los fósiles cuaternarios y terciarios de Chile*". Covacevic & Frassinetti (1980) cited the presence of *Lamna* sp. in their invertebrate fauna recovered from the Punta Alta locality and recently Suárez and Encinas (2002) yielded a brief report about the fossil vertebrate assemblage from the lower member of the Navidad Formation.

The present contribution is the result of several field trips carried out in the Navidad Formation during the years 1998-2002. These trips allowed us to gather a significant collection of fossil vertebrates, mainly fish teeth, including an unexpectedly rich elasmobranch assemblage.

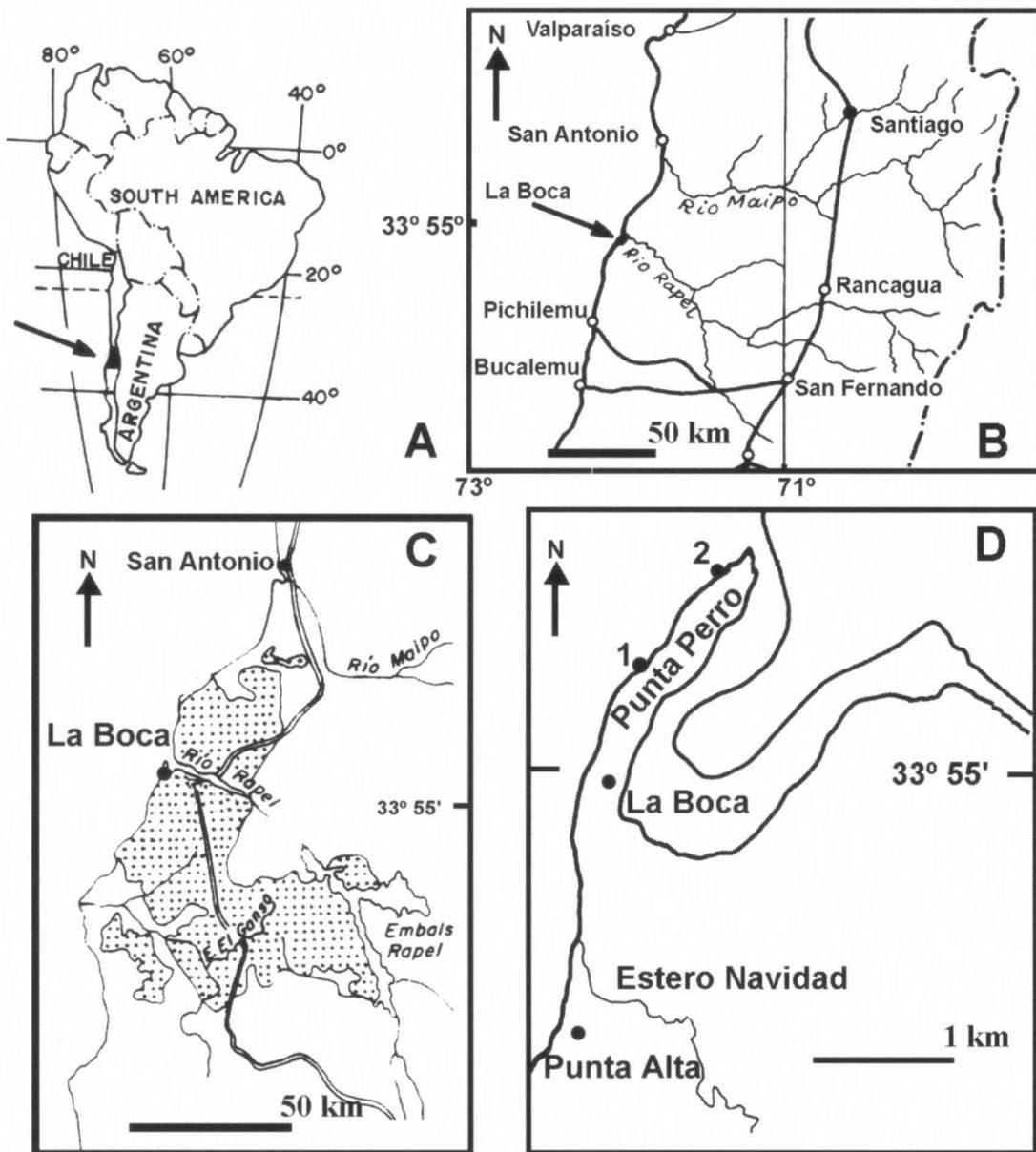


Figure 1. Location of study area. A,B- Location of study area; C- Distribution of the Navidad Formation along the coast of Central Chile; D- The Early Miocene Punta Perro and La Boca sections (indicated by '1' and '2' respectively).

The material reported in this paper comprises sharks' teeth, dental plates of rays, and holocephalians. All are new records for the Navidad Formation.

Material and methods

The material described in this paper was obtained by surface collecting from two sites located along the sea cliffs between Punta Perro and the town of La Boca (Figure 1d). It comprises shark teeth, isolated dental plates of rays, and holocephalians. Additional associated vertebrate remains, comprising both osteichthyan and cetacean teeth, were also collected but fall outside the scope of the present work. All the specimens described in this paper have been deposited in the Sección Paleontología, of the Museo Nacional de

Historia Natural (MNHN) in Santiago, Chile.

Geological setting

The Navidad Formation was first described by Darwin (1900). He assigned the term "sandstone formation at Navidad" to all the sedimentary rocks exposed between Estero Yali to the north and Punta Topocalma to the south. It consists of approximately 500 m of mudstones, siltstones, sandstones and conglomerates which form a succession of relatively undeformed strata. The Formation crops out between 33° 45' S and 34° 15' S latitude and 71° 30' W longitude, 130 kilometres southwest of Santiago, in the 6th region of Chile, and extends for 70 km north to south and 30 km east to west (Figure 1c). The Navidad Formation

crops out extensively along the coastal cliffs of the Navidad region, the eroded banks of the Rapel River and the hill-sides inland (Chambers, 1985). It rests unconformably upon the Permo-Carboniferous crystalline basement, the Cretaceous Punta Topocalma Formation, or the Eocene Río Topocalma Formation (Cecioni, 1978).

Etchart (1973), Tavera (1979) and Ceccioni (1978) studied the stratigraphy of the Navidad Formation in detail. Etchart (1973) divided the Miocene succession into the Middle Miocene La Boca Formation and the Late Miocene Navidad Formation. Tavera (1979) divided the Navidad Formation into three members, from oldest to youngest being: Navidad, Lincacheo and Rapel. Ceccioni (1970, 1978) defined the Navidad Group as formed by different units of Cretaceous-Pleistocene age. Within this group he defined the Miocene-Pliocene Punta Perro-La Era Formation, which is equivalent to the Navidad Formation of Tavera. Ceccioni divided this formation in four members: I, II, III and IV.

Age of the Navidad Formation

There is some disagreement over the age of the Navidad Formation. It has been described as Early Miocene based on macrofossils (Tavera, 1979) who suggested that the observed palaeontological differences among members could be attributed to facies variations. Osorio (1979) suggested a maximum of 11.5 Ma age based on ostracods. Martínez-Pardo (1990) suggested a 19-10 Ma age based on planktonic foraminifera. Frassinetti & Covacevic (1981) suggested an Early-Middle Miocene age for the Navidad member and based on stratigraphical correlation, and assigned a Late-Middle to Late Miocene age for the Lincacheo member. These authors proposed the same Late-Middle to Late Miocene age for the lower part of the Rapel member.

Recent investigations in the lower part of the Navidad Formation have been carried out by teams from the Columbia University, Universidad de Chile and the Museo Nacional de Historia Natural. Using Sr chemostratigraphy they analysed 24 samples of shell material from the lower member of Punta Perro and from the Matanzas area and obtained an age of 20.2 ± 0.6 Ma for Punta Perro and an age of 23.0 ± 0.6 Ma for Matanzas (K. Gregory, pers. comm.). These last ages are in agreement with those determined by the elasmobranch assemblage reported in this paper (see conclusions below) and with those determined by most of the former authors.

Localities

Over the years, amateur collectors looked for fossil invertebrates in the Navidad Formation and reported sharks' teeth and teleost fish and cetacean remains. Fossil vertebrates have also been reported farther inland from La Cueva locality (D. Frassinetti, pers. comm.) and from several other still unstudied fossiliferous localities close to the

town of Rapel (M. Suárez, personal observation). During the field trips we carried out in this area we found fossil vertebrates at several sea cliff sites between Estero Maitenlahue and the town of Pupuya.

In the northern extreme of Punta Perro, fossil sharks' teeth are found in the grey-green sandstone of the intertidal zone, immediately above the basal conglomerate. At the southern part of Punta Perro, fossil teeth become more common along the sea cliffs, within thin, discontinuous lenses of varying lithology such as conglomerates and coquina beds with gastropods, bivalves and scaphopods. South of Punta Perro, in the Punta Alta locality and near the town of Matanzas (Figure 1d), fossil teeth are scarcer and are associated with lithologies similar to those of Punta Perro (Tavera, 1979; Covacevic and Frassinetti, 1980; this paper). Two main fossiliferous sites were recognised which yielded the elasmobranch assemblages (Figure 1c). These are located along the sea cliffs between Punta Perro and La Boca town and belong to the base of this formation. The first and richest assemblage was recovered from a locality named "La Boca," to the north of La Boca town. The second locality is referred to as "Punta Perro", which is at the south of Punta Perro. Two sections, where we have found the most representative fossil assemblages, are described in detail in this section.

Stratigraphic sections

La Boca Section

This site is located about 1 km north of La Boca town and is shown as point 1 (Figure 2a). The section was measured from the intertidal zone to the top of the cliff.

BASE: Base of section lies below sea level.

UNIT 1: (3.0 m). Conglomerate with granite, tonalite and mafic rock clasts that show a huge variation in size from up to boulders exceeding one metre in diameter. The clasts are well rounded in general with the exception of the bigger ones, which are angular. The rock is clast-supported, sometimes with a sandy matrix rich in quartz, fossils are scarce, usually broken and consist mainly of bivalves, gastropods and solitary corals.

UNIT 2: (4.0 m). Medium to coarse-grained sandstone with some interbedded mudstone and siltstone. Sandstones show planar cross bedding, current ripples, high-energy parallel lamination and massive texture. Rip-up clasts, carbonized wooden fragments and pumice clasts are common in the sandstone and there are some water escape structures, as well as breccia formed by mudstone and pumice clasts. Tuffaceous mudstone and siltstone are interbedded with the sandstone forming beds several metres long which are broken and show syndepositional thrusts and are occasionally brecciated forming intraformational conglomerates. Fossils are abundant and are concentrated in lenses of dm scale within the sandstone. They include bivalves, gastropods, small solitary corals, brachiopods, scarce cetacean remains, abundant elasmobranch teeth, leaves, *Teredo* bored logs and small branches.

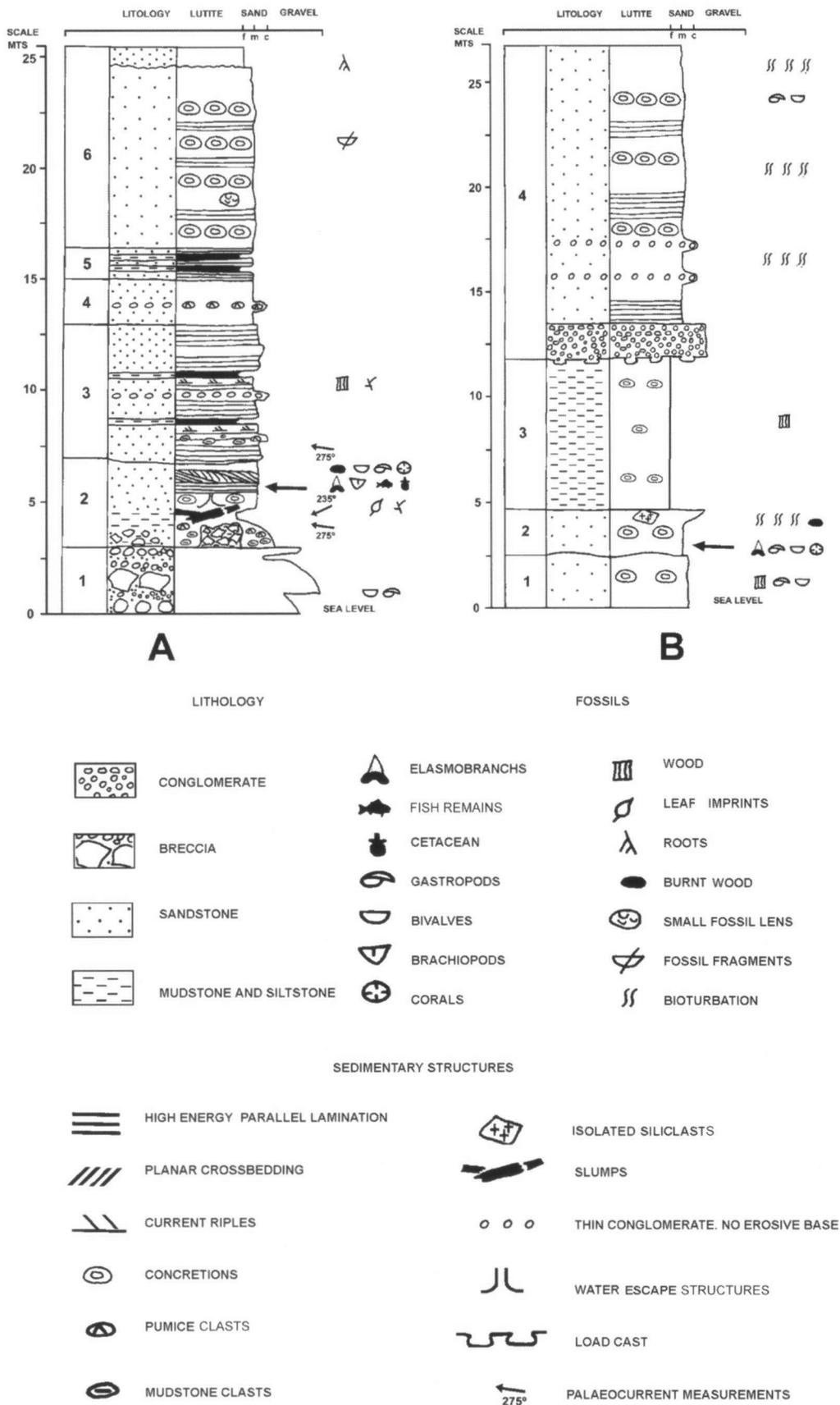


Figure 2. Stratigraphical sections with the provenance of the fossil elasmobranchs; A- Punta Perro section; B- La Boca section.

UNIT 3: (3.0 m). Coarse to medium-grained sandstone with some thin interbedded mudstone and siltstone layers. The unit has an erosive base forming a channel, several metres wide cutting the lower unit. There are some thin conglomerate beds without erosive bases, composed of angular quartz and lithic clasts interbedded with sandstones. The sandstone shows upper flow regime parallel lamination, current ripples, mudstone and pumice clasts, concretions, and logs and branches of wood that are often drilled by *Teredo*. Siltstone and mudstone contain abundant leaves.

UNIT 4: (2.0 m). Orange, light brown, medium-grained massive sandstones, occasionally with small pumice clasts, which sometimes form spherical aggregates.

UNIT 5: (1.40 m). Medium-grained sandstones alternating with siltstones in beds on a cm to dm scale. The sandstone shows upper flow regime parallel lamination.

UNIT 6: (8.0 m). Dark grey, medium-grained sandstone. They are massive in general but there are some levels that show high-energy parallel lamination. There are abundant concretions, cm to dm in diameter, that usually link up forming concretionary beds with irregular forms parallel to the bedding of the unit. The fossil content is scarce and concentrated in small lenses formed by abundant fragments of bivalves and gastropods.

TOP: (2.0 m). Dark, fine-grained homometric sandstones with a modern soil developed upon.

Punta Perro Section

This section is approximately 600 metres south of the northern end of the Punta Perro promontory as point 2 (Figure 2b). The section is measured from the intertidal zone to the top of the cliff.

BASE: Base of section lies below sea level.

UNIT 1: (2.50 m). Medium to coarse-grained quartz sandstone with irregular wavy bedding. The unit yields some very hard concretionary bands, cemented with calcite. The fossil content is low and comprising logs, many bored by *Teredo*, bivalves and gastropods.

UNIT 2: (2.15 m). Yellow-brown, medium-grained massive sandstone, rich in quartz. In the lowermost part there is an 8 cm thick fossiliferous horizon with bivalves, gastropods, solitary corals, cetaceans and elasmobranchs. This level gradually passes to the top to a 65 cm intermediate concretion horizon. The top of this unit is formed by a 70 cm thick coarse-grained sandstone, with some granite and mafic clasts up to one metre in diameter. Some of these clasts are well rounded, the bigger ones being sub-angular. This part of the unit has abundant vertical burrows and a few burnt wood fragments.

UNIT 3: (7.0 m). Light grey to white siltstone and mudstone. They show rare small spherical concretions of some cm to dm in diameter that usually contain plant fragments. There are abundant ostracods, gastropods, and planktonic foraminifera.

UNIT 4: (15.0 m). Light yellow-brown, medium-grained sandstone with load structures. Massive in general but also showing high-energy parallel lamination. At the base there is a fine conglomerate, 1 to 2 metres thick, formed by

subangular clasts of granite and volcanic rocks that passes laterally into coarse-grained sandstone. In the rest of the unit there are some thin horizons of fine conglomerates that show neither erosional contacts nor imbrication. At the top of the unit there are abundant ovoid concretions that are usually joined forming levels parallel to the main bedding of the unit. There are some vertical burrows and very few fossils, mainly bivalves and gastropods.

TOP: Recent erosional surface.

Sedimentology

The Miocene succession begins with a marine fossiliferous conglomerate that crops out only in the La Boca section (Figure 1a). The clasts are well rounded, in general mudstone or siltstone are lacking, indicating high-energy conditions. There is a huge range in clast size, from coarse sandstone to boulders that exceed one meter in diameter. This conglomerate marks the beginning of the Early Miocene marine transgression that covered most of the territory of Argentina and Brasil (Uliana & Biddle, 1988). It is interpreted as a beach where waves reworked alluvial fan sediments. The presence of huge boulders alternating with small clasts and sandstone indicates intense tectonic activity. The succession continues with mudstone, siltstone and sandstone beds. The fossiliferous content is composed of marine vertebrates and invertebrates and plant remains that indicate both marine and continental influence. There are abundant rounded pumice clasts in some layers that indicate volcanic activity contemporaneous with the sedimentation. The presence of load structures and water escape marks indicates rapid sedimentation. Brecciated horizons, large slumps, floating clasts, high energy parallel lamination and massive sandstone indicate gravity-driven transport processes in which slides, slumps, fall of clasts, granular flows and turbidity currents are the main sedimentary processes. The interbedded siltstones and mudstones have planktonic foraminifera and ostracods characteristic of deep-water sedimentation (Matínez and Valenzuela, 1979; Osorio, 1979). We interpret this part of the succession to have been formed in a submarine fan. The sedimentation would have been controlled mainly by gravity-driven processes alternating with the settling of fine grains during quiet periods. This part of the succession represents a major, very rapid sea-level rise relative to the basal beach conglomerate.

Systematic Palaeontology

(The terminology used here follows that of Cappetta, 1987)

Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Order Squaliformes Compagno, 1973
 Family Squalidae Blainville, 1816
 Genus *Squalus* Linnaeus, 1758

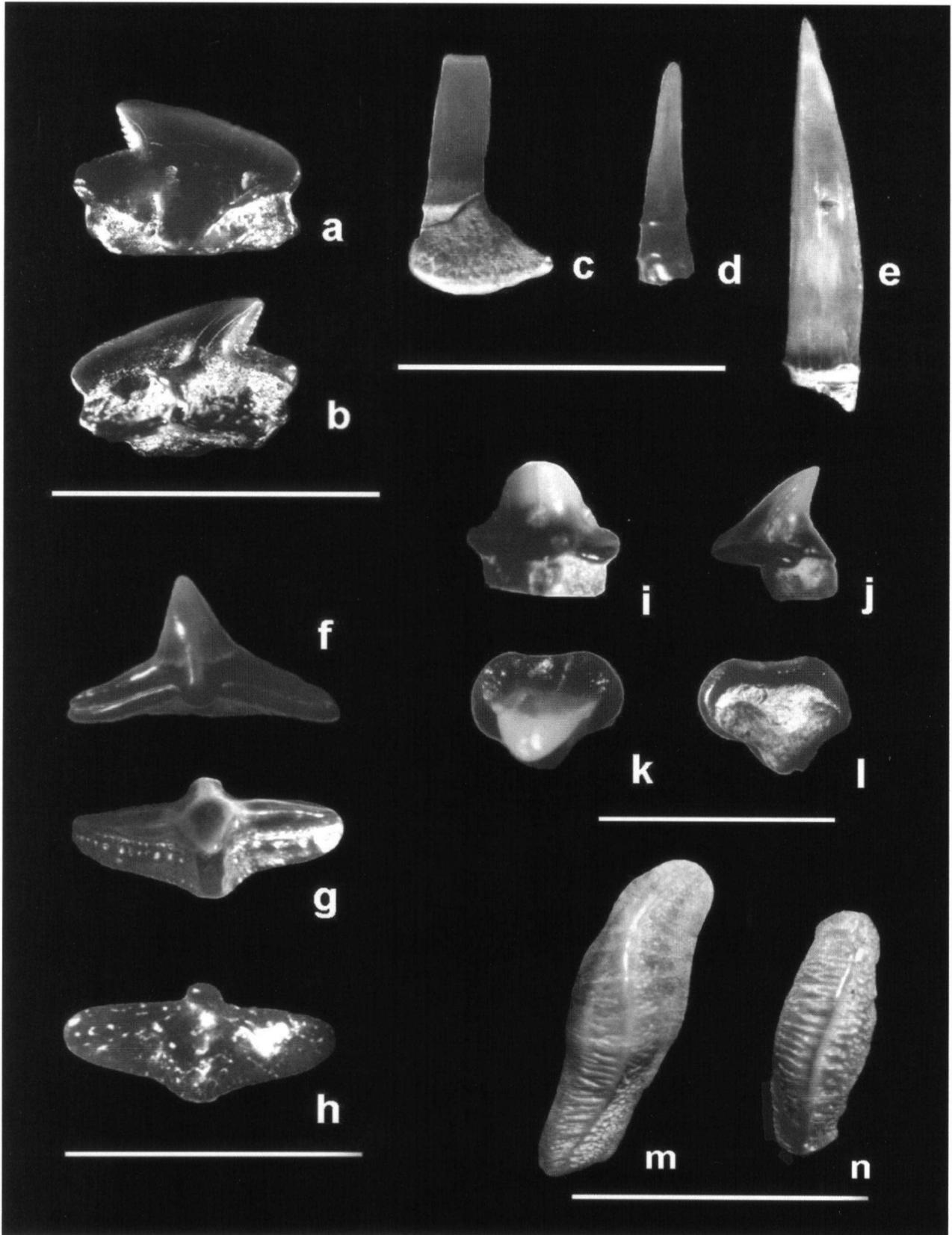


Figure 3. **a, b-** *Squalus* sp. (SGO-PV-877). Scale bar 1 cm. **(a)** lingual view, **(b)** dorsal view. **c-e-** *Pristiophorus* sp. (SGO-PV-878; 879; 880). Scale bar 1 cm. **(c)** lateral view, **(d)** mesial view, **(e)** lateral view. **f-h-** *Squatina* sp. (SGO-PV-881). Scale bar 1 cm. **(f)** lingual view, **(g)** occlusal view, **(h)** basal view. **i-l-** *Heterodontus* sp. (SGO-PV-882). Scale bar 5 mm. **(i)** lingual view, **(j)** lateral view, **(k)** occlusal view, **(l)** basal view. **m-n-** *Heterodontus* sp. (SGO-PV-883; 884). Scale bar 1 cm. **(m)** occlusal view, **(n)** occlusal view.

Squalus sp.
Figures 3a, b

Material — One tooth

Locality — La Boca

Description — The crown of this tooth is large and both lingual and labial faces are very smooth. The cusp is triangular in outline. The mesial cutting edge presents delicate serrations, while those on the distal cutting edge and distal cusplet are coarser. The crown looks rather high in labial view, having more than two times the height of the root. The apron, which reaches the floor, is well developed and is slightly backward-directed. In lingual view, the crown presents a depression on the mesial edge of the uvula. The latter is small but prominent and the infundibulum is rather large. The root is high having a row of foramina that are sub-parallel to the limit of the crown-root. Below the limit of the crown, under the mesial and distal regions, the surface presents two well-marked depressions and dispersed foramina. In basal view, the root is slightly concave exposing some small foramina with an irregular distribution.

Discussion — The mesiodistally narrow and apicobasally deep crown of this specimen suggests that it is an upper tooth. The weak serrations on the mesial cutting edge and the rather coarser cutting edges on the distal cutting edge and the distal cusplet on the single Chilean *Squalus* tooth cause it to resemble two serrate species.

1. *S. weltoni* Long 1992, from the Eocene La Meseta Formation, of Seymour Island, Antarctica (Long 1992a). This species was originally listed as *Squalus* sp. by Welton (1978 - unpublished PhD thesis) from the Late Eocene – Oligocene of the Pacific coast of the USA.

2. *Squalus occidentalis* (Agassiz 1856) (= *S. serriculus* Jordon & Hannibal, 1923) from the Middle Miocene of California, USA. The similarity in age and morphology strongly suggest that the Chilean specimen belongs to this species. However, more material is needed before it can be confidently assigned.

The Late Palaeocene species, *Megasqualus orpiensis* (Winkler 1874) differs from the Chilean specimen in having far weaker serrae on the distal cutting edge and distal cusplet.

The earliest Chilean squaloids are represented by teeth and fine spines belonging to the genus *Centrophoroides* and comes from the Late Cretaceous (Maastrichtian) of the Quiriquina Formation (Suárez, 2001; Suárez and Cappetta, 2004). The Neogene record of the genus *Squalus* in South America is scarce and is limited to material from the Early Miocene-Late Miocene of Uruguay (Perea & Ubilla, 1989). Recently Suárez *et al.* reported the presence of *Squalus* sp. from Middle-Late Miocene sediments of the Formación La Portada, northern Chile. This is the first record of *Squalus* from the Early Miocene of Chile and South America.

Order Pristiophoriformes Berg, 1958

Family Pristiophoridae Berg, 1959
Genus *Pristiophorus* Muller and Henle, 1937

Pristiophorus sp.
Figures 3c-e

Material — Three rostral spines

Localities — La Boca, Punta Alta

Discussion — One broken rostral spine from Punta Alta was included in a faunal list as *Lamna* sp. by Frassinetti & Covacevic (1981). Recent examination of this material showed that it is a pristiophorid rostral spine. Other well-preserved pristiophorid spines from La Boca locality share the characteristic elongated and laterally compressed crown with anterior and posterior cutting edges. In these teeth the peduncle is rather low and its base extended forward. The available material from the Navidad Formation, which includes rostral spines of both juveniles and adult individuals, is here assigned to *Pristiophorus* sp. This genus was recently reported from the Miocene of the Bahía Inglesa Formation (Suárez & Marquardt, 2001) but, because of its larger size, the northern specimens are markedly larger than those described here. *Pristiophorus* sp. have been reported from the Pisco Formation, Peru (De Vries & De Muizon, 1985) and from the Neogene of Argentina (Cione & Expósito, 1980; Cione, 1988; Arratia & Cione, 1996). This is the first occurrence of pristiophorids from the Early Miocene of Chile and the southernmost occurrence of this group from the western rim of South America.

Order Squatiniformes Buen, 1926
Family Squatinidae Bonaparte, 1838
Genus *Squatina* Duméril, 1906

Squatina sp.
Figures 3f-h

Material — One tooth

Locality — La Boca

Description — This single tooth possesses a low cusp, slightly recurved linguallly and distally. The specimen is elongated mesio-distally with convex lingual and labial faces. The root is almost flat in basal view and exhibits a central foramen.

Discussion — Teeth of *Squatina* exhibit a very low degree of intraspecific variation, which makes it difficult to establish species from isolated teeth. After comparing this tooth with those from jaws of extant specimens of *Squatina* sp. (probably *Squatina armata*, Phillipi) from Chilean waters (M.S. collection), it was tentatively identified as a lateral tooth (third to six position). Both the mesial and distal cus-

plets are more massive in extant specimens and the latter has a more extended angle of lateral fall in the fossil form. Such features, however, are insufficient to support a specific determination and it can only be designated as *Squatina* sp. Ward & Bonavia (2001: 142) comment similarly regarding a single tooth from the Miocene of Malta. Prior to this report, *Squatina* sp. has been recorded from the Late Cretaceous (Maastrichtian) of the Quiriquina Formation, central Chile (Suárez, 2001) and from the Middle Late Miocene of the Bahía Inglesa Formation, northern Chile (Suárez y Marquardt, 2003; Suárez *et al*, 2004). This is the first record of *Squatina* from the Early Miocene of Chile.

Order Heterodontiformes Berg, 1937
Family Heterodontidae Gray, 1851
Genus *Heterodontus* Blainville, 1816

***Heterodontus* spp.**

Figures 3i-n

Material — One anterior tooth and two lateral teeth.

Localities — Punta Perro, La Boca.

Discussion — Reif (1976) divided the extant species of *Heterodontus* into two groups, the Francisci-group, and the Portusjacksoni-group. The Portusjacksoni-group have robust clumpy anterior teeth that lack lateral cusplets in the adult, and have large ovoid molariform lateral teeth which lack or have a much reduced longitudinal ridge. Teeth of the Francisci-group of species have more gracile anterior teeth bearing at least one pair of lateral cusplets, and narrower, occlusally sigmoidal lateral teeth with a raised longitudinal ridge (Reif, 1976). The anterior tooth from the Punta Perro locality (Figures 3i-l) is characterised by a smooth rounded apical surface and absence of the lateral cusplets. This is characteristic of the Portusjacksoni-group of *Heterodontus* species (Reif, 1976). Two lateral teeth (Figures 3m-n) are rather narrow and sigmoidal in occlusal view. They show a prominent longitudinal crest from which parallel ridges radiate labially and lingually. The root is low and basally flat. These are typical of the Francisci-group.

Two interpretations of this material are possible.

1. There is a species present that shares characters of both groups.
2. There are two species present.

We are inclined towards the second possibility. Francisci-group teeth are present in the Early Cretaceous of Europe. Portusjacksoni-group teeth, the more derived condition, are present in the Late Cretaceous of Kazakhstan and Uzbekistan (David Ward, pers. observation). Both groups occur in the Paleogene of N.W. Europe. Interestingly, Casier (1966: 53), in his monograph on London Clay Fish, erroneously associated the anterior teeth of an uncommon Portusjacksoni-group species (*H. woodwardi*, Casier) with the more

lateral teeth of a more common Francisci-group species (*H. vincenti* (Leriche)). He described the anterior teeth of the Francisci-group species as a separate species; *H. wardenensis* Casier, 1966. This was because, although from a rarer species, the large Portusjacksoni-group anterior teeth are much more readily surface-collected than the smaller anterior teeth of Francisci-group species.

The Chilean Francisci-group teeth closely resemble those (unnamed) from Round Mountain Silt Member of the Middle Miocene Temblor Formation, of Bakersfield, California, USA (Shark Tooth Hill Bone Bed).

Considering the limited number of available specimens for comparison, we can only designate the Chilean material as *Heterodontus* sp. This genus has been previously reported from the Neogene of Argentina (Cione & Pandolfi, 1984), from the Pisco Basin (De Muizon & DeVries, 1985), and more recently from the Bahía Inglesa Formation, northern Chile (Suárez *et al*, 2004). This is the first record of *Heterodontus* in the Early Miocene of Chile.

Superorder Galeomorphii Compagno, 1973

Order Carcharhiniformes Compagno, 1973

Family Megascyliorhinidae Pfeil, 1984

Genus *Megascyliorhinus* Cappetta & Ward, 1977

***Megascyliorhinus trelewensis* Cione, 1986**

Figures 5g-k

Material — One tooth

Locality — La Boca

Description — This tooth is large having a crown strongly recurved lingually and flanked by one pair of cusplets. The crown has two cutting edges extending about one third of the crown's height below the apex. Both lingual and labial faces of the crown exhibit strong vertical folds, being more delicate and sinuous on the former. The root is high and wide and also shows a well-developed lingual protuberance and two divergent lobes separated by an incomplete medial groove. In lingual view the root exhibits one pair of large lateral foramina.

Discussion — Based on its unusual morphology, this tooth can be immediately assigned to the genus *Megascyliorhinus* (Cappetta & Ward, 1977). Its size, the characteristic ornamentation of the crown, and the root (with an incomplete medial groove), indicates that the Chilean material should be referred to the species *M. trelewensis* (Cione, 1986). The taxonomic relationships of this genus have been subject to a number of differing opinions. It was first considered to be a scylliorhinid by Cappetta & Ward, (1977) but later, Cappetta (1987: 113) proposed that the histology, the possession of an orthodont core, suggest that it may not be a scylliorhinid. Specimens examined more recently have an osteodont histology characteristic of carchariniiforms and some orectolobids (David Ward, pers. observation).

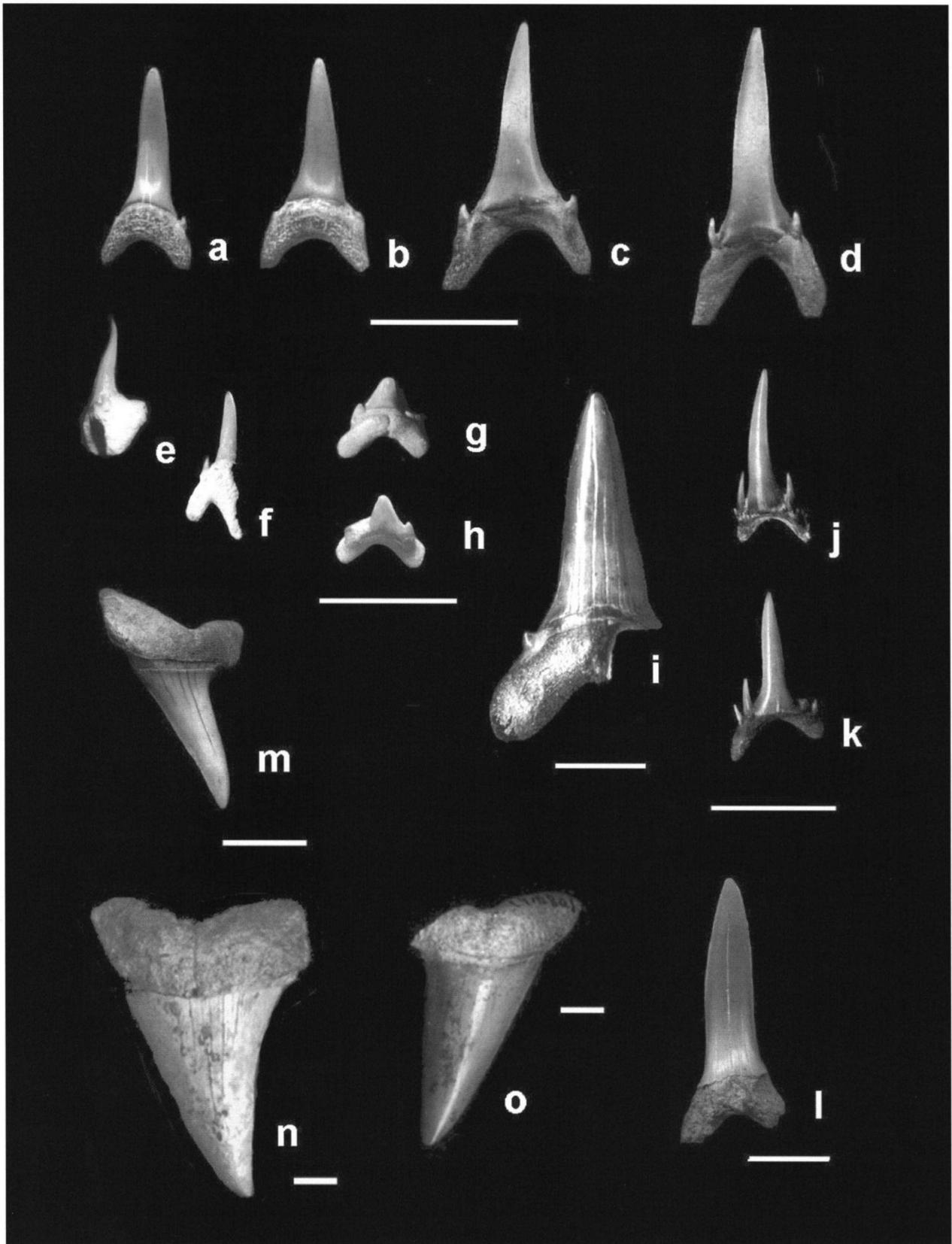


Figure 4. a-i- *Carcharias cuspidata* (SGO-PV-885; 886; 887; 888; 889; 890; 891). Scale bar 1 cm. (a) lingual view, (b) lingual view, (c) labial view, (d) labial view, (e) lateral view, (f) lingual view, (g) lingual view, (h) labial view, (i) lingual view. j, k- *Odontaspis ferox* (SGO-PV-892; 893). Scale bar 1 cm. (j) labial view, (k) labial view. l- *Carcharias* sp. (SGO-PV-897). Scale bar 1 cm. lingual view. m- *Isurus oxyrinchus* (SGO-PV-894). Scale bar 1 cm. lingual view. n, o- *Cosmopolitodus hastalis* (SGO-PV-895). Scale bar 1 cm. (n) lingual view, (o) lingual view.

Cione (1986) described *Megascyliorhinus trelewensis*, illustrating its osteodont histology with a radiograph. He referred it to galeomorphii *incertae sedis*. Nishimoto & Karasawa (1991) referred it to the orectolobiformes, as did Purdy *et al.* (2001). Nishimoto & Karasawa argued that the flattened root base and lack of labial marginal foraminae are suggestive of orectolobiforms. However, these characters are also present in many fossil carcharhiniform genera, including *Premontrea*, *Palaeogaleus*, *Stenoscyllium*, and *Scyliorhinus* and are not unique to orectolobiforms. We feel that the balance of evidence supports the placement of *Megascyliorhinus* within the carcharhiniformes, rather than the orectolobiformes.

This species is easily distinguished from the Eocene species *M. cooperi* and the Plio-Miocene *M. miocenicus* (see Cione, 1986) by its coarser crown ornamentation and root morphology (partially covered basal root groove).

The teeth of *Megascyliorhinus* are also known from the Neogene of New Zealand (Keyes, 1984; Pfeil, 1984).

The Navidad occurrence is the first fossil record of this genus in the Pacific margin of South America.

Order Lamniformes Berg, 1958

Familia Odontaspidae Muller & Henle, 1839

Genus *Carcharias* Rafinesque, 1810

Carcharias cuspidata Agassiz, 1883

Figures 4a-i

Material — Several teeth

Localities — Punta Perro, La Boca

Description — All the specimens of *C. cuspidata* from the Navidad Formation are characterised by a crown with complete or nearly complete cutting edges and a single pair of greatly reduced lateral cusplets. A large upper-anterior tooth from La Boca locality (Figure 4i) has a massive main cusp that is flanked by one pair of very small and recurved denticles. In lateral view the crown is straight, tending to be flexuous at the apex. Its lingual enameloid is smooth and its lateral cutting edges nearly reach the foot of the well-developed crown. One small tooth identified as a symphyseal (Figures 4e-f) has a strongly sigmoidal cusp, one pair of very small cusplets and a massive root. A “crusher” posterior tooth (Figures 4g-h) is small, having a heavy root and well-developed lateral cusplets. Upper and lower teeth assigned to the same species (Figures 4a-d) have more delicate main cusps characteristic of juvenile individuals.

Discussion — The teeth from the Navidad member are very similar to those of *C. cuspidata* illustrated by Purdy *et al.* (2001) from the Pungo River Formation, North Carolina. Although conventionally referred to, and superficially similar to the Recent genus *Carcharias*, the broad cusplets seen in lateral teeth would suggest that a separate genus would be more appropriate. As has been pointed out by

these authors, the teeth of *C. cuspidata* can be separated from the modern *C. taurus* due to a major development of the root in the anterior. *Carcharias cuspidata* is known in the fossil record from the Oligocene to Pliocene (Cappetta, 1987). Teeth of the genus *Carcharias* were recently reported from the Late Cretaceous (Maastrichtian) of the Quiriquina Formation, Chile (Suárez, 2001). The present is the first record of *C. cuspidata* from the Neogene of Chile.

Carcharias sp.

Figure 4l

Material — One tooth

Locality — La Boca

Discussion — Although this single large tooth lacks most of its root and denticles, it preserves the typical fine striations on the lingual face of the crown that have been traditionally used to characterise the species *O. acutissima* (Agassiz, 1843). Such striations are not present in the genus *Odontaspis* (Kemp, 1991; Ward, 2001) implying that the Navidad material represents the genus *Carcharias*. Longbottom (1979: 59) assigned it to *O. acutissima*, two teeth from the Miocene of Ecuador. These specimens are virtually identical with that discussed here from the Navidad Formation, and we believe they should be referred to as *Carcharias* sp.

Genus *Odontaspis* Agassiz, 1838

Odontaspis ferox Risso, 1826

Figures 4j-k

Material — Two teeth

Locality — La Boca

Description — The two specimens share a smooth cusp with incomplete cutting edges and exhibiting two pairs of lateral cusplets. One anterior tooth (Figure 4j) shows a strongly lingually directed cusp with one first pair of high lateral cusplets and one greatly reduced second pair. A lower tooth (Figure 4k) has a cusp which is sigmoidal in lateral view. In this specimen the first pair of lateral cusplets are twice the height of the second pair.

Discussion — The teeth of *Odontaspis* can be separated from those of *Carcharias* in that the former have more prominent and higher lateral cusplets. In addition, as is the case with the Chilean material, the cutting edges of the crown are incomplete and the root lobes are deeply arched and narrow. Oliver Schneider (1936) reported the presence of *Odontaspis elegans* teeth from the Cenozoic of La Boca, Lebu, southern Chile. Given that this material was not illustrated and has been lost, it should be considered an unreli-

able record. *Odontaspis ferox* occurs in the Neogene of the Bahía Inglesa Formation, northern Chile (Suárez *et al.*, 2003). This is the first record of this species from the early Neogene of Chile.

Genus *Isurus* Rafinesque, 1810

Isurus oxyrinchus Rafinesque, 1810

Figure 4m

Material — One upper tooth

Locality — La Boca

Discussion — This tooth is almost identical with the second upper anterior tooth of a dried jaw of *Isurus oxyrinchus* (MNHN collection). Neogene records of this species in Chile were previously reported by Long, (1993) from the Neogene of El Rincón (Coquimbo Formation) and from the Bahía Inglesa locality. This species also seems to be abundant in the Late Miocene of Pisco Perú (De Muizon & De Vries, 1985).

Genus *Cosmopolitodus* Glickman, 1964

Cosmopolitodus hastalis (Agassiz, 1843)

Figures 4n-o

Material — Two upper teeth

Locality — La Boca

Discussion — The genus “*Cosmopolitodus*” is used in recognition that the species *hastalis* is ancestral to the great white shark and not closely related to the Makos (*Isurus*) (Glyckman, 1964; Siverson, 1999 and Ward & Bonavia, 2001).

Purdy *et al.* (2001) use the name *Isurus xiphodon* for broad-crowned specimens of *hastalis*. We agree with Ward & Bonavia (2001), in considering *Isurus xiphodon* as a *nomen dubium*. Whether there was one or two coeval species of *Cosmopolitodus* in the Early Pliocene is outside of the scope of this paper, however, it does appear very unlikely. *Cosmopolitodus hastalis* (as *I. hastalis*) was previously reported from the Pisco Formation, southern Peru (De Muizon & De Vries, 1985) and from the El Rincón locality, Coquimbo Formation, Chile (Long, 1993). This is the most abundant shark species in the Middle Late Miocene of the Bahía Inglesa Formation, northern Chile (Suárez *et al.*, 2004)

Genus *Carcharoides* Ameghino, 1901

Carcharoides totuserratus Ameghino, 1901

Figures 5a-f

Localities — La Boca, Punta Perro

Description — The upper teeth have an unornamented crown with serrated cutting edges. The principal cusp is flanked by a single pair of lateral cusplets that are more massive than its lower counterparts. One upper anterior tooth (Figure 5a) is asymmetrical and shows an erect crown with an extreme apex slightly lingually directed. The labial face of the crown is rather flat and the lingual face moderately convex. In this tooth the lateral cusplets are very low and worn. The root, which is rather low, has a poorly developed lingual protuberance and short lobes. A tooth, identified tentatively as an anterior (Figure 5b), lacks the mesial cusplet (due to breakage) and shows a distally slight curvature. The mesial edge is convex, while the distal one is less so. The lateral cusplets are more developed than in the previous tooth. A more lateral tooth (Figure 5c) is strongly distally directed, having a pair of well-developed and serrated triangular cusplets. The height of the cusplets is about a quarter the height of the main cusp. The lingual and labial face of the crown is smoothly convex. Three lower teeth (Figures 5d-f) are symmetrical, having erect serrated cusps with high, slender conical cusplets. The cusplets are very fine in more anterior rows, resembling the anterior teeth of *Carcharias cuspidata* or of *Odontaspis*. As in teeth from the upper jaw, the lateral cusplets of the teeth of the lower jaw become broader at more distal positions. The serrated edges of the lower teeth may be incomplete in the most anterior teeth (Figure 5d) or complete in more distal teeth (Figure 5f).

Material — Several teeth

Discussion — Purdy *et al.* (2001) referred the fossil genus *Carcharoides* to the Recent carcharhinid genus *Triaenodon*. Ward & Bonavia (2001) rejected this assignment on the basis of its dental formula, general morphology and histology, an opinion with which we fully concur.

The Chilean material comprises serrated anterior teeth of the odontaspid-type and serrated upper lateral teeth of the lamnoid type which allows us to assign them to *Carcharoides totuserratus*, Ameghino, 1901a (Cappetta, 1987). A second species, *Carcharoides catticus* (Philippi, 1846) has non-serrated edges. The latter appears to be restricted to the Northern Hemisphere (Cione & Expósito, 1980; Cappetta, 1987) whereas *Carcharoides totuserratus*, is apparently restricted to the Southern Hemisphere (Cione & Expósito, 1980). Its presence is the first recorded for this species in Chile and its second occurrence in the Neogene of South America.

Superorder Batomorphii Cappetta, 1980 b

Order Myliobatiformes Compagno, 1973

Family Myliobatidae Bonaparte, 1838

Myliobatis sp.

Figures 5m-n

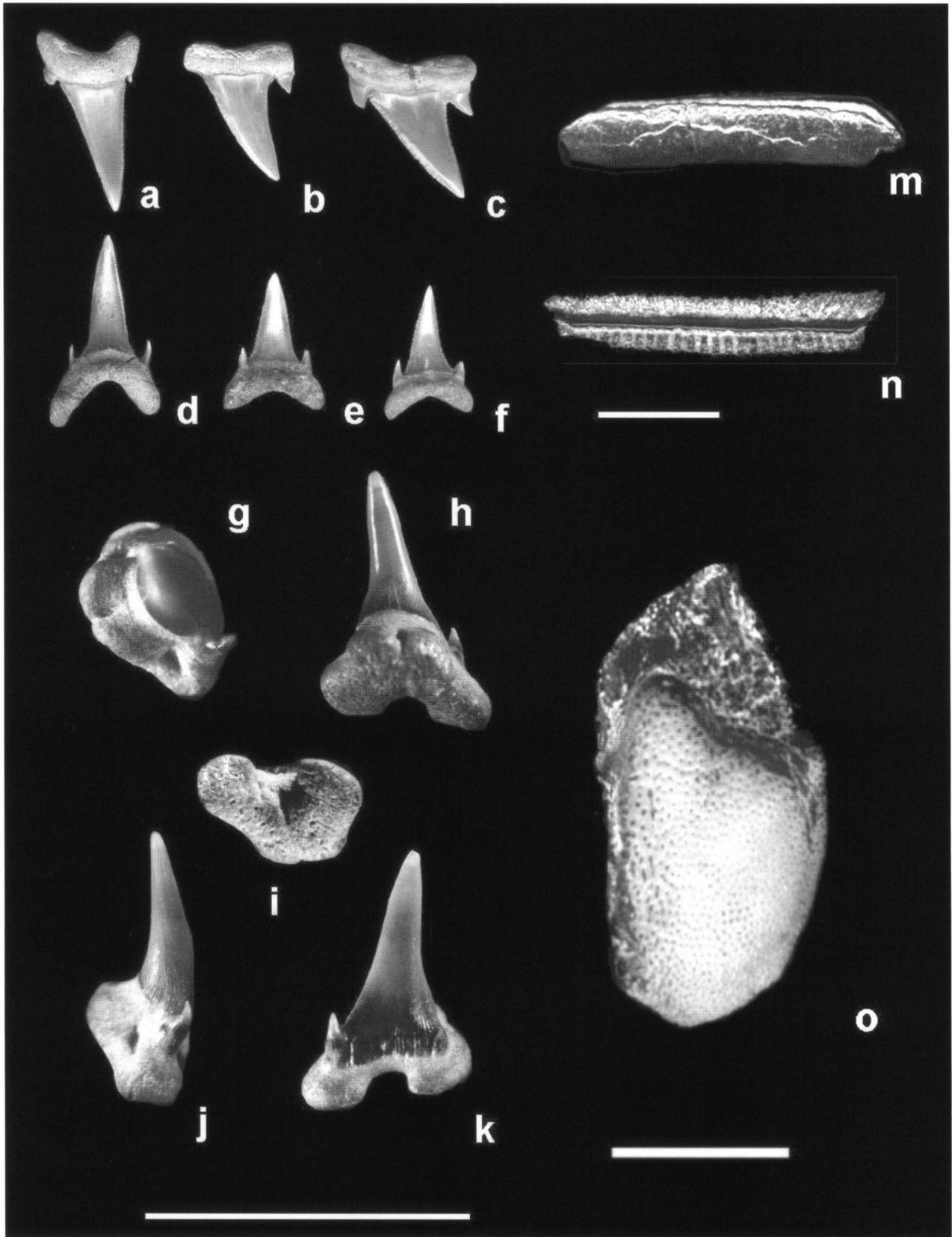


Figure 5. a-f- *Carcharoides totuserratus* (SGO-PV-898; 899; 900; 901; 902; 903). Scale bar 1 cm. (a-f) lingual view. g-k- *Megascyliorhinus trelewensis* (SGO-PV-904). Scale bar 1 cm. (g) occlusal view, (h) lingual view, (i) basal view, (j) lateral view, (k) labial view. m,n- *Myliobatis* sp. (SGO-PV-905). Scale bar 1 cm. (m) occlusal view, (n) posterior view. o-. *Callorhinchus* sp. (SGO-PV-906). Scale bar 1 cm. Occlusal view.

Material — One medial tooth

Locality — La Boca

This isolated worn, medial tooth presents a characteristic myliobatoid morphology, which includes a hexagonal contour, smooth occlusal surface and a polyaulacorhizous root.

Discussion — Taxonomical identifications based on isolated teeth of myliobatoids are extremely difficult considering the wide dental variation found within the group (Wellton & Zinsmeister, 1980; Nishida, 1990). Due to the fragmentary nature of this material, we believe that it is not reasonable to assign this specimen to any given species within *Myliobatis*. Long (1993) reported the myliobatoid *Aetobatus* from the Neogene locality of El Rincón, (Coquimbo Formation) and more recently (Suárez & Marquardt, 2003) reported *Myliobatis* sp. from the Middle-Late Miocene of the Bahía Inglesa Formation. This is the first occurrence of this genus in the Early Miocene of Chile.

Superorder Holocephali Bonaparte, 1832-41

Family Callorhynchidae Garman, 1901

Subfamily Callorhynchinae Stahl, 1999

Genus *Callorhynchus* Lacépède, 1798

Callorhynchus sp.

Figure 5o

Material — One fragmentary left mandibular dental plate.

Locality — La Boca

Description — The outline of the incomplete dental plate is rather square in shape. The symphyseal and lingual margins are a little convex and the symphyseal margin is straight. There is a single large, centrally placed, median tritor. The characteristic morphology of the plate allows us to recognize it as one left dentary (See Suárez *et al.*, 2004)

Discussion — After comparisons with dental plates from extant specimens of chimaeroid fishes from Chilean waters (eg: *Hydrolagus macrophthalmus*, *Hydrolagus* cf. *affinis* and *Callorhynchus callorhynchus*) (M.S. collection) the Navidad's material can be assigned to the genus *Callorhynchus* with any doubt. Also, because of the overall shape of its tritor, the fossil is very similar with Miocene dental plates of *Callorhynchus* sp. recently described and figured by Suárez *et al.* (2004) from the Bahía Inglesa Formation, northern Chile. Regarding the extant species these authors pointed out the shape of the tritor is strongly determined by the ontogenetic stage of the individual and the intraspecific variation. It suggests that tritor shape can't be used as a sufficient criterion to distinguish species among the genus *Callorhynchus*. Consequently we assigned the new material only as *Callorhynchus* sp. Previously (Cappetta *in* De Muizón, 1981) reported the presence

of *Callorhynchus* cf. *callorhynchus* from the Pisco Formation, Peru. However that material was not formally described or illustrated. In Chile the oldest record of holocephalian fishes comes from Late Cretaceous rocks of the Quiriquina Formation in central and southern Chile (Stahl, 2001; Suárez, 2001b).

This material is the second and oldest record of holocephalian fishes in the Miocene of Chile and the first confirmed occurrence of the group along the western margin of South America.

Palaeoecology

Although precise depths have not been estimated yet, previous authors who collected and studied microfossils from the lower member of the Navidad Formation suggested a deep environment of deposition for the sediments of this unit (Martínez & Valenzuela, 1979; Osorio, 1979). Osorio (1979) recovered ostracods from the lower member of the Navidad Formation and based on the presence of *Bradyela normani*, an ostracod species restricted to great depth, proposed a bathial environment for the deposition of the Navidad Formation. He also suggested that the occasional occurrence of some shallow water species of ostracods could be interpreted as probable redeposition in a deeper facies. Sharks from the genus *Squalus*, for example, may inhabit boreal to temperate waters ranging from the intertidal zone up to 900 m in depth (Compagno, 1984; Purdy *et al.*, 2001). Compagno, 1984 (p. 112) also commented on the distribution of this shark, which seems to be correlated with a water temperature ranging between 7° to 8° C and 12° to 15° C. Among the extant sawsharks of the genus *Pristiophorus* we can find some temperate forms that prefer shallow bays and estuaries and other forms such as the tropical species *Pristiophorus schroederi* that may occur on or near the bottom at depths from 640 to 915 m (Compagno, 1984). The angelshark *Squatina* shows a broad distribution in both cool temperate to tropical waters ranging in depth between the intertidal zone to over 1300 m (Compagno, 1984: 138).

Extant species of *Heterodontus* may occur from the intertidal zone to 275 m depth, but they are more common in waters shallower than 100m (Compagno, 1984: 154). The presence of this shark in the lower member of the Navidad Formation is remarkable because presently it is an inhabitant of warm-temperate and tropical waters that prefers temperatures above 21° C (Compagno 1984: 154).

The extant sand tiger shark *Carcharias* inhabits shallow, temperate and tropical waters from the surface zone to a maximum of 191 m depth (Purdy *et al.*, 2001). On the other hand, *Odontaspis ferox* occurs in warm temperate and tropical seas and it is believed to prefer depths up to 420 m (Compagno, 1984). *Isurus oxyrinchus* is a coastal and oceanic shark occurring in both temperate and tropical waters down to at least 152 m (Compagno, 1984: 243). Like other large lamniforms sharks, *Cosmopolitodus hastalis* was probably a cosmopolitan pelagic species during the Miocene (Cappetta, 1987; Ward, 2001). *Myliobatis* shows

a wide range of distribution between temperate and tropical waters (Cione & Expósito, 1980). *Callorhynchus* is commonly found in deep waters but it can move to relatively shallow coastal waters of 16-38 m (Didier, 1993).

Palaeoecological information about the two remaining fossil sharks found in the lower member of the Navidad Formation, *Megascyliorhinus* and *Carcharoides*, is difficult to obtain since their possible relationships with extant elasmobranch forms have not been satisfactorily clarified yet. Based upon the associated fauna and the nature of the deposits where *Megascyliorhinus* teeth have been found, Cappetta & Ward (1977) suggested that this genus inhabited depths of around 150-200 m. A pelagic habitat for this shark would be possible considering that Cione (1986: 111) noted that the teeth of *Megascyliorhinus* are similar to those reported in the three recent filter-feeding sharks: the megamouth shark *Megachasma pelagios* (Taylor *et al.*, 1983; Yabumoto *et al.*, 1997), the whale shark *Rhincodon* and the basking shark *Cetorhinus*.

The abundance of teeth of *Carcharoides totuserratus* in the lower member of the Navidad Formation, seems to be proportional to the observed abundance of *Carcharias* and it probably indicates that the former fossil species frequented shallow temperate-warm waters.

Most of the elasmobranch genera recorded in the lower member of the Navidad Formation suggest the influence of warm-temperate waters.

Palaeobiogeography

Among the fossil elasmobranch fauna of the Navidad Formation we recognised five genera that currently inhabit Chilean waters. These are *Squalus*, *Squatina*, *Isurus oxyrinchus*, *Myliobatis* and *Callorhynchus*. From the remaining taxa only *Heterodontus* and *Carcharias* are known from South American waters. *Heterodontus* occurs in waters of Peru and Ecuador while *Carcharias* is known from the Atlantic margin of southern Brasil and Argentina (Compagno, 1984). The genus *Pristiophorus*, which at present has not been recorded in South America, is common in waters of New Zealand and Southern Australia (Compagno, 1984). The fossil occurrences of *Pristiophorus* and *Heterodontus*, documented by De Muizon & De Vries (1985), Cione & Expósito (1980), Cione & Pandolfi (1984), Suárez & Marquardt (2003), Suárez *et al.*, 2004) and by the present work, indicate that during the Neogene and particularly the Miocene, sawsharks and bullhead sharks were widespread along the Pacific and Atlantic margins of South America. The Early Miocene fauna from the Navidad Formation are similar to the faunas of fossil elasmobranchs from the Late Oligocene and early Neogene from Argentina reported by Cione and Expósito (1980) and Cione (1986), sharing the presence of *Pristiophorus*, *Heterodontus*, *Isurus hastalis*, *Isurus oxyrinchus*, *Carcharoides totuserratus* and *Megascyliorhinus trelewensis*. The occurrence of the latter two species in the Navidad Formation is remarkable given the limited fossil record in South America, extending the Neogene geographical range of these taxa to the eastern

Pacific. The early Miocene elasmobranch faunas from the Navidad Formation are very similar with those reported from the Neogene of New Zealand (1984) and Late Paleogene-Early Miocene of Argentina (Cione & Expósito 1980).

General remarks and conclusions

The elasmobranch assemblage from the lower member of the Navidad Formation is currently represented by seven families: *Squalidae*, *Pristiophoridae*, *Squatinae*, *Heterodontidae*, *Lamnidae*, *Myliobatidae* and *Callorhynchidae* all which are reported for the first time from the Early Miocene of Chile. The presence of *Squalus* and *Callorhynchus* represents the first confirmed record of these two taxa in the Early Miocene of South America. The occurrence of *Carcharoides totuserratus*, an uncommon shark species with a chronostratigraphical range restricted between the Late Oligocene and Early Miocene (Suárez & Marquardt, 2003) supports a minimal Early Miocene age for the basal part of the lower member of the Navidad Formation.

Observations about habitat, distribution and biology of extant chondrychthians are certainly a useful tool for the understanding of the palaeoecological conditions of its fossil relatives from the Navidad Formation. Based on a comparison with their living relatives, the elasmobranch fauna from the lower member of the Navidad Formation represent different ecological habitats. *Squalus*, *Odontaspis*, *Megascyliorhinus* and *Callorhynchus* suggest relatively deep waters while *Heterodontus*, *Carcharias* and probably *Carcharoides totuserratus* suggest shallow waters. The remains of sharks are likely deposited together in a submarine fan or turbidite. The presence of *Heterodontus* and *Odontaspis* suggests warm-temperate waters. The latter is in agreement with evidence previously supported by micropalaeontological information (Martínez-Pardo & Valenzuela, 1979; Martínez-Pardo, 1990; Martínez-Pardo & Martínez-Gúzman, 1997) and also by macropalaeontological data (Covacevic & Frassinetti, 1980).

In comparison with other southern Neogene elasmobranch assemblages, the Navidad faunas indicate certain affinities with those previously reported from the "Patagoniano" of Argentina (Cione & Expósito, 1980; Cione, 1986) and those from New Zealand (Keyes, 1984; Pfeil, 1984).

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