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Middle Eocene chondrichthyan fauna from Antarctic Peninsula housed in the Museo de La Plata, Argentina

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Abstract In recent years, the taxonomy and systematics of the cartilaginous fish taxa from the Eocene La Meseta Formation of Seymour (Marambio) Island, Antarctica have been extensively discussed in a series of papers, resulting in a complete revision of the Antarctic Eocene ichthyofauna housed in the Vertebrate Paleontology collection of the Museo de La Plata, Argentina. This collection constitutes one of the largest and taxonomically most diverse in the world, with approximately 20000 specimens, which provides a solid database used for the analysis of qualitative and quantitative chondrichthyan taxonomic composition. The information provided herein might be useful to understand the sudden decline in chondrichthyan taxonomic diversity towards the top of La Meseta Formation as well as its potential relationship with environmental changes during the Eocene.

Keywords **Gondwana, Antarctica, Paleogene, ichthyofauna, Seymour (Marambio) Island**

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1 Introduction

Seymour (Marambio) Island, Antarctic Peninsula, once called the "Rosetta Stone" of Southern Hemisphere palaeobiology, is known for the wealth of its Paleogene cartilaginous and bony ichthyofauna. Several authors have reported chondrichthyans (sharks, rays, and holocephalans) from this island (Cione and Medina, 1987; Cione and Reguero, 1994, 1995, 1998; Cione et al., 1977; Engelbrecht et al., 2017a, 2017b, 2017c; Grande and Chatterjee, 1987; Grande and Eastman, 1986; Kriwet et al., 2016; Long, 1992; Reguero, 2019; Tonni and Cione, 1978; Ward and Grande, 1991; Welton and Zinsmeister, 1980; Woodward, 1908). Most of the published work on the Paleogene in Antarctica originates from Seymour (Marambio) Island (Figure 1), which yields one of the most diverse Paleogene chondrichthyan fauna in the Southern Hemisphere (Kriwet, 2005; Kriwet et al., 2016). Most of the vertebrate remains recovered, up to now are isolated teeth of elasmobranchs. Given that the highest diversities and quantity of cartilaginous fishes are found in the middle Eocene *Cucullaea* I Allomember (TELM 4 + TELM 5) of the La Meseta Formation (Figure 2), a predominantly temperate-adapted chondrichthyan fauna is known. As part of the doctoral dissertation of one of the authors (M. Charnelli), we conducted a comprehensive examination and qualitative

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and quantitative analyses of the chondrichthyan assemblages recorded in the *Cucullaea* I Allomember using as source the approximately 20000 specimens, cataloged specimens housed in the Museo de La Plata. This study provides a taxonomic list reporting 7 orders of selachians, consisting of 15 families, 16 genera, and 11 species; 2 orders of batoids, consisting of 3 families, 3 genera, and 1 order of holocephalans, with 1 family and 1 specie being identified (Table 1). Most of the materials come from 12 localities of the *Cucullaea* I Allomember of the La Meseta Formation (Table 2). We explored the contribution of numerical data to paleoecological interpretations.

The institutional abbreviations were given as followed. IAA: Instituto Antártico Argentino, Buenos Aires, Argentina; IAA-PV: Repositorio Antártico de Colecciones Paleontológicas y Geológicas, Instituto Antártico Argentino, San Martín, Buenos Aires, Argentina; DNA-IAA: Dirección Nacional del Antártico, Instituto Antártico Argentino; DPV: División Paleontología Vertebrados, Museo de La Plata, La Plata, Buenos Aires, Argentina; MLP: Museo de La Plata, La Plata, Buenos Aires, Argentina; MLP-PV: Colección Paleontología de Vertebrados, Museo de La Plata, La Plata, Buenos Aires, Argentina.

2 Material and methods

The material study herein comes from the *Cucullaea* I Allomember (TELMs 4 and 5 of Sadler, 1988) of the La Meseta Formation at the localities DPV 1/84, DPV 2/84, DPV 5/84, DPV 6/84, DPV 9/84, IAA 1/90, IAA 1/92, IAA 2/13, IAA 2/95 (see below). The specimens reviewed in this study, housed in the División Paleontología Vertebrados of the Museo de La Plata (MLP), Argentina, were collected during Antarctic field trips organized by the Instituto Antártico Argentino (DNA-IAA) over approximately 20 Antarctic summer campaigns from 1977 through 2015.

This material consists exclusively of isolated shark teeth, batoid dental plates, and fragmentary chimeroid tooth plates which were obtained from sediment samples (collected during the Argentine field project during the austral summers 1988 to 2013). Sediment samples were dry-sieved in the field using screens with a 2 mm mesh to produce a residue without larger stones and large

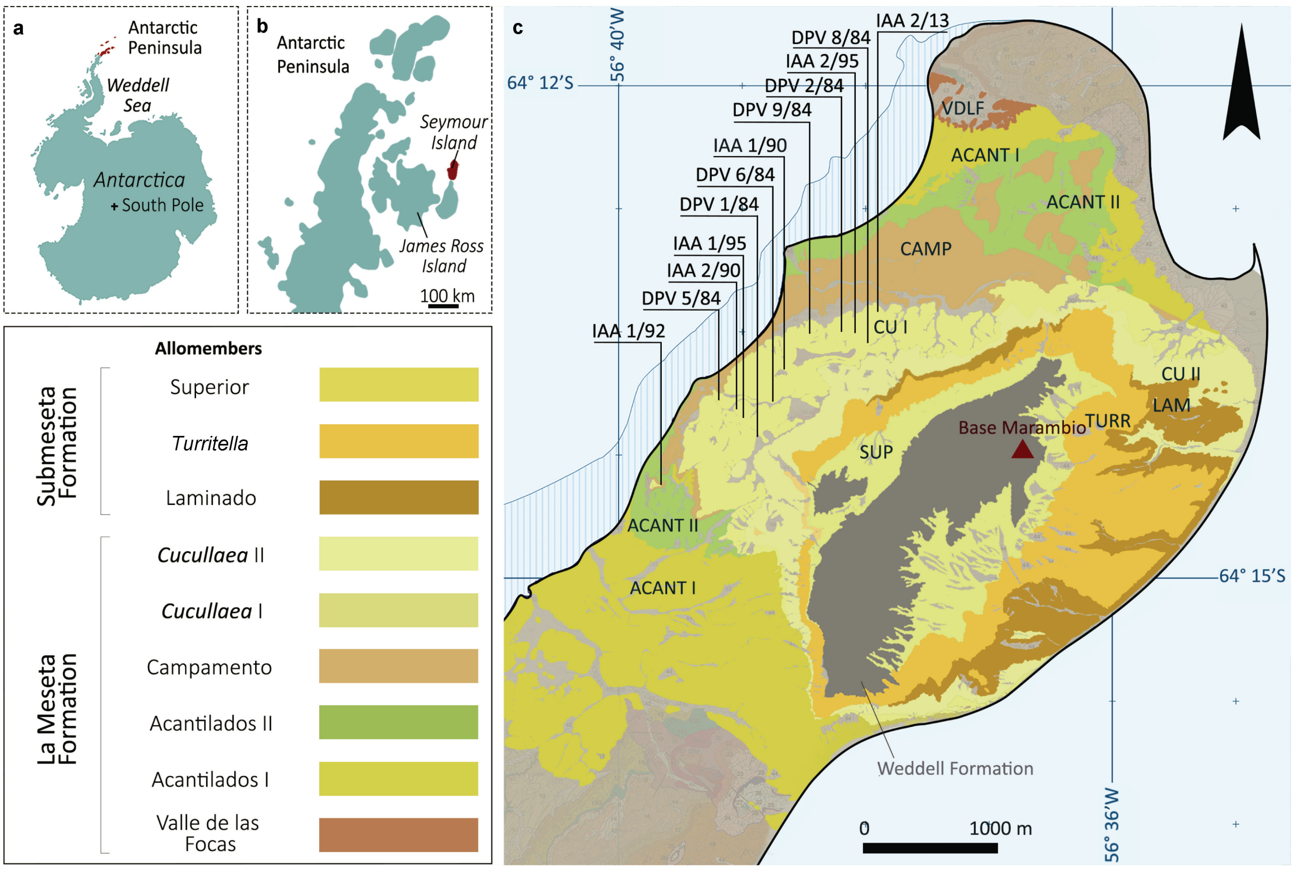

Figure 1 **a**, map of Antarctica; **b**, location of Antarctic Peninsula and Seymour (Marambio) Island; **c**, map of northwest part of Seymour (Marambio) Island; fossil chondricthyans localities on *Cucullaea* I Allomember of La Meseta Formation. Abbreviations: ACANT I, Acantilados I Allomember; ACANT II, Acantilados II Allomember; CAMP, Campamento Allomember; CU I, *Cucullaea* I Allomember; CU II, *Cucullaea* II Allomember; LAM, Laminado Allomember; SUP, Superior Allomember; TURR, *Turritella* Allomember; VDLF, Valle de las Focas Allomember.

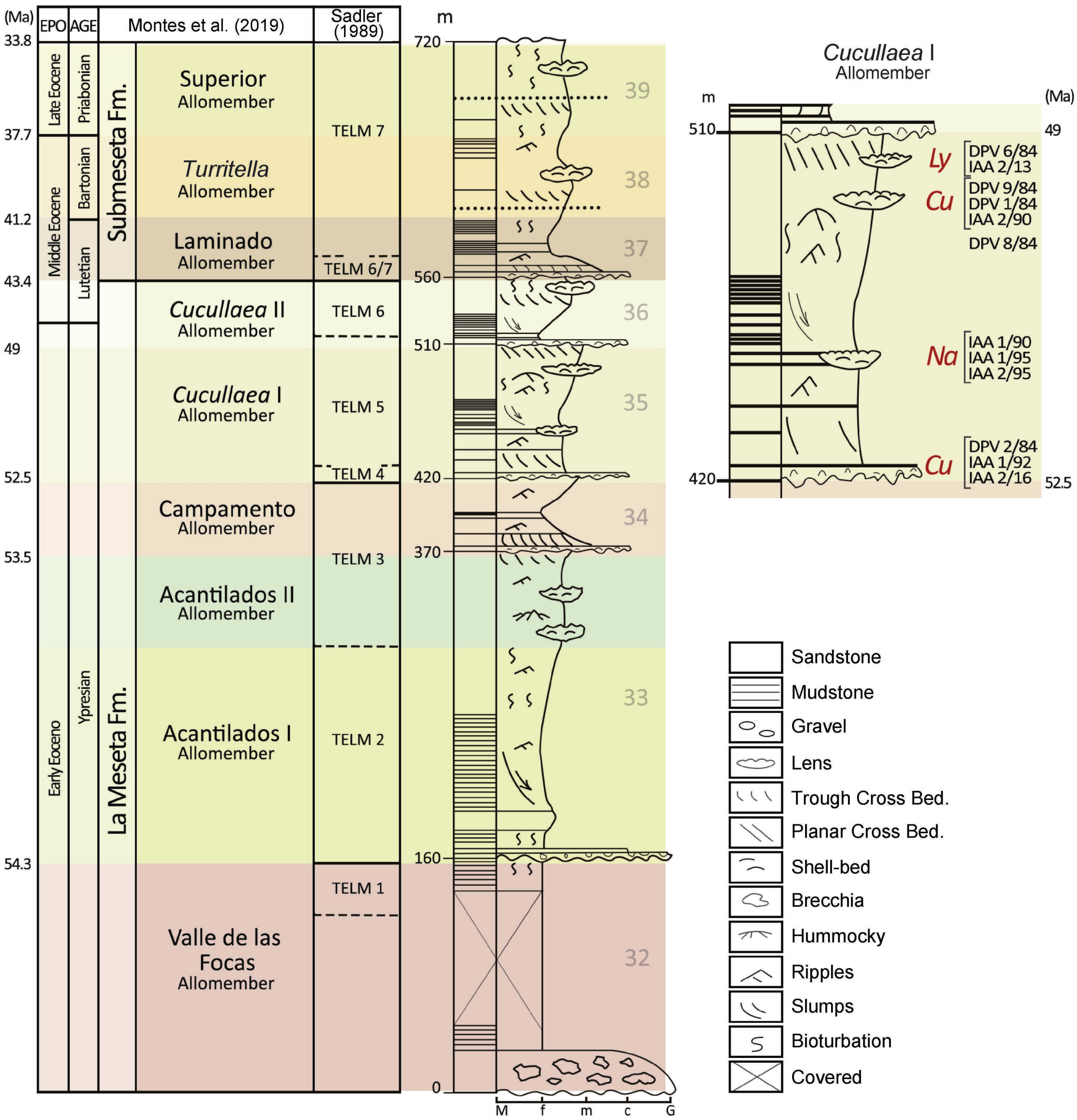

Figure 2 Stratigraphic section of La Meseta and Submeseta formations, detail showing the fossiliferous localities present in *Cucullaea* I Allomember. Abbreviations: EPO (Epoch), lower Cu (*Cucullaea* I), Na (*Natica* level), upper Cu (*Cucullaea* horizon*)* and Ly (*Lyreidus*). Modified from Montes et al. (2013). The stratigraphic position of the locality DPV 8/84 is estimated. Numbers in gray, stratigraphic levels (modified from Montes et al., 2019).

invertebrate fragments. The residue was dry-sieved again in the laboratory and separated into finer fractions > 4.0 mm, > 2.0 mm, and > 0.5 mm to collect microvertebrates. The teeth and dental plates were hand-picked using a stereomicroscope. Most of the small fossils at DPV 6/84, IAA 1/90, and IAA 2/95, were collected by dry-sieving method and only few specimens were collected by surface-prospecting, although the sediment was dry-sieved intensively in the following field seasons: 87–88, 88–89, 89–90 and 90–91. At DPV 2/84 and IAA 1/92, fossils were picked up only by surface prospecting.

The examination of the specimens was carried out using an Arcano ST30-2L binocular stereoscopic microscope. A total of 11598 teeth and dental plates were selected. Vertebrae, spines, or scales were excluded, along with heavily damaged or incomplete teeth.

Higher-level taxonomy (superfamily and up) follows Nelson et al. (2016). Sharks and rays were systematically classified following Cappetta (2012), Cappetta and Nolf (1981), Cione and Reguero (1994, 1998), Engelbrecht et al. (2016, 2017a, 2017b, 2017c), Kriwet (2005), Kriwet et al. (2016), Samonds et al. (2019) and Welten et al. (2015). Holocephalans were systematically classified following Grande and Eastman (1896), Stahl (1999, 2004), and Ward and Grande (1991).

The stratigraphic framework follows Marenssi et al. (1988), Montes et al. (2019), and Sadler (1988). All relevant information was recorded in tables and graphs.

Table 1 Chondrichthyan taxa (Class Chondrichthyes Huxley, 1880) from the *Cucullaea* I Allomember of La Meseta Formation, Seymour (Marambio) Island, Antarctica (systematics/identification, referred material, stratigraphy, assemblages and remarks)

Systematic/Identification				Referred material	Stratigraphy	Assemblages	Remarks
Subclass Holocephali Bonaparte, 1831	Order Chimaeriformes Patterson, 1965	Family Callorhynchidae Garman, 1901	*Ischyodus dolloi* Leriche, 1902	3 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Na-horizon), (Cu-horizon), (Ly-horizon)	?*Ischyodus* sp., first record from Antarctica was made by Grande and Eastman (1986). Ward and Grande (1991) reported *Ischyodus dolloi* from TELM 2, TELM 5 (RV-8200) from La Meseta Formation and TELM 6 from the Submeseta Formation. These specimens consist in fragmentary dental plates, with well-preserved oval or polygonal tritoral surfaces. Palatine dental plates are most easily identified by the arrangement of the tritors. Typical posterior and median tritors are well preserved. The distinctive multiple outer tritors allows us to assign these specimens as *I. dolloi* (Figures 3a and 3b).
			Chimaeriformes indet.	7 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Na-horizon)	First fossil of chimaeroids were reported by Grande and Eastman (1986) from Antarctica. The specimens from *Cucullaea* I Allomember bears several and well-defined tritoral surfaces but are poorly preserved and in many cases hardly damaged. Consequently, it is not possible reach a specific determination from many of them, although it's very probable that they belong to *I. dolloi* (Figure 3c).
Subclass Elasmobranchii Bonaparte, 1838	Order Orectolobiformes Applegate, 1972	Family Hemiscylliidae Gill, 1862	*Notoramphoscyllium woodwardi* Engelrecht et al., 2016	90 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Na-horizon)	This material from the *Cucullaea* I Allomember of La Meseta Formation, Seymour (Marambio) Island is a tooth very similar to *Notoramphoscyllium woodwardi* described by Engelbrecht et al. (2016). Due to its high and triangular main cusp, straight and slightly inclined backward, with absent cutting edges. The lateral cusplets are low, with oblique lateral edges in labial view. The apron is not as prominent as in *N. woodwardi* but is similar in the convex shape of its sides in labial view. Due to these features, we consider that this material fit within the variability displayed by *N. woodwardi* (Figures 3d–3l).
	Order Lamniformes Berg, 1958	Family Otodontidae Glickman, 1964	*Otodus* (*Carcharocles*) Jordan and Hannibal, 1923	7 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon)	This specimen was previously reported by Cione et al. (1977) from La Meseta Formation of Seymour (Marambio) Island as *Procarcharodon* sp. following Casier (1960). Later, Cappetta (1987) found that genus *Carcharocles* had priority. However, because the systematic discussion of this taxon is problematic and exceeds the scope of this work, we prefer to determine the specimens only at the subgenus level considering *Carcharocles* in terms of Cappetta (2012). We assigned this specimen to *Otodus* (*Carcharocles*) by the following combination of characters: larger triangular teeth with an irregular serrated cutting edge. High cusp, straight or bent distally. With moderately convex labial face which does not overhang the root. Two triangular, divergent, and serrated lateral cusplets and bulky, thick, with rather long and little extended root lobes (Figures 4a–4b).
		Family Odontaspididae Müller and Henle, 1838	*Odontaspis winkleri* Leriche, 1905	24 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon)	*Odontaspis winkleri* was previously reported by Long (1992) from *Cucullaea* I of La Meseta Formation of Seymour (Marambio) Island. In comparison with *O. winkleri* (Leriche, 1902) these specimens (Figures 4c–4d) are similar; the lateral cusplets are comparatively lower and slightly arched from the tip. The lateral tooth reports by Long (1992, his Figures 10j–10k), bears two smaller pairs of lateral cusplets in comparison. We assume that these specimens are into morphological variability among *O. winkleri.*

Continued

Systematic/Identification		Referred material	Stratigraphy	Assemblages	Remarks
	Striatolamia macrota Agassiz, 1843	1217 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon), (Ly-horizon)	*Striatolamia macrota* was previously reported by Cione et al. (1977) from La Meseta Formation of Seymour Island. Also cited by Welton and Zinsmeiser (1980) Unit II (Elliot and Trautman, 1982) and Grande and Eastman (1986). The specimens are average 2 cm high, however some specimen can reach 4 cm high (Figures 6g–6h). Several features like the intense of striation, the pronounced of sigmoidal profile, the thickness of the main cusp and the size variation are variable. We assume that they are among the normal morphologies of *S. macrota.* Cappetta (2012), Malyshkina and Ward (2016), and Ebersole et al. (2019), indicated an increase in size along the taxa record. The specimens figured here (Figures 4e–4h) belongs to base and top of the *Cucullaea* I Allomember and would support these observations.
	Odontaspididae indet.	359 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon), (Ly-horizon)	The teeth are mainly damaged, roots and main cusps are isolated. The cusplets are absent in many cases. The crown has smooth faces while some with gently striations in the lingual face. The mains cusps are slender and triangular. The cutting edge can be very sharp in some specimens but in others are completely absent or vanished. The sigmoidal profile is more or less pronounced depending on the case. The sample is integrated for few taxa, *S. macrota* and *Odontaspis* spp.
Family Jaekelodontidae Glickman, 1964	*Palaeohypotodus* sp. Glickman, 1964	40 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon)	Long (1992) reported *Palaeohypotodus rutoti* from *Cucullaea* I Allomember (TELM 5) of La Meseta Formation, Seymour (Marambio) Island. These 3 specimens show different shape, outline and cusplets arrangement, which seem to share only the presence of labial wrinkled or even ridges in the crown-root junction. The specimens report here barely resemble to the specimens of Leriche (1902) and Long (1992) in having a different cusplets (narrowed and higher). We assign these teeth to *Palaeohypotodus* sp. (Figures 4i–4l).
Family Cetorhinidae Gill, 1862	*Keasius* sp. Welton, 2013	1 specimen (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Na-horizon)	See section Systematic paleontology.
Family Lamnidae Müller and Henle, 1838	*Macrorhizodus* sp. Glickman, 1964	5 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon)	*Macrorhizodus* was previously considered synonymous with *Isurus*. Therefore, it is possible that materials previously reported as *Isurus* sp., such as the first report by Grande and Eastman (1986), or the Isurids previously reported by Elliot et al. (1975), and remains assigned with doubts to *Isurus* by Cione et al. (1977), could actually be *Macrorhizodus*. In this study, we will follow Cappetta (2012). The referred teeth are very similar to *Macrorhizodus praecursor,* however due to their state of preservation, we assign them at generic level.
	Macrorhizodus praecursor Leriche, 1905	12 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon)	*Macrorhizodus praecursor* was previously reported by Cione and Reguero (1994) in La Meseta Formation as *Isurus praecursor*. We refer these teeth to *Macrorhizodus praecursor* (Figures 4n–4o).

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Systematic/Identification			Referred material	Stratigraphy	Assemblages	Remarks
Order Carcharhiniformes Compagno, 1973	Family Triakidae Gray 1851	*Kallodentis rhytistemma* Engelbrecht et al., 2017a	4 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Na-horizon)	*Kallodentis rhytistemma* was first reported for Antarctica by Engelbrecht et al. (2017b) from the locality IAA 1/90, IAA 2/95 and IAA 1/93 from *Cucullaea* I and *Cucullaea* II allomembers, Eocene of Seymour Island, Antarctica. These specimens are very small (less than 5 mm length) the shape of the crown is barely distinguishable, because the tip of the cups and cusplets seems rounded in MLP-PV 94-III-15-521. However the outline resembles very well to some specimens of *Galeorhinus duchaussoisi*, but these teeth have fewer and relatively larger distal cusplets, plus the slightly sigmoidal mesial cutting edge. Considering these features in combination with a well-developed and broad nutritive groove and the striae of the base of the crown we assigned these specimens as *K. rhytistemma* (Figures 5a–5d).
	Family Carcharhinidae Jordan and Evermann, 1896	*Abdounia* sp. Cappetta, 1980	17 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(Na-horizon)	The genus *Abdounia* was first described for La Meseta Formation by Engelbrecht et al. (2017b), who described two species, *Abdounia mesetae* from locality IAA 1/95 and *A. richteri* from locality IAA 1/90 (*Cucullaea* I Allomember, TELM 5) of La Meseta Formation. It represents the southernmost record of this genus. A specific determination of these specimens is not possible because certain diagnostic characters cannot be observed due to preservation and breakages.
		Abdounia richteri Engelbrecht et al., 2017b	3 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Na-horizon)	The specimens corresponding to 2 anterior teeth and antero-lateral, well-preserved tooth. The anterior specimens are closely resembling to *A. beaugei* anterior tooth, however, the main cups are slightly higher than comparatively. Moreover, *A. beaugei* bears a barely sharper ended triangular main cups and the lateral teeth bear two pairs of well-defined cusplets. In comparison with anterior or antero-lateral tooth of other Ypresian species like *A. enniskilleni,* or *A. minutissima* the teeth outline hardly resembles some upper lateral tooth. In contrast, these specimens are morphologically very well comparable with the holotype and paratypes described by Engelbrecht et al. (2017b), from localities IAA 1/95 and IAA 1/90, *Cucullaea* I Allomember, for La Meseta Formation. Therefore, we consider the specimens as *A. richteri* (Figures 5e–5h).
		Rhizoprionodon sp. Whitley, 1929	1 specimen (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Na-horizon)	See section Systematic paleontology.
Order Hexanchiformes Buen, 1926	Family Hexanchidae Gray, 1851	*Hexanchus agassizi* Cappetta, 1976	1 specimen (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	?	See section Systematic paleontology.
Order Squaliformes Goodrich, 1909	Family Centrophoridae Bleeker, 1859	*Centrophorus* sp. Müller and Henle, 1837	1 specimen (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(Na-horizon), (Cu-horizon)	*Centrophorus* sp. was first reported on Seymour Island by Long (1992) RV-8200 (DPV 6/84), corresponding to TELM 5 of La Meseta Formation. However, previously Welton and Zinsmeiser (1980) reported an incomplete lower left antero-lateral tooth of and Squalidae indet., closely resembles to *Centrophorus* or *Deania* for *Cucullaea* I Allomember. The specimen is very similar with the *Centrophorus* sp. 2 report by Engelbrecht et al. (2017c) (Figures 6c–6d).

Continued

Systematic/Identification			Referred material	Stratigraphy	Assemblages	Remarks
	Family Dalatiidae Gray, 1851	*Eodalatias austrinalis* Engelbrecht, 2017c	10 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Cu-horizon)	*Eodalatias austrinalis* was reported on Seymour (Marambio) Island by Engelbrecht et al. (2017c). Long (1992) reported a specimen to *Dalastias licha* at *Cucullaea* I Allomember (TELM 5) of La Meseta Formation. The incomplete specimen described by Long (1992) closely resembles *Eodalatias austrinalis* (Engelbrecht et al., 2017c) more than *D. licha*. The specimens reported here fit very well with the description provided by Engelbrecht et al. (2017c), and therefore, we assign them as *E. austrinalis* (Figures 6e–6f).
	Family Squalidae Bonaparte, 1838	*Squalus* sp. Linnaeus, 1758	2 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon), (Ly-horizon)	*Squalus* was first reported for La Meseta Formation on Seymour (Marambio) Island by Long (1992) at localities RV-8200 (DPV 6/84) and RV-8424 (*Cucullaea* I Allomember -TELM 5) and described two new species for this genus: *S. weltoni* and *S. woodburnei.* These specimens are incomplete and badly preserved. Tentatively we assign these specimens to *Squalus weltoni.*
		Squalus weltoni Long, 1992	281 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon), (Ly-horizon)	*Squalus weltoni* was first reported by Long (1992) from RV-8200 (DPV 6/84) and RV-8424 of the *Cucullaea* I Allomember (TELM 5) from La Meseta Formation on Seymour (Marambio) Island. Squalus-like teeth are very common and relatively abundant in *Cucullaea* I Allomember. The specimens report here are small (up to 7 mm length) well preserved teeth with a triangular cusp, bents toward the rear. The cutting edge is completely serrated, and the base of the root is flat. These teeth closely resemble to the specimens described by Long (1992) as *Squalus weltoni* from *Cucullaea* I Allomember (TELM 5) (Figures 6g–6n).
		Squalus woodburnei Long, 1992	420 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(Na-horizon), (Cu-horizon), (Ly-horizon)	*Squalus woodburnei* was first reported by Long (1992) from *Cucullaea* I Allomember (TELM 5) of La Meseta Formation, Seymour (Marambio) Island. We assigned these teeth to *S. woodburnei,* they closely resemble to the specimens described by Long (1992) in a combination of the following characters: cusp labio-lingually compressed whit both smooth and convex crown faces, triangle main cusp strongly bents toward the rear with a pronounced distal heel, well developed straight lingual apron. (Figures 6o–6r).
Order Squatiniformes Buen, 1926	Family Squatinidae Bonaparte, 1838	*Squatina* sp. Duméril, 1806	2751 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon), (Ly-horizon)	Welton and Zinsmeister (1980), and Elliot and Trautman (1982) were the first authors to mention *Squatina* sp. from La Meseta Formation, Seymour (Marambio) Island, also cited by Grande and Eastman (1986). These specimens resemble *Squatina prima*. *Squatina* teeth are very conservative along the fossil record, the fossil genera are only defined by teeth, use few morphological criteria, like height-wide proportion, length of the main cusp, witch that no consider the heterodoncy along the jaws. (Figures 7a–7h).
Order Pristiophoriformes Berg, 1958	Family Pristiophoridae Bleeker, 1859	*Pristiophorus laevis* Engelrecht et al., 2017a	2551 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon), (Ly-horizon)	*Pristiophorus* was first reported by Grande and Eastman (1986) for La Meseta Formation from Seymour (Marambio) Island. Subsequently several authors (e.g. Long 1992; Otero et al., 2015; Kriwet et al., 2016) mentioned more saw shark rostral teeth from from the same unit. These specimens reported here co-occur with *P. laevis,* and resemble the rostral teeth figured for Engelbrecth et al. (2017a, the Figure 3 at page 845) (Figures 7i–7p).

Continued

Systematic/Identification				Referred material	Stratigraphy	Assemblages	Remarks
Division Batomorphii Cappetta, 1980							
	Order Rajiformes Berg, 1937	Family Rajidae Blainville, 1816	*Raja* sp. Linnaeus, 1758	300 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELM 5)	(Na-horizon)	*Raja* was previously reported by Long (1994) from the Assemblage Ly-horizon. Three species of Rajidae were described for Seymour (Marambio) Island, *Marambioraja leiostemma* (TELM 4 and TELM 5), *Raja amphitrita*, *Raja manitaria* (TELM 5 and TELM 6) by Engelbrecht et al. (2018). The MLP-PV 90-I-20-418 (Figures 7n–7o) could be a male, as its cusp is very long, as occurs in some current skates. This specimen is very similar to *R. amphitrita* Engelbrecht et al., 2019 in size, slightly more than 1 mm in width, and crown shape. The cusp on both is high, triangular, and straight, with a weakly developed labial protuberance. The cutting edges are very short, not reaching the basal part of the crown. Basal bulge continues from the mesial to the distal edge. However, it differs from *R. amphitrita* in the following aspects: the root is not as high; in lingual view, the crown changes angle towards the base instead of gradually widening, and in lateral view, the ventral edge of the crown is rather straight instead of being ventrally concave (Figures 8a–8b).
	Order Myliobatiformes Compagno, 1973	Family Myliobatidae Bonaparte, 1838	*Myliobatis* sp. Cuvier, 1817	568 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)	(35Cu-horizon), (Na-horizon), (Cu-horizon), (Ly-horizon)	*Myliobatis* sp. was previously reported for Unit II (Elliot and Trautman, 1982) by Welton and Zinsmeister (1980) from Seymour (Marambio) Island. Engelbrecht et al. (2018) reported myliobatids for TELM 2, TELM 4 and TELM 5 of the La Meseta Formation, especially for the Natica-horizon localities (IAA 1/90, IAA 1/95 and IAA 2/95). They are partially rounded, damaged and often broken, with the parallel lobes of the root filled by sediment in some cases. Both medial and lateral teeth are present in the sample. Some specimens also show a prominent curvature, but not arched as *Aeotobatus* sp. The crenulated margins of the crown are more conspicuous in the lateral teeth, which has typically hexagonal, pentagonal or distorted rhombic silhouette (Figures 8c–8d).
		Family Rhinopteridae Jordan and Evermann, 1896	*Rhinoptera* sp. Cuvier, 1829	5 specimens (see Appendix)	La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5)		See section “Systematic paleontology”.

Notes: Stratigraphic abbreviations were given as followed. 35Cu-horizon: channelized level with gravels and *Cucullaea* I coquina, informally referred to as “*Cucullaea* I level”; Cu-horizon: sandstone levels with *Cucullaea*; Na-horizon: naticid conglomerate bank; Ly-horizon: *Lyreidus* bank.

Photographs of the specimens were taken using a Nikon Coolpix L840 camera and an AmScope Microscope Digital Camera model MU1803 USB 3.0 DC 5V/900 mA. Images were processed using AmScope software and Adobe Photoshop.

Proposed ecological roles were determined using criteria from Ebert et al. (2021) and Myers et al. (2007), and taxonomic correspondence with extant taxa and faunal associations were established according to Kriwet et al. (2016).

3 Stratigraphical setting and age

Seymour (Marambio) Island is located at the southeastern tip of the Antarctic Peninsula, in the northwestern Weddell Sea (Figures 1a and 1b). The material discussed in this contribution comes from La Meseta Formation, exposed in the northeastern part of Seymour (Marambio) Island (Figure 1c).

Marenssi et al. (1998) organized this sequence into

Table 2 Summary of the fossiliferous localities within the *Cucullaea* I Allomember, La Meseta Formation, Seymour (Marambio) Island. DPV 8/84 is not associated with any of the coquina levels

Localities	Chondrichthyans assemblages and TELMS (Sadler, 1988)	Allomember (Montes et al., 2019)	Mapped	GPS (Latitude, Longitude)	
DPV 6/84	Ly-horizon (TELM5)		X	64°14'21.782"S	56°39'44.840"W
IAA 2/13	Ly-horizon (TELM5)		X	Not available	
DPV 8/84	(TELM 5)		X	Not available	
DPV 9/84	Cu-horizon (TELM 5)		X	64°14'09"S	56°39'55.1"W
DPV 1/84	Cu-horizon (TELM 5)		X	Not available	
IAA 2/90	Cu-horizon (TELM 5)		X	Not available	
IAA 1/90	Na-horizon (TELM 5)	*Cucullaea* I	X	64°14'06"S	56°39'57.1"W
IAA 1/95	Na-horizon (TELM 5)		X	64°14'28.55"S	56°40'18.59"W
IAA 2/95	Na-horizon (TELM 5)		X	64°13'57.67"S	56° 39'5.87"W
DPV 2/84	35Cu-horizon (TELM 4)		X	64°13'51.195"S	56°39'21.992"W
IAA 1/92	35Cu-horizon (TELM 4)		X	64°14'43.9"S	56°41'9.9"W
DPV 5/84	35Cu-horizon (TELM 4)		X	64°14'16.5"S	56°40'38.6"W

erosionally based internal units or allomembers. The La Meseta Formation includes six allomembers (in ascending temporal order): Valle de Las Focas, Acantilados I, Acantilados II, Campamento, *Cucullaea* I, and *Cucullaea* II (Montes et al., 2013, 2019). The overlying Submeseta Formation (Montes et al., 2013) was divided into three main allomembers (in ascending temporal order): *Turritella*, Laminado, and Superior (Montes et al., 2019) (Figure 2).

The age of the middle part of La Meseta Formation, including the *Cucullaea* I and *Cucullaea* II allomembers (Figure 2), remains uncertain. Based on palynofloral analysis made by Askin (1988), this interval is suggested to be middle Eocene, which corresponds with the $^{87}Sr/^{86}Sr$ ages reported by Dutton et al. (2002) for TELM 5 (equivalent to most of *Cucullaea* I and all *Cucullaea* II), and marine and terrestrial vertebrates by Reguero and Marenssi (2010). However, as noted by Ivany et al. (2008), chronological relationships based solely on individual $^{87}Sr/^{86}Sr$ measurements of presumed Eocene age do not provide definitive chronological results due to minimal changes in the global seawater curve during this period.

The *Cucullaea* I Allomember (TELMs 4 and 5 of Sadler, 1988) of the La Meseta Formation, from which most of the materials comes, primarily consists of well-sorted sands with thick shelly conglomerates and frequent intercalations of sand/mud channel fills. Sadler's (1988) characterization of TELM 4 focused on its thickness, coarseness, and the high presence of teeth and bones. This horizon is predominantly marked by the pelecypod *Cucullaea* and darwinellid gastropods (Reguero et al., 2012). In general, TELM 5 sediments comprise laminated fine-grained sandstones and silty clays with interbedded conglomeratic sandstones (Sadler, 1988). The distinct presence of *Cucullaea* shells in this unit indicates a shallow marine environment near the coast (Stilwell and Zinsmeister, 1992). The Assemblage Na-horizon of the *Cucullaea* I Allomember (Figure 2) yielded a substantial amount of material, including marine mollusks, sharks, skates, and rays (Long, 1992; Kriwet et al., 2016; Stilwell and Zinsmeister, 1992).

Within this allomember we identify 12 localities and four assemblages (Table 2).

(1) Assemblage 35Cu-horizon (TELM 4) represented in the following localities: DPV 2/84, "de Miles" with an erosive base. This horizon has an erosive base and a thickness of 4 m, which can be traced laterally for several kilometers (Marenssi et al., 1998). The deposits here are intensely reworked from the underlying materials of the Campamento Allomember, IAA 1/92; and DPV 5/84, outcropping at "Sergios Point". This horizon is mapped as "level 35 Cu" in Montes et al. (2013).

(2) Assemblage Na-horizon (TELM 5), includes the following localities: IAA 1/90, also informally referred to as Ungulate Site (Marenssi et al., 1994), IAA 1/95 and IAA 2/95 or "Marsupial Site".

(3) Assemblage Cu-horizon (TELM 5) which includes the following localities: DPV 1/84, informally known as "El Cangrej al"; DPV 9/84 (IAA 1/80). IAA 2/90, equivalent to IAA 4/80.

(4) Assemblage Ly-horizon (TELM 5) includes: DPV 6/84, also known as RV-8200, or "Mammal site" or "Rocket site". This was the first locality where fossils of land mammals were found in Antarctica (Woodburne and Zinsmeister, 1984). IAA 2/13, informally known as "Simil RV" which beds are correlated with DPV 6/84.

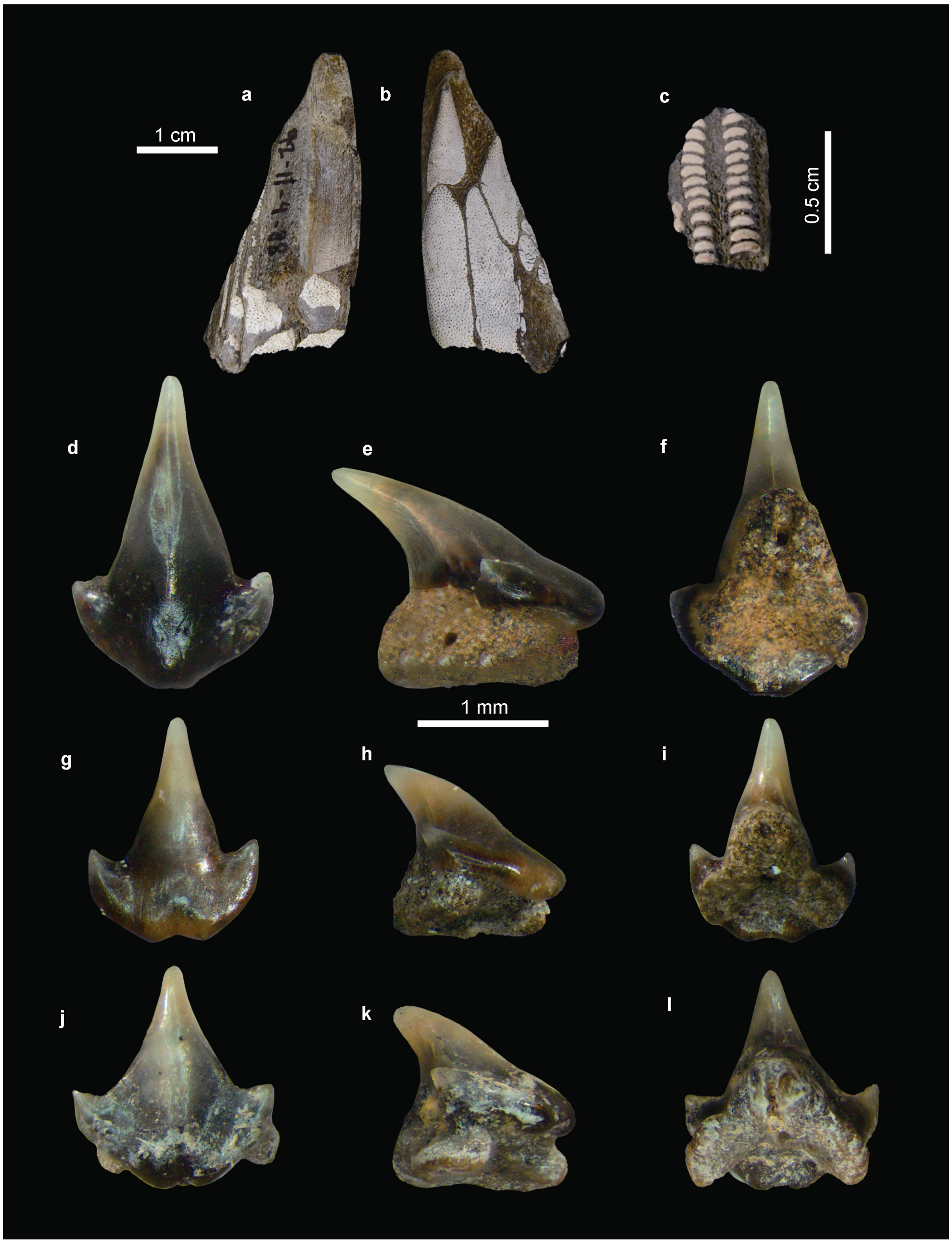

Figure 3 Remains of Chimaeriformes and Orectolobiformes. **a**–**c**, Chimaeriformes; **d**–**l**, Hemiscyllidae. **a**–**b**, *Ischyodus dolloi*, left palatine dental plate, MLP-PV 92-II-4-88, in aboral view (**a**) and oral view (**b**); **c**, Chimaeriformes indet., left mandibular dental plate, MLP-PV 94-III-15-171, in lingual view; **d**–**f**, *Notoramphoscyllium woodwardi*, anterior tooth, MLP-PV 95-I-10-290, in labial view (**d**), profile (**e**) and oblique lingual view (**f**); **g**–**i**, *N. woodwardi*, MLP-PV 92-II-2-21, in labial view (**g**), profile (**h**) and oblique lingual view (**i**); **j**–**k**, *N. woodwardi*, MLP 94-III-15-516, in labial view (**j**), profile (**k**) and oblique lingual view (**l**).

4 Systematic paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Orden Lamniformes Berg, 1958
Family Cetorhinidae Gill, 1862
Genus *Keasius* Welton, 2013
Type Species—*Squalus maximus* Gunner, 1765

Keasius sp. (Figure 4m)

Referred material: MLP-PV 96-I-5-42, a proximal fragment of the gill raker.

Geographic and stratigraphic occurrence: IAA 1/90. Seymour (Marambio) Island, Antarctica; La Meseta Formation, *Cucullaea* I Allomember (TELM 5).

Description: A proximal fragment of a gill raker, small in size, approximately 6.3 mm long. The base is wide and flat. The medial process is short, with a bight width barely

Figure 4 Specimens of Lamniformes. **a**–**b**, Otondontidae; **c**–**h**, Odontaspididae; **i**–**l**, Jaekelodontidae; **m**, Cetorhinidae; **n**–**o**, Lamnidae. *Otodus* (*Carcharocles*), lower tooth, MLP-PV 94-III-15-145, in labial view (**a**) and lingual view (**b**); *O. Winkleri*. ?lateral tooth, MLP-PV 94-III-15-523, in labial view (**c**) and lingual view (**d**); *Striatolamia macrota*. ?lower left anterior tooth, MLP-PV 91-II-4-180, in labial view (**e**) and lingual view (**f**); *S. macrota*, upper right anterior tooth, MLP-PV 14-I-10-203, in labial view (**g**) and lingual view (**h**); *Palaeohypotodus* sp., lower right anterior tooth, MLP-PV 91-II-4-165, in labial view (**i**) and lingual view (**j**); *Palaeohypotodus* sp., lateral tooth, MLP-PV 88-I-1-76, in labial view (**k**) and lingual view (**l**); **m**, Cetorhinidae, *Keasius* sp., the proximal part of a gill raker, MLP-PV 96-I-5-42, in lateral view (**m**); *Macrorhizodus praecursor*, lower anterior tooth, MLP-PV 94-III-15-517, in labial view (**n**) and lingual view (**o**). For **a**–**b**, 1 cm small scale bar; for **c**–**l**, **n**–**o** 1cm large scale bar.

wide, and a subangular shape. The mesial edge of the medial process is moderately convex, with a rounded basal angle. The filament portion is short, appearing flat and weak, weakly curved above its basal junction. The characteristics of the medial process can be well observed in Cione and Reguero (1998), where it is seen complete.

Remarks: MLP-PV 96-I-5-42 was previously reported by Cione and Reguero (1998) as *Cetorhinus* sp. Malyshkina et al., 2022 refer to this material as *Keasius*, according to the description of gill raker of Welton (2013). Herein we agree with Malyshkina et al. (2022) and consider this specimen as a gill rakers of *Keasius* sp., as *Keasius* compared with *Cetorhinus* has a shorter medial process, a broadly rounded subangular bight shape, and a narrow and rounded base and a wide and weakly curved filament base.

Order Carcharhiniformes Compagno, 1973

Family Carcharhinidae Jordan and Evermann, 1896

Genus *Rhizoprionodon* Whitley, 1929

Type Species—*Carcharias* (*Scoliodon*) *crenidens* Klunzinger, 1880.

Rhizoprionodon sp. (Figures 5i–5j)

Referred material: MLP-PV 96-I-5-89, a (?upper) lateral tooth.

Geographic and stratigraphic occurrence: IAA 1/90. Seymour (Marambio) Island, Antarctica. La Meseta Formation, *Cucullaea* I Allomember (TELM 5).

Description: Small tooth width is greater than height, 7.7 mm in length. The triangular-shaped main cusp is barely inclined distally, labio-lingually flattened. Smooth enameloid. Well-defined cutting edge, the base of the mesial heel bears some irregular serrations. The mesial edge is concave and the distal edge is much straighter and orthogonal to the plane of the root. In labial view, the distal heel has a well-defined edge and bears three cusplets with straight margins, which are smaller to the rear. Labially the crow/root junction seudo-horizontal, lingually, it is strongly concave. The root lobes in the baso-lingual view are sub triangular, wider than they are tall, separated by a well-defined groove. On the lingual face of the root, aligned foramina are present.

Remarks: *Rhizoprionodon* is a genus present in the lower Ypresian Eocene in Europe and North Africa, currently inhabiting tropical waters of the Atlantic and Indo-Pacific. The specimen from La Meseta Formation represent the southernmost record and also the first of this genus in Antarctica. This specimen is contemporaneous with *Rhizoprionodon ganntourensis* from the lower Eocene, Ypresian, Morocco, and Africa. Several specimens with certain morphological variability can be observed, in Arambourg's original description (Arambourg, 1952), nonetheless, this specimen has cusplets aligned like a staircase with straight and almost orthogonal edges, and a well-developed main cusp that is barely wider at its base than in the middle portion, sub triangular, flat, with well-defined convex anterior cutting edges. In addition to these differences, the enamel is very thin on the mesial cutting edge. According Ebersole et al. (2023), this

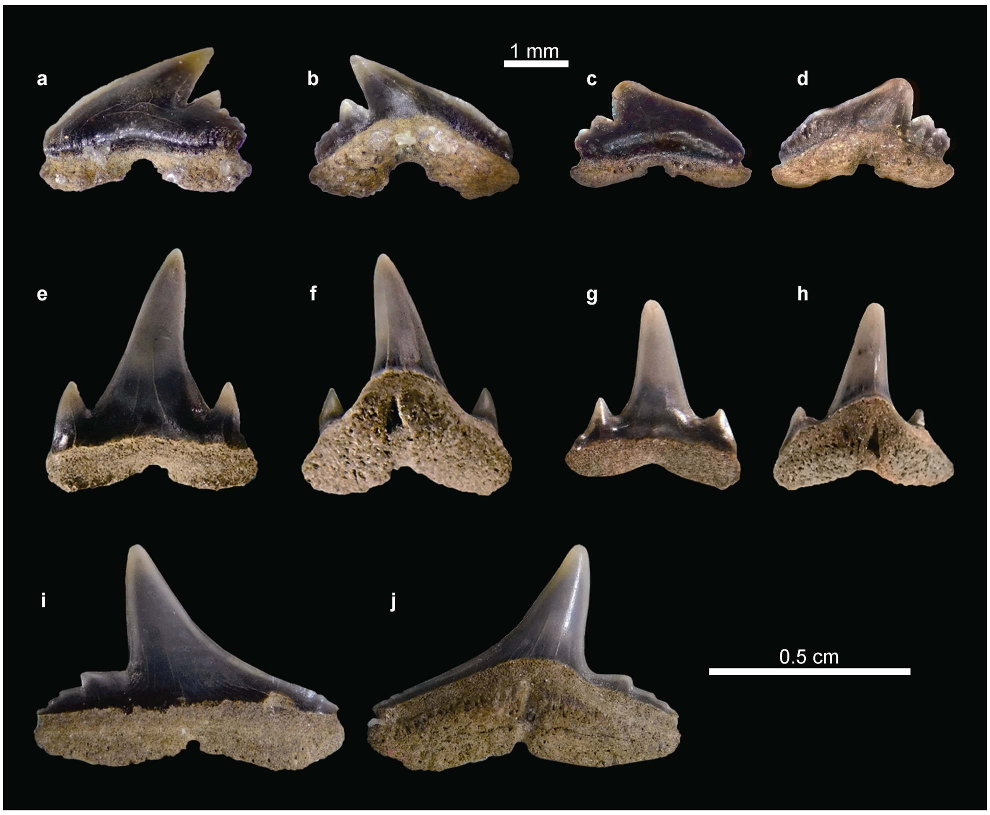

Figure 5 Remains of Carcharhiniformes. **a–d**, Triakidae; **e–j**, Carcharhinidae. *Kallodentis rhytistemma*, anterior tooth, MLP-PV 94-III-15-521, in labial view (**a**) and linguobasal view (**b**); *K. rhytistemma*, anterior tooth, MLP-PV 94-III-15-544, in labial view (**c**) and linguobasal view (**d**); *Abdounia richteri*, anterior teeth, MLP-PV 94-III-15-518, in labial view (**e**) and lingual view (**f**); *Abdounia richteri*, anterior teeth, MLP-PV 94-III-15-519, in labial view (**g**) and lingual view (**h**); *Rhizoprionodon* sp., MLP-PV 96-I-5-89, ?upper left lateral tooth, in labial view (**i**) and linguobasal view (**j**). For **a–d**,1 mm scale bar; for **e–j**, 0.5 cm scale bar.

variability fit between the morphology displays for this taxon. This leads to speculation that this form could be a heterodonty variation for *Rhizoprionodon ganntourensis*.

Order Hexanchiformes Compagno, 1973
Family Hexanchidae Gray, 1851
Genus *H*exanchus Rafinesque, 1810
Type Species—*Squalus griseus* Bonnaterre, 1788
Hexanchus agassizi Cappetta, 1976 (Figures 6a–6b)

Referred material: MLP-PV 88-I-1-384, incomplete isolated lower left lateral tooth.

Geographic and stratigraphic occurrence: DPV 8/84, Seymour (Marambio) Island, Antarctica; La Meseta Formation, *Cucullaea* I Allomember (TELM 5).

Description: A left Lower anterolateral tooth, partially complete. The anterior portion of the main cusp and mesio-distally edges of theroot are missing. The mesio-distallylength of the specimen is 24.2 mm, approximately twice as long as height. The main cusp (acrocone), barely bigger than the following 8 cusplets, which ones are decreasing, first rapidly then gradually, in size toward the distal margin, this gives a concave silhouette. Transversally, the cusplets are flat in the labial face and convex in the lingual face. The main cusp has almost straight edges, the

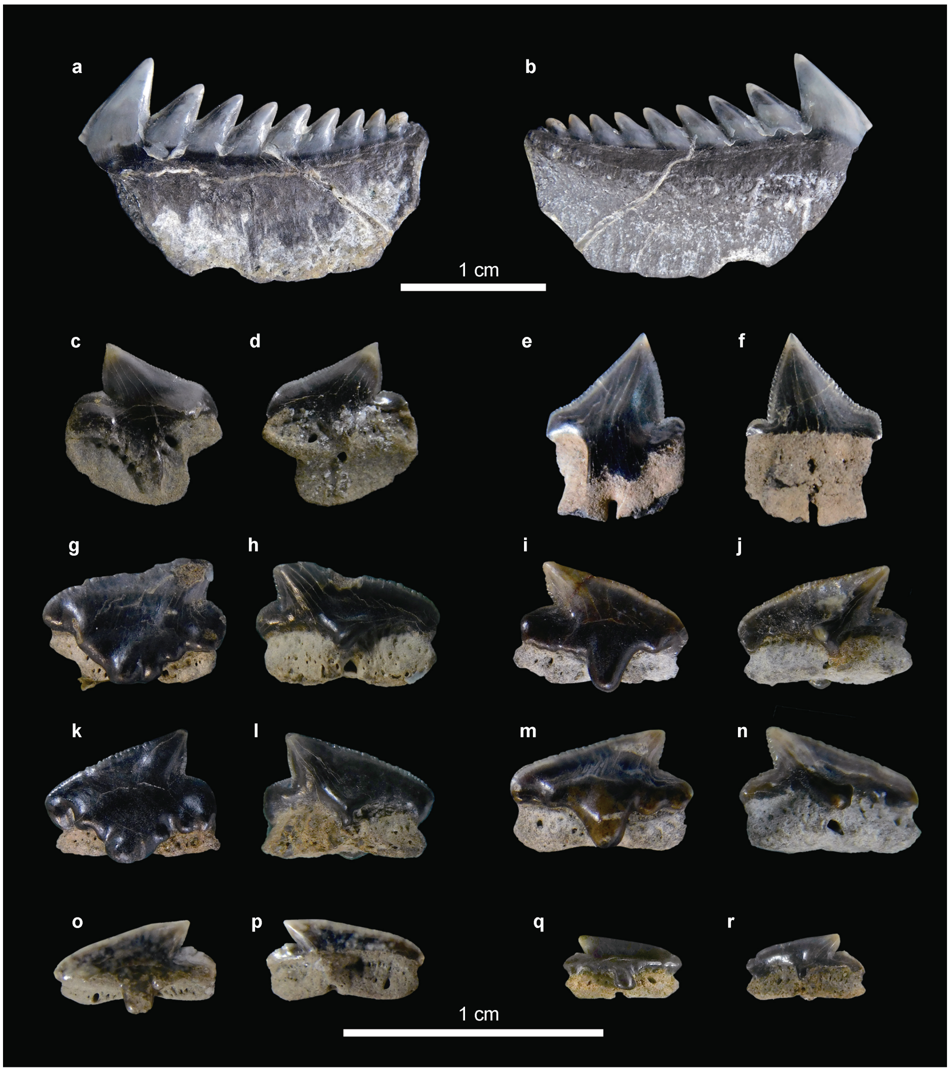

Figure 6 Remains of *Hexanchus agassizi* (**a**–**b**) and Squaliformes (**c**–**r**). *Hexanchus agassizi*, lower left lateral tooth, MLP-PV 88-I-1-384, in labial view (**a**) and lingual view (**b**); Centrophoridae, *Centrophorus* sp., lower right lateral tooth, MLP-PV 91-II-4-159, in labial view (**c**) and lingual view (**d**); Dalatidae, *Eodalatias austrinalis*, lower left lateral tooth, MLP-PV 94-III-15-522, in labial view (**e**) and lingual view (**f**); Squalidae, *Squalus weltoni*, ?upper right lateral tooth, MLP-PV 95-I-20-291, in labial view(**g**) and lingual view (**h**); Squalidae, *S. weltoni*, upper left lateral tooth, MLP-PV 95-I-20-292, in labial view(**i**) and lingual view (**j**); Squalidae, *S. weltoni*, upper right lateral tooth, MLP-PV 95-I-20-293, in labial view (**k**) and lingual view (**l**); Squalidae, *S. weltoni*, ?lower left lateral tooth, MLP-PV 95-I-20-294, in labial view (**m**) and lingual view (**n**); Squalidae *Squalus Woodburnei*, ?lower left lateral tooth, MLP-PV 90-I-20-421, in labial view (**o**) and lingual view (**p**); Squalidae *S. Woodburnei*, upper right lateral tooth, MLP-PV 90-I-20-419, in labial view (**q**) and lingual view (**r**). For *Hexanchus agassizi* (**a**–**b**), upper scale bar; for Squaliformes (**c**–**r**) lower scale bar.

one bear some little constrictions, which indicates the beginning of mesial serration. The root is high, flattened labio-lingually. The crown-root junction is slightly concave in the labial face. Lingually, the crown-root junction is convex bellow the main cusp, and straight under the cusplets. The lingual protuberance is parallel to the crow-root junction line.

Remarks: Cione and Reguero (1994) reported the first occurrence of the genus *Hexanchus* sp. at Marambio, based on MLP-PV 88-I-1-384, a lower incomplete tooth Cione and Reguero (1994, the Figure 4, page 4 in their paper) found in the DPV 8/84 locality, which is exclusive to this specimen. This locality belongs to *Cucullaea* I Allomember but cannot be correlated with the horizons described above. However, the available geographic information about DPV 8/84, allows us to include the specimen in our analysis as a member of TELM 5. Initially, Cione and Reguero (1994), discussed the resemblance of the specimen among *Hexanchus* spp. However, because of some characters it would not be possible to make a specific determination. Even more so if it is considered that this specimen was larger than the largest tooth of *Hexanchus* reported up to that moment from the Cretaceous to Eocene time lapse (*H. agassizi* 25 mm in length; Ward, 1979). The specimen was determinate only on generic level.

Adnet (2006) suggested that the variability exhibits in the morphologies of lower antero-lateral teeth responds ontogeny, and the Paleogene species *H. hookeri* and *H. collinsonae* could be different ontogenetic states of *H. agassizi.* Furthermore, the increase in tooth size during the end of the Paleogene to Neogene of *Hexanchus* spp. (more than 20 mm) could indicate the rise of a new group of large *Hexanchus*, perhaps the first representatives of the extant grisiform lineage better known in Neogene and recent oceans (Adnet, 2006). According to Ward (1979), the Cenozoic *Hexanchus* shows two morphological types of lower teeth: grisiform and vituliform. *H. hookeri*, *H. collinsonae* and *H. agassizi* here will be consideration in Adnet (2006) terms, like ontogenetic states of *H. agassizi*, a vituliform type according to Ward (1979). Following Adnet (2006), there is no clear evidence that the grisiform lineage has been found prior to the middle Eocene (Adnet, 2006), a fact that suggest the great modern Hexanchiforms grisiforms rised form vituliforms. Considering all of this, MLP-PV 88-I-1-384, could represent these transitional forms. However, as this discussion goes beyond the purpose of this article and given the morphology resembles both *H. agassizi* and *H. griseus*, with the former being contemporary with this specimen. We assigned MLP-PV 88-I-1-384 to a large *H. agassizi*, a precursor to *H. griseus*.

Superorder Batomotphii Cappetta, 1980
Order Myliobatiformes Compagno, 1973
Family Rhinopteridae Jordan and Evermann, 1896
Genus *R*hinoptera Cuvier, 1829
Type Species—*Raja aquila* Linnaeus, 1758

Rhinoptera sp. (Figures 8e–8f)

Referred material: Specimens in Appendix.

Geographic and stratigraphic occurrence: MLP-PV 91-II-4-189, MLP-PV 95-I-10-143 (Figures 7p–7q) come from DPV 2/84; MLP-PV 13-XI-28-339 come from IAA 1/90. Seymour (Marambio) Island, Antarctica. La Meseta Formation, *Cucullaea* I Allomember (TELMs 4 and 5).

Description: Dental plates are wider than their length, straight or slightly lingually arched, with a hexagonal shape in occlusal view. The crowns are thick, whit smooth margins and straight and sometimes wrinkled, labial, and lingual faces. The base of lingual face bears a rounded transverse ridge. The surface of the dental plate is almost flat, with only a slight curve in the front face. The polyaulacorhize root is apicobasally shorter than the crown. The lateral teeth are asymmetrical in labial view, and the mesial side of the crown is higher than the distal side.

Remarks: At first glance, *Rhinoptera* and *Myliobatis* isolated teeth have many characters in common, such as the hexagonal shape in the occlusal view of the medial teeth or high crowns with straight faces. Therefore, damaged specimens are hard to identify. The samples show heterogeneous preservation and many dental plates very often are broken or rounded, and the most relevant characters are erased. *Rhinoptera* and *Myliobatis* are differentiated by: the shape of the junction surface with the transverse ridge, asymmetries in the crown high in the lateral plates and the smoothness of the edges of the crown, although this is not always clear. Other characteristics, like the wrinkled ornamentation in the crown faces, are useless in many cases considering the vanished surfaces, broken or the enameloid is chipped. These specimens represent the southernmost record as well as the first of the genus *Rhinoptera* in Antarctica.

5 Concluding remarks

In the study area, 20 chondrichthyan genera, belonging to 10 orders and 18 families were documented (Table 1). Approximately 7779 shark teeth, 578 ray tooth plates, and 300 ray teeth, and 8 chimera dental plates were reviewed (Table 3). *Rhinoptera* is added to the taxonomic list. Other work provides extensive lists of materials reported for these formations, focusing on the presence of taxa (Engelbrecht et al., 2016; Long, 1992; Reguero, 2019). This study recognizes 4 new taxonomic assemblages within the *Cucullaea* I Allomember.

Most of the material was obtained by dry-sieving and surface prospecting in the field from different coquinas from the *Cucullaea* I Allomember. These techniques were widely employed in DPV 5/84 DPV 2/84, IAA 1/90, IAA 1/95, IAA 2/95, RV-8200, and IAA 2/13. In DPV 2/84 the majority of recovered teeth, such as *Otodus* (*Carcharocles*) and *Striatolamia macrota*, were collected through surface prospecting, while very few specimens, e.g., *Pristiophorus*,

Figure 7 Remains of Squatiniformes and Pristiophoriformes. *Squatina* sp., anterior teeth, MLP-PV 88-I-1-508, in labial view (**a**), basal view (**b**), lingual view (**c**) and occlusal view (**d**); *Squatina* sp., anterior teeth, MLP-PV 88-I-1-509, in labial view (**e**), basal view (**f**), lingual view (**g**) and occlusal view (**h**); **i–n**, *Pristiophorus* sp., rostral teeth from the middle part of the rostrum, left rostral tooth (MLP-PV 14-XI-27-305 in dorsal view (**i**) and basal view (**j**), MLP-PV 14-XI-27-302 in dorsal view (**k**) and basal view (**l**), MLP-PV 14-XI-27-303 in basal view (**m)** and dorsal view (**n**); **o–p**, *Pristiophorus* sp., rostral teeth from the middle part of the rostrum, right rostral tooth, MLP-PV 14-XI-27-304 in basal view (**o**) and dorsal view (**p**).

Squalus, *Squatina*, were recovered after intensive dry-sieving. It is worth to note that the diversity in this locality is higher than the diversity in modern cool temperate faunas and nearly equal to a present-day tropical fauna (Reguero et al., 2012). Interestingly, the occurrence of several taxa i.e., *Abdounia* sp., *Notoramphoscyllium woodwardi*, *Centrophorus* sp. in the Assemblage Na-horizon are absent in the rest of the assemblages of the *Cucullaea* I Allomember, so it could represent a collecting bias rather than a real pattern (Table S1).

The middle Eocene marine sediments of the La Meseta Formation have yielded a very diverse chondrichthyan fauna, with an abundance of epipelagic forms and large predators such as *Macrorhizodus praecursor*, *Striatolamia macrota*, and *Otodus* (*Carcharocles*). However, *Striatolamna macrota*, *Odontaspidaie* indet., *Myliobatis* sp., *Pristiophorus* sp, and *Squatina* sp., are most abundant in *Cucullaea* I Allomember (Figure S1 and Table S2).

The comparison of the chondrichthyan ichthyofauna studied here with the extant ichthyofauna allows us to estimate the paleoecology and paleoenvironments zonation for each taxon (Table 4). In general, many of these taxa correspond to shallow waters near the coast. However, there are also pelagic forms with a wide distribution, such as Lamniformes, and taxa living in open and deep waters like *Hexanchus* and *Dalatias licha* (Figure 9).

Stratigraphically the chondrichthyan material reviewed here is distributed unevenly between four main different shell beds (assemblages) of the *Cucullaea* I Allomember: 35Cu-horizon, Na-horizon, Cu-horizon, and Ly-horizon (Table S2). The Assemblage 35Cu-horizon (Figure 10) exhibits a higher abundance of coastal epipelagic forms, such as *Striatolamia macrota* and *Odontaspididae* indet., and to a lesser extent *Myliobatis* sp. and *Pristiophorus laevis*., primarily from the continental shelf. The highest number of *Otodus* (*Carcharocles*) teeth is recorded in this horizon (Table 3).

Figure 8 Remains of Rajiformes and Myliobatiformes. Rajidae, *Raja* sp. anterior tooth MLP-PV 90-I-20-418, in lingual view (**a**) and profile (**b**); Myliobatidae, *Myliobatis* sp. median tooth, MLP-PV 13-XI-28-562, occlusal view (**c**) and basal view (**d**); *Rhinoptera* sp. median tooth, MLP-PV 95-I-10-143, in occlusal view (**e**) and basal view (**f**). For **a–b**, 1 mm scale bar; for **c–f**, 1cm scale bar.

The Assemblage Na-horizon yields the most diverse and productive Paleogene chondrichthyan fauna from Antarctica (Figure 11) and probably from the Southern Hemisphere to date and provides a unique opportunity to study composition and faunal turnover in Eocene ecosystems (Kriwet, 2005; Kriwet et al., 2016). In turn, among the Na-horizon localities (IAA 1/90, IAA 1/95, IAA 2/95), IAA 1/90 is undoubtedly the most productive localities for sharks. The Na-horizon, is a shell bed not reworked, characterized by abundant coastal and estuarine forms i.e., *Squatina* sp., *Pristiophorus laevis*, *Striatolamna macrota* and *Squalus* spp. Other shallow water taxa, i.e., *Myliobatis* sp., *Raja* sp. and *Notoramphoscyllium woodwardi* are present in large quantities in this horizon (Figure 10). Carcharhiniformes, like *Abdounia* spp., *Kallodentis rhytistemma* and *Rhizoprionodon* sp, are also associated with shallow waters along the continental shelf and wide distribution species like *Ischyodus dolloi*, *Macrorhizodus praecursor*, and *Centrophorus* sp., associated with continental shelf and upper slope (Table 4). A single specimen of a basking shark, *Keasius* sp., (Reguero et al., 2013) with a wide range of zonation, is recorded in this level.

The Assemblage Cu-horizon contains the most commonly found taxa reported in the Assemblage Na-horizon (Figure 10). However, *Macrorhizodus praecursor* and Carcharhiniformes and *Raja* sp. are absent, but *Pristiophorus* and *Striatolamna macrota* are abundant, albeit with significantly fewer specimens (Table 3). It is worth noting that while the number of specimens found in the Cu-horizon is relatively small, the material is large (over 1 cm) making them easy to spot.

In the Assemblage Ly-horizon an intensive dry sieving was carried out; however, very few chondrichthyan materials were collected (Table 3). In Ly-horizon, the dominant species include *Pristiophorus laevis*, *Squatina* sp., and *S. macrota*, with a lower number of specimens compared to the previous level (Figure 10). Squaliformes such as *Squalus woodburnei* and *Eodalatias austrinalis* are present.

These data reveal a consistent and increasing prevalence of Lamniformes in the lower coquina levels of *Cucullaea* I (35Cu-horizon and Na-horizon), gradually decreasing towards the top (Cu-horizon and Ly-horizon). In general, *Striatolamna macrota, Squatina* sp., *Pristiophorus laevis*, and *Myliobatis* sp. dominate the assemblages, closely followed by squaliforms and *Raja* sp. Other groups, such as Orectolobiformes and Carcharhiniformes, are generally found in much smaller proportions (Table 3). The sporadic presence of some taxa such as *Hexanchus*,

Table 3 Chondrichthyans recovered from the *Cucullaea* I Allomember of the La Meseta Formation. The numbers indicate the number of specimens recovered

Taxa	TELM 4	TELM 5		
	(35Cu-horizon)	(Na-horizon)	(Cu-horizon)	(Ly-horizon)
Squalus sp.	1			1
Rhinoptera sp.	2	3		
Macrorhizodus sp.	1	4		
Otodus (*Carcharocles*)	5	2		
Macrorhizodus praecursor	5	7		
Odontaspis winkleri	1	22	1	
Striatolamia macrota	333	703	60	71
Odontaspididae indet.	121	185	85	1
Myliobatis sp.	30	493	35	15
Pristiophorus laevis	31	2326	68	126
Squatina sp.	8	2669	1	71
Squalus weltoni	1	275	2	3
Palaeohypotodus sp.	1	36	1	2
Ischyodus dolloi		2	1	1
Squalus woodburnei		417		3
Eodalatias austrinalis		9		1
Centrophorus sp.		1		
Notoramphoscyllium woodwardi		90		
Raja sp.		300		
Abdounia sp.		18		
Abdounia richteri		3		
Chimaeriformes indet.		6		
Kallodentis rhytistemma		4		
Rhizoprionodon sp.		1		
Keasius sp.		1		

Notes: The colors pale blue for the minor values (1–39), the light yellows (40–150) and the light oranges (151–1000) for middle values, and pale red for highest values (over 2000).

Table 4 Water column distribution of the reported chondrichthyans of the *Cucullaea* I Allomember of La Meseta Formation. Zonation according to Ebert (2021). Table modified from Kriwet et al. (2016)

Taxa	Living analogue	Zonation
Otodus (*Carcharocles*)	*Carcharodon carcharias*	Very shallow water inshore to the continental shelfs.
Keasius sp.	*Cetorhinnus maximus*	Coast to the continental shelves edge and slope/open marine.
Macrorhizodus praecursor	*Isurus oxyrhynchus*	Coastal and oceanic.
Raja sp.	*Bathyraja* sp.	Coastal to deep-water.
Squatina sp.	*Squatina squatina*	Inshore/coasts and stuaries on continental shelves.
Rhizoprionodon sp.	*Rhizoprionodon porosus*	Close inshore on continental and insular shelves and also offshore.
Notoramphoscyllium woodwardi	*Brachaelurus* spp.	Coral reef, sands between reefs and offshore sediments.
Striatolamia macrota	*Carcharias taurus*	Coastal waters/surf zone to offshore reefs.
Ischyodus dolloi	*Chimaera* spp.	Continental and insular shelves and uppermost slopes
Myliobatis sp.	*Myliobatis* sp.	Continental and insular shelves to offshore.

Continued

Taxa	Living analogue	Zonation
Abdounia sp.	*Carcharhinus* sp.	Continental and insular shelves to offshore.
Hexanchus sp.	*Hexanchus griseus*	Continental and island shelves and slope, seamounts and mid-ocean ridges.
Odontaspis winkleri	*Odontaspis ferox*	Continental and island shelves and upper slopes.
Squalus spp.	*Squalus acanthias*	Continental and island shelves.
Centrophorus sp.	*Centrophorus granulosus*	Continental shelves and slope.
Pristiophorus laevis	*Pristiophorus cirratus*	Continental shelves and upper slope.
Kallodentis rhytistemma	*Galeorhinus galeus*	Continental shelves.
Rhinoptera sp.	*Rhinoptera* sp.	Continental shelves.
Eodalatias austrinalis	*Dalatias licha*	Deep water/outer continental shelves and slopes.

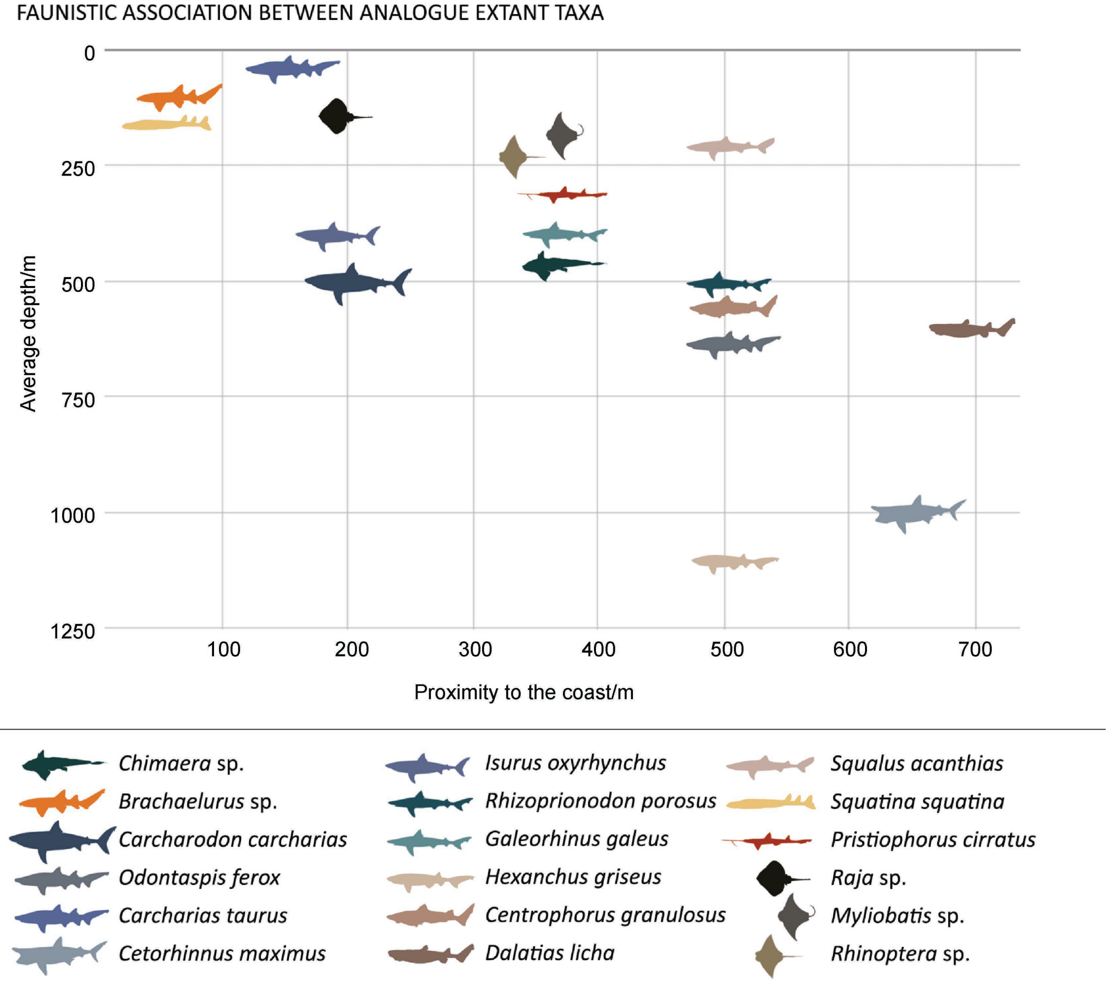

Figure 9 Environmental distribution of living analogs of chondrichthyans present in the *Cucullaea* I Allomember. The colored silhouettes depict the maximum ranges of proximity to the coast and depth inhabited by the living analogs of the taxa reported for *Cucullaea* I in this study. Zonation according to Ebert (2021).

typically from deep waters, milk sharks or basking shark, from the continental shelf and continental shelf edge and slope, as well as other species that currently inhabit from the coast to open waters, for example, *Carcharodon Carcharias* (analogous to *Otodus* (*Carcharocles*)) are present in a low number, they could be considered less representative of these associations.

As described by Long (1992) and other authors, the *Cucullaea* I Allomember of La Meseta Formation is primarily defined as an estuarine environment, aligning with the results obtained for the Na-horizon (estuarine, and continental shelf environment). The Assemblage Na-horizon might represent an environment slightly farther from the coast and potentially warmer waters, considering

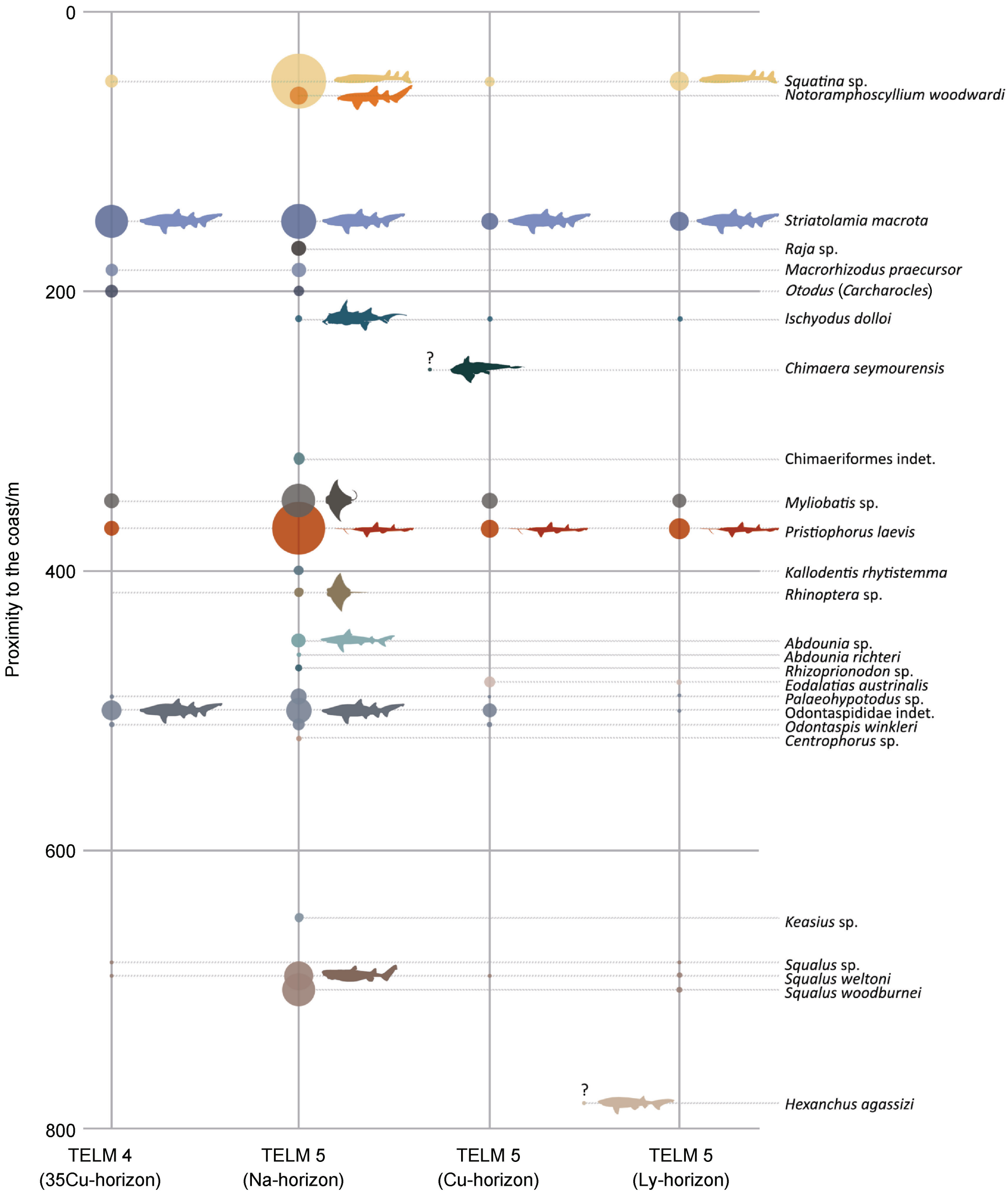

Figure 10 Taxonomic assemblages proposed for the four coquina levels based on the distribution of current equivalent taxa or their present representatives. The question mark applies to those specimens whose location cannot be directly related to any coquina level. The size of the dots indicates their density, quantified by the number of specimens. The vertical axis depicts the approximate proximity to the coast.

the presence of taxa such as *Eodalatias austrinalis*, *Rhinoptera* sp. and *Centrophorus*, which are currently associated with warm temperate and tropical waters, nonetheless, are extremely infrequent and might be no-representative, such as *Hexanchus* and holocephalans. Finally, the Assemblages Cu-horizon and Ly-horizon may be linked to a coastal environment. However, it exhibits significant numerical impoverishment and a decrease in taxonomic diversity. It is necessary to consider that most sharks can migrate along coasts seeking the right temperature throughout the year. Open water and/or deep-water taxa on coasts appear sporadically.

Taxonomic composition, habitat preferences and palaeobathymetric analyses support the hypothesis that these assemblages occupied temperate marine shallow waters (likely up to 50 m deep) of the inner portion of the James Ross Basin. The taxonomic composition of the four assemblages is considerably different from that of any other contemporaneous chondrichthyan assemblages.

Figure 11 A life reconstruction of chondrichthyan taxa from *Natica* level of the La Meseta Formation (Artwork by Martina Charnelli).

The early Eocene Climatic Optimum event that occurred approximately between 51 Ma and 53 Ma ago at the onset of the Campamento Allomember (Figure 2) and persisted until the *Cucullaea* I Allomember. The temperature of 15 ℃ inferred for this period could somehow explain the high diversity exhibited. Subsequently, in the middle Eocene, specifically at the boundary between *Cucullaea* I and *Cucullaea* II (Figure 2), there was an estimated temperature decrease of around 10 ℃, as indicated by Ivany et al. (2008). This event surely had an effect on organisms more sensitive to specific conditions of salinity, pH, and temperature, prompting them to migrate.

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Supplementary Tables, Figure and Appendix

Table S1 List of chondrichthyan taxa present four assemblages from the *Cucullaea* I Allomember of the La Meseta Formation, Seymour Island, Antarctica

TELM 4	TELM 5		
(35Cu-horizon)	(Na-horizon)	(Cu-horizon)	(Ly-horizon)
Squalus sp.			*Squalus* sp.
Rhinoptera sp.	*Rhinoptera* sp.		
Macrorhizodus sp.	*Macrorhizodus* sp.		
Otodus (*Carcharocles*)	*Otodus* (*Carcharocles*)		
Macrorhizodus praecursor	*Macrorhizodus praecursor*		
Odontaspis winkleri	*Odontaspis winkleri*	*Odontaspis winkleri*	
Striatolamia macrota	*Striatolamia macrota*	*Striatolamia macrota*	*Striatolamia macrota*
Odontaspididae indet.	Odontaspididae indet.	Odontaspididae indet.	Odontaspididae indet.
Myliobatis sp.	*Myliobatis* sp.	*Myliobatis* sp.	*Myliobatis* sp.
Pristiophorus laevis	*Pristiophorus laevis*	*Pristiophorus laevis*	*Pristiophorus laevis*
Squatina sp.	*Squatina* sp.	*Squatina* sp.	*Squatina* sp.
Squalus weltoni	*Squalus weltoni*	*Squalus weltoni*	*Squalus weltoni*
Palaeohypotodus sp.	*Palaeohypotodus* sp.	*Palaeohypotodus* sp.	*Palaeohypotodus* sp.
	Ischyodus dolloi	*Ischyodus dolloi*	*Ischyodus dolloi*
	Squalus woodburnei		*Squalus woodburnei*
	Eodalatias austrinalis		*Eodalatias austrinalis*
	Centrophorus sp.		
	Notoramphoscyllium woodwardi		
	Raja sp.		
	Abdounia sp.		
	Abdounia richteri		
	Chimaeriformes indet.		
	Kallodentis rhytistemma		
	Rhizoprionodon sp.		
	Keasius sp.		

Table S2 The percentage of chondrichthyan specimens present in four assemblages from the *Cucullaea* I Allomember of the La Meseta Formation, Seymour Island, Antarctica

Taxa	TELM 4	TELM 5		
	(35Cu-horizon)	(Na-horizon)	(Cu-horizon)	(Ly-horizon)
Squalus sp.	0.01%			0.01%
Rhinoptera sp.	0.02%	0.03%		
Macrorhizodus sp.	0.01%	0.05%		
Otodus (*Carcharocles*)	0.06%	0.02%		
Macrorhizodus praecursor	0.06%	0.08%		
Odontaspis winkleri	0.01%	0.25%	0.01%	
Striatolamia macrota	3.84%	8.11%	0.69%	0.82%
Odontaspididae indet.	1.40%	2.13%	0.98%	0.01%
Myliobatis sp.	0.35%	5.69%	0.40%	0.17%

Continued

Taxa	TELM 4	TELM 5		
	(35Cu-horizon)	(Na-horizon)	(Cu-horizon)	(Ly-horizon)
Pristiophorus laevis	0.36%	26.84%	0.78%	1.45%
Squatina sp.	0.09%	30.80%	0.01%	0.82%
Squalus weltoni	0.01%	3.17%	0.02%	0.03%
Palaeohypotodus sp.	0.01%	0.42%	0.01%	0.02%
Ischyodus dolloi		0.02%	0.01%	0.01%
Squalus woodburnei		4.81%		0.03%
Eodalatias austrinalis		0.10%		0.01%
Centrophorus sp.		0.01%		
Notoramphoscyllium woodwardi		1.04%		
Raja sp.		3.46%		
Abdounia sp.		0.21%		
Abdounia richteri		0.03%		
Chimaeriformes indet.		0.07%		
Kallodentis rhytistemma		0.05%		
Rhizoprionodon sp.		0.01%		
Keasius sp.		0.01%		

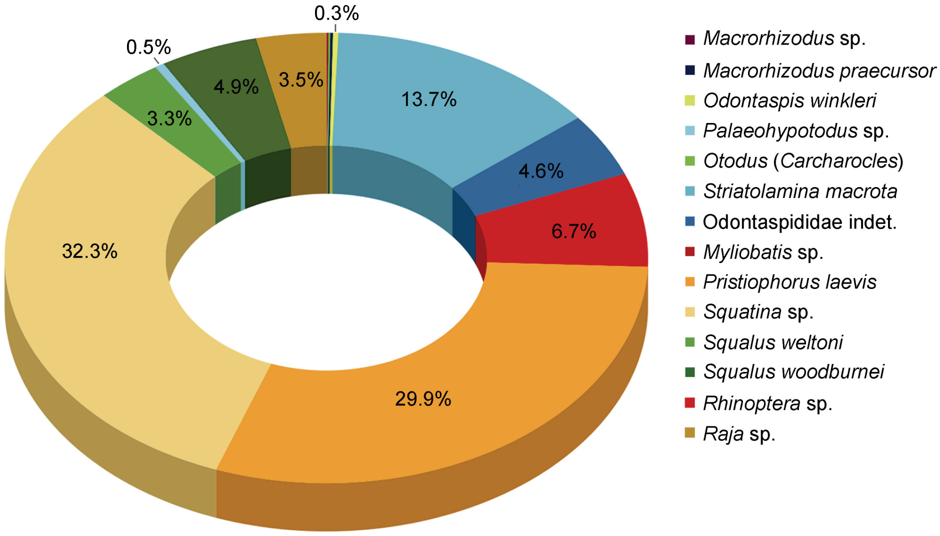

Figure S1 The percentage of chondrichthyan specimens present in the *Cucullaea* I Allomember.

Appendix Referred material list

Order Chimaeriformes Patterson, 1955
Family Callorhynchidae Garman, 1901
Genus *Ischyodus* Egerton, 1843

Ischyodus Dolloi Leriche, 1902

Referred material:
MLP-PV 90-I-20-265, 1 dental plate.
Locality DPV 9/84

MLP-PV 96-I-5-76, 1 dental plate.
Locality DPV 6/84.

MLP-PV 92-II-4-88, 1 dental plate (Figures 3a–3b).
Locality IAA 1/90

Chimaeriformes indet.

Referred material:
MLP-PV 94-III-15-171, 1 dental plate (Figure 3c).
Locality IAA 2/94

MLP-PV 95-I-10-100, batch of 2 dental plates.
Locality IAA 1/90

MLP-PV 95-I-10-241, batch of 4 dental plates.
Locality IAA 2/95

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Order Orectolobiformes Applegate, 1972
Family Hemiscylliidae Gill, 1862
Genus *Notoramphoscyllium* Engelrecht et al., 2016

Notoramphoscyllium woodwardi Engelrecht et al., 2016

Referred material:
MLP-PV 90-I-20-401, batch of 71 teeth.
MLP-PV 92-II-2-21, 1 tooth (Figures 3g–3i).
MLP-PV 94-III-15-135, 2 teeth.
MLP-PV 94-III-15-516, 1 tooth (Figures 3j–3k).
MLP-PV 95-I-10-107, 6 teeth.
MLP-PV 95-I-10-202, 4 teeth.
MLP-PV 95-I-10-290, 1 tooth (Figures 3d–3f).
MLP-PV 96-I-5-59, 3 teeth.
Locality IAA 1/90

MLP-PV 96-I-5-53, 1 tooth.
Locality IAA 2/95

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Order Lamniformes Berg, 1958
Family Otodontidae Glickman, 1964
Genus *Otodus* Agassiz, 1843

Otodus (*Carcharocles*) Jordan and Hannibal, 1923

Referred material:
MLP-PV 91-II-4-190, 1 tooth.
MLP-PV 91-II-4-194, 1 tooth.
Locality DPV 2/84

MLP-PV 91-II-4-199/200, 2 teeth.

MLP-PV 92-II-2-7a, 1 tooth.
Locality DPV 5/84
MLP-PV 94-III-15-145, 1 tooth (Figures 4a–4b).
MLP-PV 94-III-15-35, 1 tooth.
Locality IAA 1/90

Family Odontaspididae Müller and Henle, 1838
Genus *Odontaspis* Agassiz, 1843

Odontaspis winkleri Leriche, 1905

Referred material:
MLP-PV 94-III-15-217, 1 tooth.
Locality DPV 5/84
MLP-PV 91-II-4-259, 1 tooth.
Locality DPV 9/84
MLP-PV 96-I-5-95, batch of 21 teeth.
MLP-PV 94-III-15-523 1 tooth (Figures 4c–4d).
Locality IAA 1/90

Genus *Striatolamia* Glickman, 1964

Striatolamia macrota Agassiz, 1843

Referred material:
MLP-PV 84-II-1-571, 5 teeth.
MLP-PV 88-I-1-489, batch of 27 teeth.
MLP-PV 89-III-2-42, 7 teeth.
MLP-PV 90-I-20-312, 5 teeth.
MLP-PV 91-II-4-180, 1 tooth (Figure 4e–4f).
MLP-PV 91-II-4-201, 3 teeth.
MLP-PV 92-II-2-120, 9 teeth.
MLP-PV 92-II-2-127, batch of 103 teeth.
MLP-PV 92-II-2-132, batch of 12 teeth.
MLP-PV 94-III-15-103, batch of 18 teeth.
Locality DPV 2/84

MLP-PV 92-II-2-147, 2 teeth.
MLP-PV 93-X-1-163, 1 tooth.
Locality IAA 1/92

MLP-PV 92-II-2-140, batch of 67 teeth.
MLP-PV 94-III-15-213, batch of 71 teeth.
MLP-PV 94-III-15-216, 2 teeth.
Locality DPV 5/84

MLP-PV 88-I-1-193/196, 4 teeth.
MLP-PV 90-I-20-301, batch of 43 teeth.
MLP-PV 95-I-10-174, 3 teeth.
Locality DPV 1/84

MLP-PV 90-I-20-412, 5 teeth.
MLP-PV 91-II-4-147, 39 teeth.
MLP-PV 91-II-4-156, 29 broken teeth.
MLP-PV 92-II-2-93, 4 teeth.
MLP-PV 92-II-2-105, batch of 57 teeth.
MLP-PV 92-II-2-116, batch of 31 teeth.
MLP-PV 92-II-2-153, 4 teeth.
MLP-PV 92-II-2-154, 8 teeth.
MLP-PV 94-III-15-111, batch of 11 teeth.
MLP-PV 94-III-15-137, 2 teeth.
MLP-PV 94-III-15-191, 2 teeth.
MLP-PV 94-III-15-193, batch of 64 teeth.
MLP-PV 94-III-15-198, batch of 147 teeth.
MLP-PV 94-III-15-241, 7 teeth.
MLP-PV 95-I-10-105, batch of 33 teeth.
MLP-PV 96-I-5-33, batch of 52 teeth.
MLP-PV 12-I-20-317, 1 tooth.
MLP-PV 12-I-20-318, 2 teeth.
Locality IAA 1/90

MLP-PV 13-XI-28-72, 3 teeth.
MLP-PV 13-XI-28-82, batch of 10 teeth.
Locality IAA 1/95

MLP-PV 95-I-10-33/69, batch of 37 teeth.
MLP-PV 95-I-10-79, batch of 68 teeth.
MLP-PV 96-I-5-14, batch of 74 teeth.
MLP-PV 12-I-20-321, 1 tooth.
MLP-PV 13-XI-28-76, batch of 12 teeth.
Locality IAA 2/95

MLP-PV 89-III-2-3/12, batch of 10 teeth.
MLP-PV 91-II-4-204, batch of 34 teeth.
Locality DPV 9/84

MLP-PV 94-III-15-30/33, 4 teeth.
MLP-PV 94-III-15-36/47, 12 teeth.
Locality IAA 2/90

MLP-PV 88-I-1-365, batch of 27 teeth.
MLP-PV 90-I-20-293, 6 teeth.
MLP-PV 91-II-4-121/128, 9 teeth.
MLP-PV 94-III-15-99, 3 teeth.
MLP-PV 95-I-10-82/83, 2 teeth.
MLP-PV 13-XI-28-38, 7 teeth.
Locality DPV 6/84

MLP-PV 13-XI-28-111, batch of 10 teeth.
MLP-PV 14-I-10-180, 6 tooth.
MLP-PV 14-I-10-203, 1 tooth (Figures 4g–4h).
Locality IAA 2/13

Odontaspididae indet.

Referred material:
MLP-PV 84-II-1-575, 1 tooth.
MLP-PV 88-I-1-500, 6 teeth.
MLP-PV 89-III-2-44, 1 tooth
MLP-PV 92-II-2-124, 4 teeth.
MLP-PV 92-II-2-160, 2 teeth.
MLP-PV 92-II-2-162, batch of 56 teeth.
Locality DPV 2/84

MLP-PV 88-I-1-76/77, 2 teeth.
MLP-PV 90-I-20-113/114, 2 teeth.
MLP-PV 90-I-20-322, 2 teeth.
MLP-PV 90-I-20-323, batch of 33 teeth.
MLP-PV 91-II-4-268, 3 teeth.
MLP-PV 91-II-4-269, batch of 30 teeth.
MLP-PV 91-II-4-270, batch of 56 teeth.
MLP-PV 92-II-2-142, 2 teeth.
MLP-PV 92-II-2-163, 2 teeth.
MLP-PV 94-III-15-195, batch of 18 teeth.
MLP-PV 94-III-15-261, 8 teeth.
MLP-PV 94-III-15-262, 8 teeth.
MLP-PV 94-III-15-263, 6 teeth.
Locality IAA 1/90

MLP-PV 92-II-2-137, 2 teeth.
MLP-PV 92-II-2-161, batch of 12 teeth.
MLP-PV 94-III-15-256, batch of 36 teeth.
Locality DPV 5/84.

MLP-PV 90-I-20-320, batch of 33 teeth.
Locality DPV 1/84

MLP-PV 92-II-2-122, 1 tooth.
Locality IAA 1/92

MLP-PV 96-I-5-54, batch of 11 teeth.
MLP-PV 13-XI-28-76, 2 teeth.
Locality IAA 2/95

MLP-PV 91-II-4-266, batch of 14 teeth.
MLP-PV 88-I-1-499, 5 teeth.
Locality DPV 9/84

MLP-PV 91-II-4-255, 1 tooth.
Locality DPV 6/84

Family Jaekelodontidae Glickman, 1964
Genus *Palaeohypotodus* Glickman, 1964

Palaeohypotodus sp.

Referred material:
MLP-PV 88-I-1-76, 1 tooth (Figures 4k–4l).
MLP-PV 88-I-1-77, 1 tooth.
Locality DPV 6/84

MLP-PV 94-III-15-48, 1 tooth.
Locality IAA 2/90

MLP-PV 94-III-15-215, 1 tooth
Locality DPV 5/84.

MLP-PV 95-I-10-70/77, 8 teeth.
Locality IAA 2/95

MLP-PV 91-II-4-165, 1 tooth (Figures 4i–4j).
MLP-PV 91-II-4-166, 1 tooth.
MLP-PV 92-II-2-9/10, 2 teeth.
MLP-PV 92-II-2-73, batch of 14 teeth.
MLP-PV 94-III-15-129, 1 tooth.
MLP-PV 95-I-10-104, 5 teeth.
MLP-PV 96-I-5-93, 4 teeth.
Locality IAA 1/90

Family Cetorhinidae Gill, 1862
Genus *Keasius* Welton, 2013

Keasius sp.

Referred material:
MLP-PV 96-I-5-42, proximal fragment of a gill raker (Figure 4m).
Locality IAA 1/90

Family Lamnidae Müller and Henle, 1838
Genus *Macrorhizodus* Glickman, 1964

Macrorhizodus sp.

Referred material:
MLP-PV 92-II-2-28/30, 3 teeth.
MLP-PV 95-I-10-188, 1 tooth.
Locality IAA 1/90

MLP-PV 92-II-2-123, 1 tooth.
Locality IAA 1/92

Macrorhizodus praecursor Leriche, 1905

Referred material:
MLP-PV 91-II-4-167/168, 2 good teeth.
Locality DPV 2/84

MLP-PV 94-III-15-153, 1 tooth.
MLP-PV 96-I-5-57, 4 teeth.
MLP-PV 94-III-15-517, lower anterior tooth (Figures 4n–4o)
Locality IAA 2/95

MLP-PV 78-X-26-43, 1 tooth.
MLP-PV 91-II-4-169, 1 tooth.
MLP-PV 91-II-4-209, 1 tooth.
Locality DPV 5/84

MLP-PV 94-III-15-190, 1 tooth.
Locality IAA 1/90

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Order Carcharhiniformes Compagno, 1973
Family Triakidae Gray 1851
Genus *Kallodentis* Engelbrecht et al., 2017a

Kallodentis rhytistemma Engelbrecht et al., 2017a

Referred material:
MLP-PV 94-III-15-521 1 tooth (Figures 5a–5b).
MLP-PV 94-III-15-544, 1 tooth (Figures 5c–5d).
MLP-PV 95-I-10-169, 1 tooth.
MLP-PV 96-I-5-65, 1 tooth.
Locality IAA 1/90

Family Carcharhinidae Jordan and Evermann, 1896
Genus *Abdounia* Cappetta, 1980

Abdounia sp.

Referred material:
MLP-PV 90-I-20-142, 1 tooth.
MLP-PV 90-I-20-396, 1 tooth.
MLP-PV 91-II-2-162, 1 tooth.
MLP-PV 94-III-15-250, 1 tooth.
MLP-PV 94-III-15-512, 1 tooth of *Abodunia* and 1 tooth of *Odontaspis* sp.
MLP-PV 95-I-10-205, 4 teeth.
MLP-PV 96-I-5-66, 7 teeth.
MLP-PV 96-I-6-7, 1 broken tooth.
Locality IAA 1/90

Abdounia richteri Engelbrecht et al., 2017b

Referred material:
MLP-PV 94-III-15-518, 1 anterior tooth (Figures 5e–5f).
MLP-PV 94-III-15-519 1 anterior tooth (Figures 5g–5h).
MLP-PV 94-III-15-520 1 anterior tooth.
Locality IAA 1/90

Genus *Rhizoprionodon* Whitley, 1929

Rhizoprionodon sp.

Referred material:
MLP-PV 96-I-5-89, a (?upper) lateral tooth (Figures 5i–5j).
Locality IAA 1/90

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Order Hexanchiformes Buen, 1926
Family Hexanchidae Gray, 1851
Genus *Hexanchus* Rafinesque, 1810

Hexanchus agassizi Cappetta, 1976

Referred material:
MLP-PV 88-I-1-384, incomplete isolated lower left lateral tooth (Figures 6a–6b).
Locality DPV 8/84

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

Centrophorus sp.

Referred material:
MLP-PV 91-II-4-159, 1 tooth (Figures 6c–6d).
Locality IAA 1/90

Family Dalatiidae Gray, 1851
Genus *Eodalatias* Engelbrecht, 2017c

Eodalatias austrinalis Engelbrecht, 2017c

Referred material:
MLP-PV 91-II-4-253, 1 tooth.
Locality DPV 6/84

MLP-PV 94-III-15-133, 8 teeth.
MLP-PV 94-III-15-522 (Figures 6e–6f), lower left lateral tooth.
Locality IAA 1/90

Family Squalidae Bonaparte, 1838
Genus *Squalus* Linnaeus, 1758

Squalus sp.

Referred material:
MLP-PV 94-III-15-101, 1 tooth.
Locality DPV 2/84

MLP-PV 88-I-1-368, 1 tooth.
Locality DPV 6/84

Squalus weltoni Long, 1992

Referred material:
MLP-PV 92-II-2-94, 41 teeth.
MLP-PV 96-I-5-98, batch of 30 teeth.
MLP-PV 92-II-2-159, batch of 86 teeth.
MLP-PV 95-I-10-109, batch of 30 teeth.
MLP-PV 95-I-10-212, 11 teeth.
MLP-PV 95-I-10-215, batch of 24 teeth.
MLP-PV 95-I-20-291, 1 tooth (Figures 6g–6h).
MLP-PV 95-I-20-292, 1 tooth (Figures 6i–6j).
MLP-PV 95-I-10-293, 1 tooth (Figures 6k–6l).
MLP-PV 95-I-20-294, 1 tooth (Figures 6m–6n).
Locality IAA 1/90

MLP-PV 88-I-1-201, 1 tooth.
Locality DPV 1/84

MLP-PV 88-I-1-495, 3 teeth.
Locality DPV 6/84

MLP-PV 94-III-15-208, 1 tooth.
Locality DPV 5/84

MLP-PV 94-III-15-50, 1 tooth.
Locality IAA 2/90

MLP-PV 96-I-5-41, batch of 49 teeth.
Locality IAA 2/95

Squalus woodburnei Long, 1992

Referred material:
MLP-PV 88-I-1-494, 3 teeth.
Locality DPV 6/84

MLP-PV 90-I-20-399, batch of 22 teeth.
MLP-PV 90-I-20-419, 1 tooth (Figures 6q–6r).
MLP-PV 90-I-20-421, 1 tooth (Figures 6o–6p).
MLP-PV 91-II-4-154, 365 teeth.
MLP-PV 91-II-4-261, 4 teeth.
MLP-PV 92-II-2-125, 3 teeth.
MLP-PV 92-II-2-158, 6 teeth.
MLP-PV 95-I-10-85, 2 teeth.
MLP-PV 96-I-5-34, batch of 11 teeth.
MLP-PV 96-I-5-97, 2 teeth.
Locality IAA 1/90

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Order Squatiniformes Buen, 1926
Family Squatinidae Bonaparte, 1838
Genus *Squatina* Dumeril, 1806

Squatina sp.

Referred material:
MLP-PV 83-V-20-382/383, 2 teeth.
MLP-PV 92-II-2-128, 4 teeth.
MLP-PV 95-I-10-146, 2 teeth.
Locality DPV 2/84

MLP-PV 88-I-1-209, damaged tooth.
Locality DPV 1/84

MLP-PV 90-I-20-68-85, batch of 18 teeth.
MLP-PV 91-II-4-154, batch of 365 teeth.
MLP-PV 91-II-4-241, 2 teeth.
MLP-PV 92-II-2-103, batch of 550 teeth.
MLP-PV 92-II-2-25/27, 3 teeth.
MLP-PV 92-II-2-86/87, 2 teeth.
MLP-PV 94-III-15-112, batch of 675 teeth.
MLP-PV 94-III-15-123, 2 teeth.
MLP-PV 94-III-15-143, batch of 19 teeth.
MLP-PV 94-III-15-239, 1 tooth.
MLP-PV 95-I-10-108, batch of 178 teeth.
MLP-PV 95-I-10-170, 1 tooth.
MLP-PV 95-I-10-209, batch of 48 teeth.
MLP-PV 96-I-5-26, batch of 324 teeth.
MLP-PV 96-I-6-9, 1 tooth.
Locality IAA 1/90

MLP-PV 89-III-2-19/21, 3 teeth.
MLP-PV 12-I-20-322, batch of 17 teeth.
MLP-PV 14-XI-27-268, batch of 19 teeth.
MLP-PV 95-I-10-78, batch of 283 teeth.
MLP-PV 96-I-5-40, batch of 157 teeth.
Locality IAA 2/95

MLP-PV 90-I-20-285/286, 2 teeth.
Locality DPV 9/84

MLP-PV 13-XI-28-82, 1 tooth.
Locality IAA 1/95

MLP-PV 87-II-1-35, 1 tooth.
MLP-PV 88-I-1-369, batch of 55 teeth.
MLP-PV 88-I-1-373, 4 teeth.
MLP-PV 88-I-1-508, 1 tooth (Figures 7a–7d).
MLP-PV 88-I-1-509, 1 tooth (Figures 7e–7h).
MLP-PV 90-I-20-300, 4 teeth.
MLP-PV 91-II-4-250, 3 teeth.
MLP-PV 95-I-10-31/32, 2 teeth.
Locality DPV 6/84

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Order Pristiophoriformes Berg, 1958
Family Pristiophoridae Bleeker, 1859

Genus *Pristiophorus* Müller and Henle, 1837

Pristiophorus laevis Engelrecht et al., 2017a

Referred material:

MLP-PV 91-II-4-28, 1 rostral tooth.
MLP-PV 92-II-2-126, 12 rostral teeth.
MLP-PV 95-I-10-147, 3 rostral teeth.
Locality DPV 2/84

MLP-PV 94-III-15-207, 15 rostral teeth.
Locality DPV 5/84
MLP-PV 88-I-1-197/200, 4 rostral teeth.
MLP-PV 90-I-20-303, 9 rostral teeth.
MLP-PV 95-I-10-177, 1 rostral tooth.
Locality DPV 1/84

MLP-PV 90-I-20-402, batch of 31 rostral teeth.
MLP-PV 91-II-4-155, batch of 205 rostral teeth.
MLP-PV 91-II-4-243, 2 rostral teeth.
MLP-PV 92-II-2-106, batch of 389 rostral teeth.
MLP-PV 92-II-2-117, 1 rostral tooth.
MLP-PV 94-III-15-110, batch of 496 rostral teeth.
MLP-PV 94-III-15-188, 3 rostral teeth.
MLP-PV 94-III-15-513, 8 rostral teeth.
MLP-PV 95-I-10-112, batch of 81 rostral teeth.
MLP-PV 95-I-10-208, 19 rostral teeth.
MLP-PV 95-I-10-87, batch of 130 rostral teeth.
MLP-PV 96-I-5-27, batch of 127 rostral teeth.
MLP-PV 96-I-5-68, 4 rostral teeth.
MLP-PV 96-I-5-92, 19 rostral teeth.
MLP-PV 12-I-20-315, 2 rostral teeth.
MLP-PV 13-XI-28-325, batch of 22 rostral teeth.
MLP-PV 13-XI-28-529, 2 rostral teeth.
MLP-PV 13-XI-28-530, 6 rostral teeth.
MLP-PV 14-I-10-164, 1 rostral tooth.
Locality IAA 1/90

MLP-PV 95-I-10-81, batch of 416 rostral teeth.
MLP-PV 96-I-5-13, batch of 253 rostral teeth.
MLP-PV 08-XI-30-214, batch of 22 rostral teeth.
MLP-PV 12-I-20-323, 13 damaged rostral teeth.
MLP-PV 13-XI-28-78, batch of 10 rostral teeth.
MLP-PV 13-XI-28-321, 12 rostral teeth.
MLP-PV 14-I-10-157, 4 rostral teeth.
MLP-PV 14-XI-27-264, batch of 36 rostral teeth.
MLP-PV 14-XI-27-302, 1 rostral tooth (Figures 7 k–7l).
MLP-PV 14-XI-27-303, 1 rostral tooth (Figures 7m–7n).
MLP-PV 14-XI-27-304, 1 rostral tooth (Figures 7o–7p).
MLP-PV 14-XI-27-305, 1 rostral tooth (Figures 7i–7j).
MLP-PV 14-I-10-191, 8 rostral teeth.
Locality IAA 2/95

MLP-PV 90-I-20-284, batch of 12 rostral teeth.
MLP-PV 91-II-4-207, 28 rostral teeth.
MLP-PV 91-II-4-245, 1 rostral tooth.
Locality DPV 9/84

MLP-PV 94-III-15-34, 13 broken rostral teeth.
Locality IAA 2/90

MLP-PV 87-II-1-36, 1 rostral tooth.
MLP-PV 88-I-1-364, batch of 57 rostral teeth.
MLP-PV 88-I-1-490, 2 rostral teeth.
MLP-PV 90-I-20-299, batch of 11 rostral teeth.
MLP-PV 91-II-4-134/139, 6 rostral teeth.
MLP-PV 91-II-4-249, 5 rostral teeth.
MLP-PV 94-III-15-100, 3 rostral teeth.
MLP-PV 95-I-10-24/30, 6 rostral teeth.
MLP-PV 13-XI-28-38, 1 rostral tooth.
MLP-PV 13-XI-28-351, 3 rostral teeth.
Locality DPV 6/84

MLP-PV 14-I-10-72, 2 rostral teeth.
MLP-PV 14-I-10-96, 3 rostral teeth.
MLP-PV 14-XI-27-272, batch of 26 rostral teeth.
Locality IAA 2/13

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Order Rajiformes Berg, 1937
Family Rajidae Blainville, 1816
Genus *Raja* Linnaeus, 1758

Raja sp.

Referred material:

MLP-PV 90-I-20-404, 270 teeth.
MLP-PV 90-I-20-418, 1 tooth (Figures 8a–8b).
MLP-PV 92-II-2-42/70, batch of 29 teeth.
Locality IAA 1/90

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Order Myliobatiformes Compagno, 1973
Family Myliobatidae Bonaparte, 1838

Genus *Myliobatis* Cuvier, 1817

Myliobatis sp.

Referred material:
MLP-PV 84-II-1-170a, 1 dental plate.
MLP-PV 91-II-4-181/183, 6 dental plates.
MLP-PV 94-III-15-226, 1 dental plate.
Locality DPV 2/84

MLP-PV 94-III-15-212, 22 dental plates.
Locality DPV 5/84

MLP-PV 88-I-1-208, 1 dental plate.
Locality DPV 1/84

MLP-PV 90-I-20-287, 30 dental plates.
MLP-PV 91-II-4-197, 4 dental plates.
Locality DPV 9/84

MLP-PV 84-II-1-574, 2 dental plates.
MLP-PV 87-II-1-33, 1 dental plate.
MLP-PV 88-I-1-35/43, 9 dental plates.
MLP-PV 94-III-15-232, 2 dental plates.
MLP-PV 96-I-5-75, 1 dental plate.
Locality DPV 6/84

MLP-PV 92-II-2-85, 19 lateral dental plates.
MLP-PV 92-II-2-151, 2 dental plates.
MLP-PV 94-III-15-132, 2 dental plates.
MLP-PV 94-III-15-144, 37 teeth.
MLP-PV 94-III-15-194, batch of 166 dental plates.
MLP-PV 94-III-15-197, 7 dental plates, 1 tooth.
MLP-PV 94-III-15-243, 8 dental plates.
MLP-PV 95-I-10-113, 88 dental plates.
MLP-PV 95-I-10-166, 1 tooth.
MLP-PV 95-I-10-206, 3 dental plates, 4 teeth from Rajidae indet.
MLP-PV 96-I-6-8, 1 dental plate.
MLP-PV 96-I-5-90, 1 dental plate.
Locality IAA 1/90

MLP-PV 95-I-10-246, batch of 83 complete and fragmented dental plates.
MLP-PV 96-I-5-16, batch of 69 dental plates.
Locality IAA 2/95

MLP-PV 13-XI-28-562, dental plate (Figures 8c–8d).
Locality IAA 1/95

Family Rhinopteridae Jordan and Evermann, 1896
Genus *Rhinoptera* Cuvier, 1829

Rhinoptera sp.

Referred material:
MLP-PV 91-II-4-189, 1 dental plate.
MLP-PV 95-I-10-143, 1 dental plate (Figures 8e–8f).
Locality DPV 2/84

MLP-PV 13-XI-28-339, 3 dental plates.
Locality IAA 1/90