

THE SOUTHERNMOST OCCURRENCE OF *BRACHYCARCHARIAS* (LAMNIFORMES, ODONTASPIDIDAE) FROM THE EOCENE OF ANTARCTICA PROVIDES NEW INFORMATION ABOUT THE PALEOBIOGEOGRAPHY AND PALEOBIOLOGY OF PALEOGENE SAND TIGER SHARKS

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Abstract. The first record of one of the most common and widespread Paleogene selachians, the sand tiger shark *Brachycarcharias*, in the Ypresian strata of the La Meseta Formation, Seymour Island, Antarctica, is provided herein. Selachians from the early Eocene horizons of this deposit represent the southernmost Paleogene occurrences in the fossil record, and are represented by isolated teeth belonging to orectolobiforms, lamniforms, carcharhiniforms, squatiniforms and pristiphoriforms. The combination of dental characters of the 49 isolated teeth collected from the horizons TELMs 2, 4 and 5 supports their assignment to the odontaspidae *Brachycarcharias lerichei* (Casier, 1946), a lamniform species widely spread across the Northern Hemisphere during the early Paleogene. The unambiguous first report of this lamniform shark in the Southern Hemisphere in the Eocene of the La Meseta Formation improves our knowledge concerning the diversity and paleobiology of the cartilaginous fishes of this deposit, and provides new insights about the biotic turnovers that involved the high trophic levels of the marine settings after the end-Cretaceous extinction and before the establishment of the modern marine ecosystems.

INTRODUCTION

Living sand tiger sharks of the possibly paraphyletic family Odontaspidae include three large sized species within the order Lamniformes, today inhabiting marine tropical outer shelf and mesopelagic habitats (*Carcharias taurus*) and cool-water inner shelf habitats (*Odontaspis ferox* and *O. noronhai*) of the Atlantic, Indian, and Pacific oceans (Compagno 1984, 2002; Cappetta 2012; Nelson et al. 2016). Although recent morphological and molecular analyses suggested that Odontaspidae might not be monophyletic (e.g., Shimada 2005; Martin et al. 2002;

Naylor et al. 2012), several authors have recognized a set of plesiomorphic characters that are traditionally used to distinguish sand tiger sharks from all other lamniforms, including a short to moderately long, conical or slightly depressed snout, weakly protrusible jaws, first dorsal fin in front of the pelvic origin, last gill-slit in front of the pectoral origin, 156 to 183 vertebral centra, monognathic tooth heterodonty, tearing-type dentition, teeth arranged in less than 60 rows in each jaw having a tall and slender main cusp, one to three pairs of lateral cusplets, and a root with well-separated lobes and marked by a strong nutritive furrow (Compagno 1999, 2002; Cappetta 2012; Nelson et al. 2016).

Although *Carcharias* and *Odontaspis* are the only genera having modern representatives within

this family (Compagno 1999; Nelson et al. 2016), the odontaspimid fossil record has a wide temporal and geographic distribution, being indeed comprised of at least 20 extinct genera with more than 50 species dating back to the Lower Cretaceous (Cappetta 2012; Shimada et al. 2015; Cappetta & Case 2016). Selachians from Paleogene sites, such as the La Meseta Formation on Seymour Island (NE of the Antarctic Peninsula), are of utmost importance for understanding of the general patterns of abiotic disruptions during the Paleogene. In fact, these predators can document profound changes and turnovers in marine ecosystems in concomitance to the Paleocene – Eocene Thermal Maximum (PETM; ca. 55.5 Ma) and subsequent cooling phase towards the establishment of the Antarctic ice sheet. PETM was followed by a middle to late Eocene transition from the greenhouse world to icehouse conditions (ca. 49–34 Ma) with marked deep-sea cooling of about 7°C (e.g., Zachos et al. 2001, 2008; Miller et al. 2005). The final cooling phase across the Eocene – Oligocene (E–O) boundary (ca. 33.7 Ma) resulted in the disappearance of chondrichthyans from Antarctica (e.g., Kriwet et al. 2016). The vertebrate fossils of the La Meseta Formation are mainly represented by cartilaginous fishes, which seemingly represents the major faunal components of the pre-Oligocene Antarctic fish faunas (Kriwet et al. 2016). Fossil chondrichthyans include more than 35 species within 22 families of selachians, batoids, and chimaeroids, which have been reported from different levels within the La Meseta Formation and at different localities on Seymour Island (see Welton & Zinsmeister 1980; Jerzemska 1988, 1991; Eastman & Grande 1989, 1991; Long 1992a, b, 1994; Balushkin 1994; Cione & Reguero 1995, 1998; Doktor et al. 1996; Long & Stilwell 2000; Kriwet 2005; Engelbrecht et al. 2016, 2017; Kriwet et al. 2016). The Ypresian strata from which the elasmobranch material of this study originated, date back about 15 Ma after the end-Cretaceous extinction, coinciding with a period of maximum morphological diversification of major bony and cartilaginous fish lineages (e.g., Kriwet & Benton 2004; Friedman 2009, 2010; Sorenson et al. 2014; Frédérich et al. 2016; Marramà & Carnevale 2017; Marramà et al. 2016a, b, 2017a) and correspond to the latest phase of the early Eocene Climatic Optimum (e.g., Reguero et al. 2012; Kriwet et al. 2016). For this reason, these strata are crucial to reconstruct evolutionary dynamics of

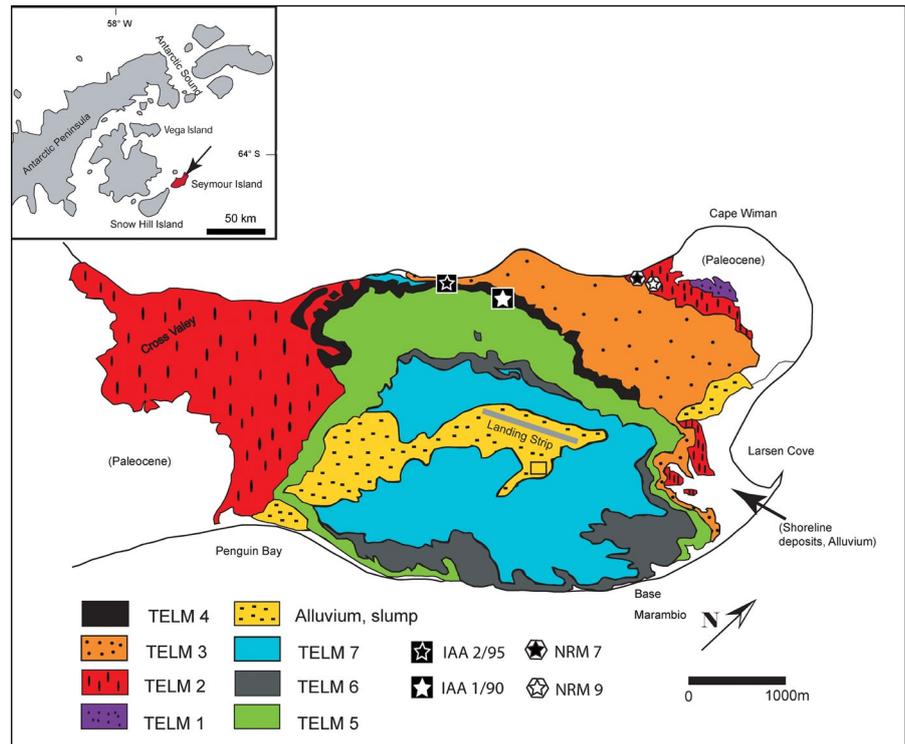
chondrichthyans across the Paleogene of Antarctica.

The aim of this paper is to provide the first unambiguous record of one of the most common and widespread early Paleogene marine top predators, *Brachycarcharias* Cappetta & Nolf, 2005, in the early Eocene La Meseta Formation of Seymour Island. Paleobiogeographic, paleobiological and paleoecological implications based on this occurrence provide new insights into the biotic turnovers that occurred at a high trophic level of the marine food chain during the Paleogene.

GEOLOGICAL SETTING

The Eocene La Meseta Formation is exposed on Seymour Island, which is situated approximately 100 kilometers SE of the northern tip of the Antarctic Peninsula (Fig. 1). The highly fossiliferous sediments of the 720-m-thick La Meseta Formation represent the uppermost part of the infill of the James Ross Basin, a back-arc basin developed on the eastern flank of the Antarctic Peninsula (Elliot 1988; Del Valle et al. 1992; Hathway 2000; Marensi et al. 2006). This formation comprises mostly poorly consolidated clastic fine-grained sediments, which were deposited in a deltaic, estuarine and shallow marine environment (Marensi 1995; Marensi et al. 1998a, b). The fossiliferous sediments belong to two groups, the lower Marambio Group of Late Cretaceous to Paleocene age including the Lopez de Bertodano and Sobral formations and the overlying Seymour Island Group comprising the Cross Valley (middle – earliest late Paleocene), La Meseta (late Paleocene – early middle Eocene), and Submeseta (middle Eocene – early Oligocene) formations (e.g., Zinsmeister 1982; Grande & Chatterjee 1987; Marensi 2006; Montes 2013). The La Meseta and Submeseta formations, which have yielded most vertebrate material up to now, are separated and bounded by a prominent erosional surface (Marensi 2006). The La Meseta Fm ranges from the Thanetian to the Lutetian, whereas the Submeseta Fm ranges from the late Lutetian to the Priabonian/Rupelian. The La Meseta Fm is further subdivided into six allomembers, namely: Valle de las Focas (TELM 1), Acantillado I and II (TELMs 2 and 3 in partem), Campamento (TELMs 3 in partem and TELM 4), and *Cucullaea* I and II (TELMs 5, and 6

Fig. 1 - Location and geological map of the Seymour Island, showing the Ypresian horizons TELMs 2, 4 and 5 where teeth of *Brachycarcharias lerichei* (Casier, 1946) were found.



in partem), respectively, whereas the Submeseta Fm includes three allomembers, Submeseta I (TELMs 6 in partem and 7 in partem), Submeseta II (TELM 7 in partem), and Submeseta III (upper TELM 7) (Montes et al. 2013). Both stratigraphic schemes, allomembers and TELMs (= Tertiary Eocene La Meseta; see Sadler 1988), are widely used and we use both schemes to indicate where the material comes from to provide as much stratigraphic information as possible.

The material that forms the focus of this study was recovered from three different TELMs. Most of the material described and discussed herein (29 teeth, representing about 60% of the entire sample) was collected from TELM 5 of the *Cucullaea* I Allomember (mostly at localities IAA [Instituto Antártico Argentino] 1/90 and IAA 2/95) which is Ypresian in age. From the underlying TELM 4 of the *Cucullaea* I Allomember, (localities IAA 1/90, IAA 2/95 and NRM [Naturhistoriska riksmuseet] 10), which also is Ypresian in age, 16 teeth (32%) were collected. TELM 2 produced the fewest material, comprising four teeth (8%), and is early Ypresian in age. No teeth referable to *Brachycarcharias lerichei* were recovered from TELM 3 (Ypresian), but this is probably due to sampling bias since very few samples were collected from this layer (M.R., and M.T., pers. obs.). On the contrary, the absence of *B. lerichei* teeth from TELMs 6 (Lutetian) and 7

(Priabonian) may represent a real paleoecological and stratigraphic signal since very few taxa adapted to cool waters have been recovered in these levels (Kriwet et al. 2016).

The *Cucullaea* I Allomember crops out all around the foothills of the Meseta in the northern part of Seymour Island and has a maximum thickness of 90 m. It is composed of shelly channel fills, sand-mud alternations, and cross-bedded fine sands. The unit was deposited in estuarine to shallow marine estuary settings (Marensi et al. 1998a, b, 2002).

The *Acantilados* Allomember crops out along the seacliffs and has a maximum thickness of 210 m. The remarkably faulted sediments are mainly composed of mudstones and very fine sandstones with prominent breccia horizons. The depositional setting is interpreted as a progradational/aggradational tide-dominated and wave-influenced delta front/delta plain which developed within a incised valley (Marensi et al. 1998a, b, 2002).

MATERIAL AND METHODS

The present study is based on 49 isolated teeth from the fossiliferous strata of the TELMs 2, 4 and 5 of the La Meseta Formation, Seymour Island, in Antarctica, and collected during three summer campaigns in 2011, 2012 and 2013. All material is housed in the collections of the Swedish Natural History Museum, Stockholm, with NRM-PZ collection numbers.

All the specimens were extracted by hand-quarrying from the

matrix and some of them were mechanically prepared with needles to reveal fine details. The material was examined using a Leica MZ12 stereomicroscope and photographed with a reflex camera and/or a 3D digital microscope Keyence VHX-1000D 3D. Subsequently, all the teeth were measured to the nearest 0.01 mm by using the software package TPSdig 2.19 (Rohlf 2005) and assigned to their respective positions using characters observed in *Brachycarcharias lerichei* mostly following Cappetta & Nolf (2005), Van Den Eeckhaut & De Schutter (2009), Cappetta (2012), and Cappetta & Case (2016). Morphological tooth terminology follows Cappetta (2012). Morphometric terminology is adopted and modified from Kriwet et al. (2015).

SYSTEMATIC PALEONTOLOGY

Class **CHONDRICHTHYES** Huxley, 1880

Subclass **ELASMOBRANCHII** Bonaparte, 1838

Order **Lamniformes** Berg, 1958

Family Odontaspidae Müller & Henle, 1839

Genus *Brachycarcharias* Cappetta & Nolf, 2005

Type species: *Lamna lerichei* Casier, 1946; from lower Eocene, Ypresian; Forest-lez-Bruxelles, Belgium

Brachycarcharias lerichei (Casier, 1946)

Figs 2, 3

See Cappetta & Nolf (2005) for a complete list of synonyms.

1946 *Lamna lerichei* Casier, p. 80, pl. 2, fig. 7a-b [after *Lamna vincenti* Winkler, 1874, pars, in Leriche (1906)]

1952 *Odontaspis vincenti* - Arambourg, p. 84, fig. 19 and pl. 13

1992a ?*Lamna* cf. *L. nasus* - Long, p. 27, fig. 9c-d

2005 *Brachycarcharias lerichei* - Cappetta & Nolf, p. 241, pl. 2

2009 *Brachycarcharias lerichei* - Van Den Eeckhaut & De Schutter, p. 5, pl. 7, figs. 1-11; pl. 8, figs. 1-5

2012 *Brachycarcharias lerichei* - Cappetta, p. 193, fig. 182

2016 *Brachycarcharias lerichei* - Cappetta & Case, p. 49, pl. 3, figs. 8-22

2017b *Brachycarcharias lerichei* - Marramà et al., p. 3, figs. 2, 3

Referred material: 49 isolated teeth: TELM 2, Early Ypresian, early Eocene: south of NRM 9 (NRM-PZ P15870), NRM 9 (NRM-PZ P15883); NRM 7 (NRM-PZ P15858) and *Natica*-Horizon, (NRM-PZ P15838). TELM 4, Ypresian, early Eocene: NRM 6 (NRM-PZ P15846); NRM 1 (NRM-PZ P15929, NRM-PZ P15930, NRM-PZ P15876, NRM-PZ P15846, NRM-PZ P15849, NRM-PZ P15852), *Cucullaea* I, (NRM-PZ P15847, NRM-PZ P15871), Center of Shark Basin (NRM-PZ P1886, NRM-PZ P15774), below IAA 1/90 (NRM-PZ P15773), Jaw Site (NRM-PZ P15926), below IAA 1/90 (NRM-PZ P15840) and IAA 1/11 (NRM-PZ P15777). TELM 5, Ypresian, early Eocene: NRM 10 (NRM-PZ P15771, NRM-PZ P15775, NRM-PZ P15836, NRM-PZ P15841, NRM-PZ P15853, NRM-PZ P15854), IAA 2/95 and IAA 1/95, 'Marsupial site' (NRM-PZ P15772, NRM-PZ P15837, NRM-PZ P15839, NRM-PZ P15806, NRM-PZ P15878, NRM-PZ P15789, NRM-PZ P15842, NRM-PZ P15778, NRM-PZ P15798, NRM-PZ P15796); NRM 11 (NRM-PZ P15859, NRM-PZ P15776, NRM-PZ P15885); IAA 1/90, 'Ungulate Site' (NRM-PZ P15779, NRM-PZ P15843, NRM-PZ P15845, NRM-PZ P15872, NRM-PZ P15887); *Natica*-Horizon (NRM-PZ P15780, NRM-PZ P15873, NRM-PZ P15874); Pass Site (NRM-PZ P15848); 'Monotreme Site' (NRM-PZ P15882); DPV 6/84 (NRM-PZ P15857); South of Marsupial Site (NRM-PZ P15888).

Locality and age: Seymour Island, Antarctica; TELMs 2, 4 and 5 of the La Meseta Formation, Ypresian, early Eocene (see Reguero et al. 2012).

Remarks. The genus *Brachycarcharias* was introduced by Cappetta & Nolf (2005) based on the revision of the odontaspidae material from the Ypresian of Belgium previously referred to *Lamna vincenti* Winkler, 1876, or *L. lerichei* Casier, 1946. The presence of *L. vincenti* had been reported from several other Ypresian deposits of Europe, North America, and Africa (e.g., Bassani 1897; Woodward 1899; Casier 1946; Arambourg 1952; Noubhani & Cappetta 1997). In the revision of the Ypresian material from Belgium, Casier (1946) assigned to *L. lerichei* the specimens previously assigned to *L. vincenti*. Later, Cappetta & Nolf (2005) observed that teeth of *L. lerichei* are morphologically different from those of any other known odontaspidae or lamnid species and therefore erected the odontaspidae genus *Brachycarcharias* to include *Lamna vincenti* and *L. lerichei*. Purdy & Francis (2007) challenged the validity of *Brachycarcharias*; however, according to Cappetta (2012) evidence for synonymy with previously described genera or species was never provided. More recently, Marramà & Kriwet (2017) demonstrated through a quantitative morphometric analysis that teeth of *Brachycarcharias* and *Lamna* are morphologically different, excluding definitively the hypothesis of Purdy & Francis (2007). Three other species within the genus *Brachycarcharias* (*B. atlasi*, *B. koerti*, and *B. mississippiensis*) have been recognised based on some qualitative morphological differences. Teeth from the Thanetian to the Ypresian of Northern Africa traditionally referred to *Odontaspis atlasi* by Arambourg (1952) were subsequently transferred to *Brachycarcharias* by Cappetta & Nolf (2005). Cappetta (2006) considered *B. mississippiensis* from the Thanetian to the Ypresian of North America (see also Case 1994) to be a junior synonymy of *B. lerichei*; Case et al. (2015) considers *B. mississippiensis* to be a valid species. Finally, isolated teeth of Lutetian to Priabonian age of North Africa, America, and Asia traditionally assigned to *Otodus koerti* (Stromer, 1910) and to *Lamna* or *Creto-lamna twiggensis* (see e.g., Case 1981) were included in *Brachycarcharias* by Underwood et al. (2011). The validity of *B. twiggensis* was later questioned by Adnet et al. (2011) and, more recently, Cappetta & Case (2016) transferred this species in *Tethylamna*, a genus erected for material recovered from the Lutetian of

| Specimen | TELM | BCT | BCW | CH | DCL | DS | LCH | LCW | MCL | PCH | PCW | RA | RW | RH | RT | TH | Position |
|---------------|------|-----|------|------|------|------|-----|-----|------|------|------|-------|------|-----|-----|------|----------------------|
| NRM-PZ P15771 | 5 | 2.5 | | 9.65 | - | 8.38 | 2.2 | 2.2 | 12.5 | 8.53 | 7.53 | - | - | - | 5.2 | - | upper lateral |
| NRM-PZ P15772 | 5 | 2.6 | 11 | 9.71 | 10.6 | 8.14 | 2.8 | 1.8 | 11.9 | 8.56 | 6.91 | 121.7 | 11.7 | 3.4 | 5 | 13.1 | upper antero-lateral |
| NRM-PZ P15773 | 4 | 2.6 | 10.4 | 9.41 | 9.94 | 13.7 | 2.3 | 2.2 | 11.8 | 8.56 | 6.31 | 122.7 | 11.7 | 3.6 | 3.9 | 13 | upper lateral |
| NRM-PZ P15774 | 4 | 2.1 | - | - | - | 15.8 | - | - | - | 7.05 | 6.06 | - | - | - | - | 3.7 | upper lateral |
| NRM-PZ P15775 | 5 | 2 | - | 8.62 | - | 4.19 | 1.9 | 1.3 | 9.86 | 7.57 | 5.11 | - | - | 3.5 | 4.1 | 12.1 | upper antero-lateral |
| NRM-PZ P15776 | 5 | - | - | - | - | 0.5 | 2.1 | 1.6 | - | - | 6.31 | - | - | 3.3 | - | - | lower lateral |
| NRM-PZ P15777 | 4 | 2.2 | 7.74 | 9 | 9.74 | 0.66 | 2.6 | 1.6 | 9.8 | 7.94 | 4.73 | 123.9 | 9.95 | 3 | 3.7 | 12 | lower antero-lateral |
| NRM-PZ P15779 | 5 | 3 | 9.42 | 9.15 | 10.3 | 1.8 | 2.2 | 1.9 | 10.3 | 8.11 | 5.69 | 117.2 | 11.6 | 3.8 | 4.1 | 12.9 | lower lateral |
| NRM-PZ P15780 | 5 | 2.4 | 8.44 | 3.2 | 4.88 | 17.6 | 1 | 1.8 | 5.83 | 2.71 | 5.05 | 112.8 | 10.8 | 5.1 | 4.3 | 8.31 | upper lateralmost |
| NRM-PZ P15789 | 5 | 2.6 | - | 7.65 | - | 14 | 2.5 | 2.1 | 10.6 | 6.1 | 6.25 | - | - | - | 5.2 | - | upper lateral |
| NRM-PZ P15796 | 5 | 2.9 | 11.5 | 11 | 11.6 | 13.4 | 2.5 | 2.1 | 13.4 | 9.99 | 7.2 | 133.6 | 15.4 | 4.4 | 4.7 | 15.4 | upper lateral |
| NRM-PZ P15798 | 5 | 2.5 | - | 9.61 | 10 | 9.36 | 2.8 | 1.6 | 11.5 | 8.91 | 6.04 | - | - | - | - | 4.7 | upper lateral |
| NRM-PZ P15806 | 5 | 1.8 | 8.93 | 7.42 | 8.38 | 6.64 | 1.6 | 1.6 | 8.99 | 6.66 | 5.85 | 130.7 | - | 2.9 | 2.9 | 10.4 | upper lateral |
| NRM-PZ P15836 | 5 | 2.2 | 7.97 | 8.14 | 9.19 | 1.8 | 2 | 1.5 | 8.87 | 7.23 | 4.57 | 123.7 | 9.6 | 2.7 | 2.9 | 10.9 | lower lateral |
| NRM-PZ P15837 | 5 | 2.8 | - | 11.4 | - | 8.85 | 3.2 | 2.1 | 13.8 | 9.26 | 6.78 | - | - | 5.1 | 5.4 | 16.4 | intermediate |
| NRM-PZ P15838 | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | upper lateral |
| NRM-PZ P15839 | 5 | 2.5 | - | 9.56 | - | 0.5 | 2.4 | 1.6 | 10.6 | 8.57 | 6.19 | - | - | 4 | 3.6 | 13.5 | lower lateral |
| NRM-PZ P15840 | 4 | 2.1 | - | 10.2 | 10.6 | 16.2 | 2.4 | 1.8 | - | 9.29 | 6.7 | - | - | 3.6 | 4.3 | 13.8 | upper lateral |
| NRM-PZ P15841 | 5 | - | 10.6 | 7.21 | 7.89 | 16.7 | 1.8 | 2.3 | 10.2 | 6.31 | 6.55 | 138 | 11.4 | 3.2 | - | 10.4 | upper lateral |
| NRM-PZ P15842 | 5 | 2.9 | - | 10 | 10.8 | 0.2 | 2.6 | 1.5 | - | - | 5.34 | - | - | - | 4 | - | anterior |
| NRM-PZ P15843 | 5 | 2 | 6.33 | 7.2 | 7.82 | 2 | 2 | 1.2 | 7.92 | 6.23 | 3.9 | - | - | - | 4 | - | lower antero-lateral |
| NRM-PZ P15845 | 5 | 2.1 | - | 8.56 | 9.32 | 1.65 | 1.8 | 1.5 | - | 7.77 | 4.75 | - | - | 4.2 | 4.5 | 12.7 | lower antero-lateral |
| NRM-PZ P15846 | 5 | 2.2 | 10.6 | 9.38 | 9.8 | 15.1 | 2.3 | 2 | 12.2 | 8.4 | 6.47 | - | - | - | 3.2 | - | upper lateral |
| NRM-PZ P15847 | 4 | 2.7 | - | 9.76 | 10.7 | 0.3 | 2 | 1.5 | - | 8.51 | 6.16 | - | - | 2.6 | - | 12.4 | lower antero-lateral |
| NRM-PZ P15848 | 5 | 2 | 11.5 | 10.2 | 10.6 | 16.7 | 2 | 2.2 | 13.3 | 9.39 | 6.96 | 132.3 | 14.2 | 3.3 | 3.7 | 13.5 | upper lateral |
| NRM-PZ P15849 | 5 | 2.9 | 10.7 | 10.6 | 11.1 | 11.9 | 2.1 | 1.9 | - | 9.53 | 7.49 | - | - | - | 4.4 | - | upper lateral |
| NRM-PZ P15852 | 5 | - | - | 10.1 | 14 | 17.2 | 2.2 | 2.3 | - | 9.32 | 9.18 | - | - | - | - | - | upper lateral |
| NRM-PZ P15853 | 5 | 2.4 | - | 8.64 | 9.76 | 0.7 | 2.5 | 1.8 | - | 7.75 | 5.22 | - | - | - | 4 | - | lower antero-lateral |
| NRM-PZ P15854 | 5 | 1.6 | - | 6.59 | 7.41 | 0.8 | 1.8 | 1.5 | - | 5.89 | 3.78 | - | - | - | - | - | lower antero-lateral |
| NRM-PZ P15857 | 5 | 2.6 | 11.3 | 9.52 | 10 | 12.6 | 2.9 | 2.2 | 12.5 | 8.22 | 6.87 | 130.5 | 12.9 | 3.2 | 4.3 | 12.7 | upper lateral |
| NRM-PZ P15858 | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| NRM-PZ P15859 | 5 | 3.1 | 8.98 | 9.58 | 10.5 | 1 | 2.5 | 1.7 | 10.6 | 8.47 | 5.23 | - | - | 3.4 | - | 13 | lower antero-lateral |
| NRM-PZ P15870 | 2 | 2.6 | - | 10.6 | 11.5 | 0.5 | 2.2 | 1.6 | 11.5 | 9.41 | 5.94 | - | - | 2.8 | 3.7 | 13.5 | lower antero-lateral |
| NRM-PZ P15871 | 4 | 2.5 | - | 9.57 | 8.36 | 0.3 | 2.3 | 1.9 | - | 7.96 | - | - | - | 4.3 | 4.1 | 13.9 | lower antero-lateral |
| NRM-PZ P15872 | 5 | 3.3 | 12.3 | 12 | 12.2 | 18.5 | 2.8 | 2.1 | 15.4 | 10.2 | 8.1 | - | - | 5.4 | 5.8 | 17.4 | upper lateral |
| NRM-PZ P15873 | 5 | 2.4 | - | 8.9 | 10.1 | 1.65 | 2.2 | 2.3 | - | 8 | 5.72 | - | - | 3.7 | 4 | 12.6 | lower antero-lateral |
| NRM-PZ P15874 | 5 | 2.3 | 9.41 | 8.4 | 9.23 | 11.7 | 1.8 | 1.8 | 10.3 | 7.86 | 6.74 | 142.5 | 11.5 | 3.4 | 3.5 | 11.8 | upper lateral |
| NRM-PZ P15876 | 4 | 3 | 10.2 | 9.63 | 10.4 | 5.05 | 2.3 | 2 | 11.4 | 8.44 | 6.34 | 130.3 | - | 2.6 | - | 12.2 | upper antero-lateral |
| NRM-PZ P15878 | 5 | 3 | - | 12.9 | 13.6 | 14.9 | - | - | - | 11.8 | 8.08 | - | - | - | 5.2 | - | upper lateral |
| NRM-PZ P15882 | 5 | 3.2 | - | 11.5 | - | 11.7 | 2.4 | 1.9 | 14.1 | 9.89 | 8.59 | - | - | 3.8 | 5.4 | 15.3 | upper lateral |
| NRM-PZ P15883 | 2 | 2.9 | - | 10.3 | - | 13 | 2.3 | 2 | 13.2 | 9.23 | 6.98 | - | - | - | 5.8 | - | upper lateral |
| NRM-PZ P15885 | 5 | 2.5 | - | 8.6 | - | 4.99 | 2.1 | 1.8 | 11 | 7.37 | 6.9 | 128.7 | - | 2.9 | 4.9 | 11.5 | upper antero-lateral |
| NRM-PZ P15886 | 4 | 1.9 | 8.41 | 6.22 | 6.74 | 12.7 | 1.7 | 1.4 | 8.56 | 5.44 | 5.15 | 135.6 | - | 2.5 | 3.3 | 8.69 | upper lateral |
| NRM-PZ P15887 | 5 | 2.5 | - | 9.25 | - | 13.2 | 2 | 1.7 | 11.6 | 8.18 | 7.46 | 147.4 | - | 2 | 3.6 | 11.2 | upper lateral |
| NRM-PZ P15888 | 5 | 2.5 | 9.52 | 8.14 | 9.12 | 3.43 | 2.5 | 1.9 | 9.84 | 6.98 | 5.61 | 125.5 | 12.3 | 3.2 | 3.4 | 11.3 | lower lateral |
| NRM-PZ P15926 | 4 | 2.6 | - | 8.88 | 9.97 | 1 | 1.9 | 1.9 | - | 7.76 | 5.64 | - | - | 3.5 | 3.9 | 12.4 | lower antero-lateral |
| NRM-PZ P15928 | 5 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| NRM-PZ P15929 | 4 | 2.5 | 7.95 | 8.23 | 8.9 | 3.96 | 1.8 | 1.3 | 9.46 | 7.44 | 5.3 | - | - | 3.7 | 3.7 | 11.9 | lower lateral |
| NRM-PZ P15930 | 4 | 1.8 | - | 9.31 | 10 | 12.5 | 2.3 | 2.1 | - | 8.25 | 6.79 | - | - | - | - | - | upper lateral |

Tab. 1 - Tooth measurements (lengths in mm; angles in degree) and related position. Abbreviations: BCT, basal crown thickness; BCW, basal crown width; CH, crown height; DCL, distal crown edge length; DS, degree of slant; LCH, height of lateral cusplets; LCW, width of lateral cusplets; MCL, mesial crown edge length; PCH, height of principle cusp; PCW, width of principle cusp; RA, angle between root lobes; RH, root height; RW, root width; RT, root thickness; TH, total height of tooth.

Alabama. Moreover, *Carcharias borodini* and *C. hynei* from the Thanetian to Ypresian of Mississippi (see Case 1994) are considered to be junior synonyms of *B. lerichei* by Cappetta (2006).

Long (1992a, fig. 9c-d) described and figured teeth as belonging to the porbeagle *Lamna* cf. *nasus* from the early Eocene strata of the La Meseta Formation of Seymour Island, although he regarded

the entire succession as Middle-Late Eocene in age. Based on this occurrence, Long (1992a) therefore supposed the presence of the earliest representative of the genus *Lamna* in the Eocene La Meseta Formation. It must be pointed out that this genus has been used traditionally as repository basket taxon for fossil teeth having similar morphologies (Cappetta 2012). Teeth of *L. nasus* are characterized by

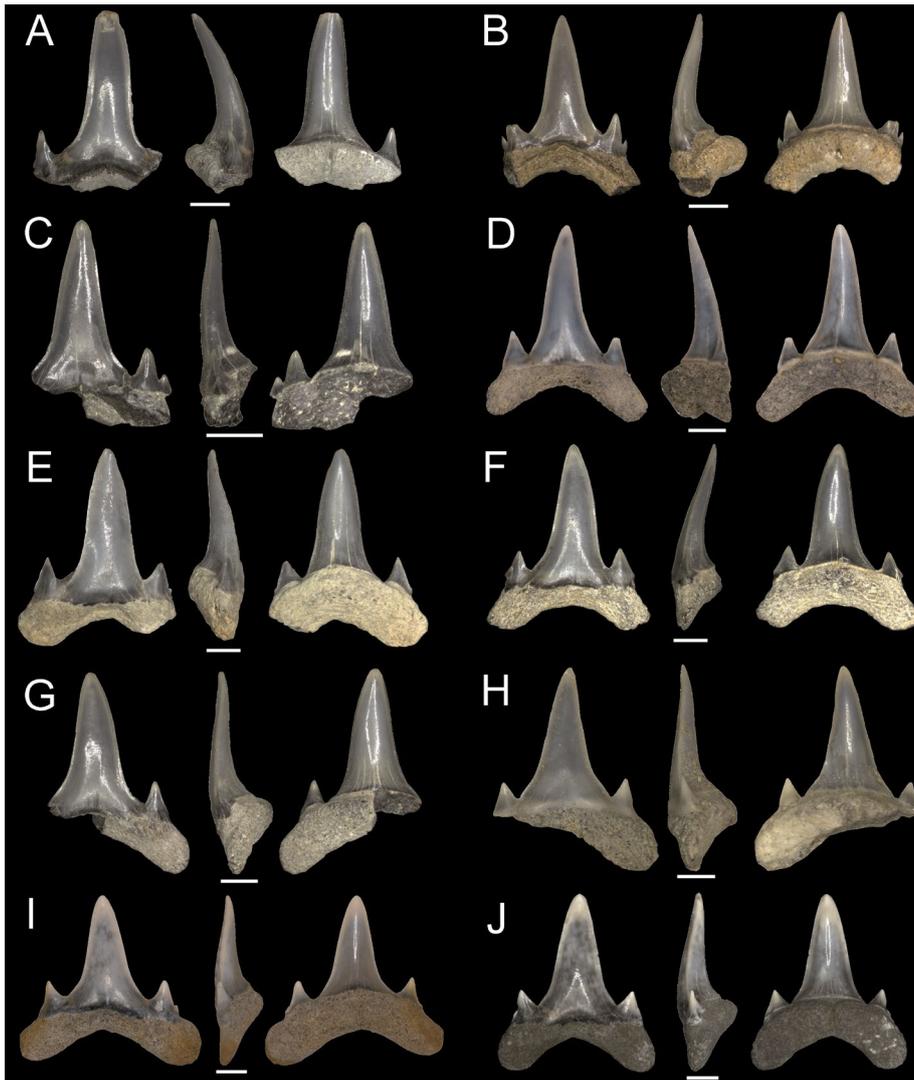


Fig. 2 - *Brachycarcharias lerichei* (Casi-
er, 1946) from the Ypresian
(early Eocene) of La Me-
seta Formation, Seymour
Island, Antarctica. Each
tooth is shown (from left
to right) in labial, profile
and lingual view. Anterior
tooth: A) NRM-PZ
P15842. Lower lateral
teeth: B) NRM-PZ P15843;
C) NRM-PZ P15854;
D) NRM-PZ P15777;
E) NRM-PZ P15859; F)
NRM-PZ P15836; G)
NRM-PZ P15839; H)
NRM-PZ P15929; I) NRM-
PZ P15888; J) NRM-PZ
P15779. Scale bars 2 mm.

small and not very high lateral cusplets that may be absent in anterior and lateral teeth (see Cappetta 2012; Marramà & Kriwet 2017), whereas those described by Long (1992a) appears in our opinion more consistent with the diagnosis of the lower antero-lateral or lateral teeth of *Brachycarcharias*, although we do not exclude that they might belong to *Isurolamna*. In this perspective, the presence of *Lamna* in the La Meseta Formation and more generally in the Eocene can be definitively excluded, thus supporting the hypothesis that the origin of the genus is probably Oligocene or Miocene (Cappetta 2012), since the earliest fossil occurrences so far of true *Lamna nasus* are from late Miocene of the North Sea (Peters 2009; Mollen 2010).

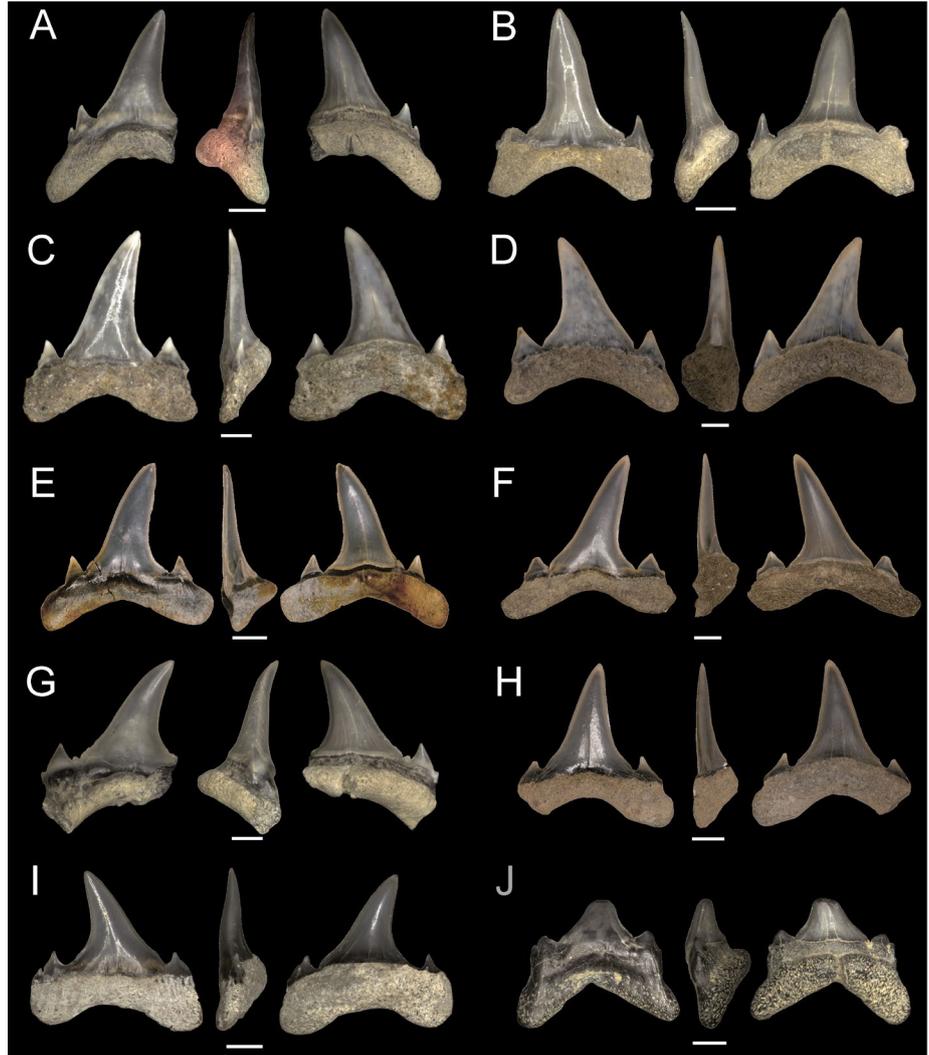
Based on the present study, the morphology of the isolated teeth from the Ypresian of the La Meseta Formation here studied, as well as those reported by Long (1992a) as *Lamna* cf. *nasus*, are consistent with the diagnosis of teeth of *Brachycarcharias*

lerichei described and figured by Cappetta & Nolf (2005), Van Den Eeckhaut & De Schutter (2009), Cappetta (2012), Cappetta and Case (2016), and Marramà et al. (2017b).

Description. A detailed list of tooth measurements is given in Table 1. The largest tooth is an upper lateral tooth of 17.41 mm total height (TH), slightly smaller than the maximum size of 25 mm reported by Cappetta (2012) for the species. Teeth belonging to different jaw positions (upper and lower teeth, anteriors, antero-laterals and laterals) have different morphologies, therefore suggesting that the dentition is monognathic and dignathic heterodont and of tearing type.

The single anterior tooth recognized in our sample (NRM-PZ P15842; Fig. 2A) shows a straight and triangular cusp, which is not very high and regularly decreasing in width from the base to the apex. The cutting edges reach the base of the crown, and

Fig. 3 - *Brachycarcharias lerichei* (Casi-
er, 1946) from the Ypresian
(early Eocene) of La Me-
seta Formation, Seymour
Island, Antarctica. Each
tooth is shown (from left
to right) in labial, profile
and lingual view. Inter-
mediate tooth: A) NRM-
PZ P15837. Upper lateral
teeth: B) NRM-PZ P15772;
C) NRM-PZ P15773; D)
NRM-PZ P15857; E)
NRM-PZ P15796; F) NRM-
PZ P15848; G) NRM-
PZ P15789; H) NRM-
PZ P15806; I) NRM-PZ
P15841; J) NRM-PZ P15780
(lateralmost tooth). Scale
bars 2 mm.



its profile is slightly curved. The lingual crown face of the cusp shows a strongly convex profile and short lingual folds are present. The labial crown face of the cusp overhangs the root by a little protruding bulge, and is characterised by the presence of very short and slender folds close to the crown-root junction. There was originally a single pair of high and upright cusplets, well separated from the main cusp, although only one is preserved in the specimen. The root is missing.

The cusp of lower antero-lateral teeth is upright and almost symmetrical in labial and lingual views (e.g., Fig. 2B–D). The base of the crown is larger than that of the anterior tooth. Lower antero-lateral teeth bear one to two pairs of lateral cusplets: the proximal one is always large, triangular in shape, with apices often diverging from the main cusp. The distal lateral cusplets, when present, are smaller than the proximal ones. The holaulacrhizous root lobes have flat distal extremities.

The nutritive axial furrow on the lingual protuberance is deep and strongly developed with a marked nutritive foramen. More lateral teeth of the lower jaw (e.g., Fig. 2G–J) possess a lower cusp with respect to antero-lateral ones.

A single probable upper intermediate tooth of about 10 mm TH has been recognized in our sample (NRM-PZ P15837; Fig. 3A). The crown height is about 60% of TH. The labial bulge of the crown is wide. The main cusp is distally bent. There are two lateral cusplets with the distal one being smaller than the proximal one.

In upper antero-lateral teeth (e.g., Fig. 3B) the main cusp is slightly distally inclined. The mesial cutting edge is oblique and almost straight, whereas the distal one is more vertical and slightly sigmoidal. A weak depression is recognizable at the base of the crown in labial view. Short and faint folds are always present basally on lingual face. The proximal lateral cusplets are broad, and a smaller second pair of

distal cusplets can be recognised at least partially in NRM-PZ P15772 (Fig. 3B). The root is asymmetric with a mesial lobe that is longer than the distal one.

Upper teeth of more lateral position (Fig. 3C–I) have a triangular cusp, which is strongly bent distally. The cusp appears slightly flattened labio-lingually. The labial face of the crown is smooth and almost flat with only a shallow median concavity at base. The lingual face is gently convex; short and weak lingual folds are present at the base of the crown. The cutting edges extend from the apex down to the base of the crown. The mesial cutting edge of the main cusp is oblique and slightly convex, whereas the distal one is concave. The labial bulge of the crown is wide and distinctly overhangs the root. There are often two pairs of lateral cusplets: the proximal lateral cusplets are broad and triangular, whereas the distal ones are significantly reduced. The cutting edges of the proximal cusplets are separated from those of the main cusp by a distinct notch. The root is low and broad, with well-separated lobes. The lingual furrow on the protuberance is weak or sometimes appears absent.

In the single upper lateralmost tooth recognized (Fig. 3J) the main cusp is strongly bent distally and its crown is reduced in size. The labial bulge of the crown is mesio-distally wide. The two pairs of lateral cusplets are low and the apices of the proximal ones appear rounded, although we cannot exclude that this is due to abrasion. The root is bulky and wider than the total height of the tooth.

DISCUSSION

Comparisons. The analysis of the material from the La Meseta Formation on Seymour Island has revealed the presence of several characters that support the assignment of these teeth to the family Odontaspidae, including a monognathic and dignathic heterodonty, a tearing type dentition, well-developed and separated root lobes, a marked nutritive furrow, and a tall and slender main cusp (Compagno 1984, 1999; Cappetta 2012).

Teeth of this Ypresian sand tiger shark of Antarctica can be distinguished from other Eocene odontaspids, and in particular from those occurring in the same horizons on Seymour Island (i.e., *Odontaspis*, *Palaeohypotodus* and *Striatolamia*) by their unique combination of characters such as a trian-

gular, not very high cusp, which decreases regularly in width distally. For the same reason they can also be easily separated from those of *Jaekelotodus* (wide and bulky cusp), *Carcharias* (very sharp and high cusp), and *Hypotodus* (robust cusp) (see Cappetta & Nolf 2005; Cappetta 2012). The presence of fine folds on the basal labial face of the main cusp distinguishes the teeth from those of *Araloselachus*, *Glueckmanotodus*, *Hypotodus*, *Jaekelotodus*, *Odontaspis*, and *Orpodon* which lack any labial or lingual crown ornamentation, whereas *Palaeohypotodus* is characterized by a series of tubercles or strong ridge-like folds boarding the base of the labial face (Leriche 1951; Cappetta & Nolf 2005). The cutting edges in *B. lerichei* extend the full height of the crown. This character additionally separates the teeth from the La Meseta Fm from those of *Araloselachus*, *Carcharias*, *Hypotodus*, and *Odontaspis*, in which the cutting edges do not reach the base of the crown (Cappetta & Nolf 2005; Mannering & Hiller 2008; Cappetta 2012). Although the cutting edges reach the base in *Jaekelotodus* and *Sylvestrilamia*, the teeth of the former are larger (up to 45 mm high) and have a wide and bulky main cusp that is almost the same height as the root, whereas *Sylvestrilamia* possesses a main cusp with a more flexuous profile and always bears single pair of small lateral cusplets, a feature that also characterizes the teeth of *Hypotodus* (Cappetta & Nolf 2005; Cappetta 2012). The teeth from the La Meseta Fm can be easily separated from those of *Araloselachus*, *Borealotodus*, *Carcharias*, *Glueckmanotodus*, *Hypotodus*, *Jaekelotodus*, *Mennerotodus*, *Sylvestrilamia*, *Tethylamna*, and *Turania* by the presence of well-developed lateral cusplets (Cappetta & Nolf 2005; Cappetta 2012; Cappetta & Case 2016). *Odontaspis*, *Orpodon*, and *Palaeohypotodus* also possess tall lateral cusplets but, contrary to *Brachycarcharias*, teeth of *Orpodon* are much smaller (less than 12 mm), *Odontaspis* possess a very high, sharp and non-sigmoidal main cusp that is often flanked by up to three pairs of cusplets in lateral teeth, whereas *Palaeohypotodus* possesses short and strong folds on the labial bulge, and strong and irregular serrations at the base of the cutting edges (Compagno 1984; Cappetta 2012). Finally, the stratigraphic age of the teeth can provide additional information for separating the teeth described here from *Araloselachus*, *Orpodon*, and *Tethylamna* since these genera are unknown from Ypresian deposits (Cappetta & Nolf 2005; Cappetta 2012; Cappetta & Case 2016). How-

ever, stratigraphic distribution might not be a valid reason for distinguishing taxa.

Currently, four valid species are recognized within the genus *Brachycarcharias*: *B. atlasi*, *B. koerti*, *B. lerichei*, and *B. mississippiensis* (see also ‘Remarks’ above). Teeth from the La Meseta Fm can be easily separated from those of *B. atlasi* in the absence of strong lingual folds and a well-developed second pair of lateral cusplets (Arambourg 1952) and from those of *B. koerti* for the presence of lower and broader lateral cusplets (see Darteville & Casier 1943; Underwood et al. 2011). Finally, although teeth of *B. lerichei* are morphologically very similar to those of *B. mississippiensis*, which Cappetta (2006) considers to be synonymous with *B. lerichei*, we can exclude that our teeth pertain to this species mostly for biogeographic reasons, since *B. mississippiensis* was only restricted to the eastern coasts of North America according to our current knowledge (Case 1994; Case et al. 2015).

The significance of *B. lerichei* in the Eocene of Antarctica. This report represents the southernmost occurrence of the extinct sand tiger shark *Brachycarcharias*. The abundance of *Brachycarcharias lerichei* teeth in TELMs 2, 4 and 5 of the La Meseta Fm on Seymour Island is in accordance with the increase in species richness of elasmobranchs and holocephalans detected from the earliest to the latest Ypresian of the La Meseta Formation (Kriwet et al. 2016). This Ypresian occurrence in Antarctica supports the hypothesis that this species was probably an opportunistic top predator having a wide range of habitats and feeding preferences (Marramà et al. 2017b). Remains of *B. lerichei* were in fact abundantly recovered from tropical shallow- to deep-water deposits of the Northern Hemisphere (see e.g., Arambourg 1952; Ward & Wiest 1990; Case 1994; Noubhani & Cappetta 1997; Smith et al. 1999; Cappetta & Nolf 2005; Adnet & Cappetta 2008; Diedrich 2012; Cicimurri & Ebersole 2015; Cappetta & Case 2016). More recently, isolated teeth of this species have been also reported from the celebrated Ypresian Bolca Lagerstätte of Italy (Marramà et al. 2017b, c). It has been suggested that the mean annual surface seawater paleotemperatures for this early Eocene deposit located in Tethys realm was very high (Giusberti et al. 2014). In fact, the fossil occurrence of the specialized marine water strider *Halobates* suggested that sea surface paleotemper-

atures in the Bolca paleobiotope exceeded 20°C, representing the lower temperature tolerated by the extant species of this genus (Andersen et al. 1994; Cheng et al. 2012). This concurs to suggest a tropical environment with high mean annual surface paleotemperature for the Bolca paleobiotoxes (see also Carnevale et al. 2014; Marramà et al. 2016c). On the contrary, paleotemperatures detected for TELMs 2 to 5 of the La Meseta Fm of the Antarctic Peninsula were remarkably lower, around 10–11°C, as suggested by Ivany et al. (2008), thus resulting in an association of chondrichthyans adapted to cooler waters (Kriwet et al. 2016), although non-resident warm-water genera as *Carcharhinus* and *Pristis* have been also reported (Kriwet 2005). The first unambiguous occurrence of *B. lerichei* from the Southern Hemisphere therefore supports the hypothesis of Marramà et al. (2017b) that this species was an opportunistic cosmopolitan top predator having a wide range of habitat preferences, contrary to the hypothesis of Maisch et al. (2014) who supposed a life style more similar to that of the living porbeagle shark, *Lamna nasus*, a lamnid species today only restricted to temperate and cool waters and never occurring in tropical seas (Compagno 1984; Compagno et al. 2005), although more recent studies suggest that *L. nasus* might be more heat-tolerant than previously thought (Campana et al. 2010). In this perspective, we also hypothesize that *B. lerichei* might have been an eurytherm species, tolerating wide ranges of temperatures, from tropical warm waters of the Bolca Lagerstätte to the cooler contexts of the La Meseta Formation. This remarkable adaptation probably enabled this lamniform shark to become one of the most successful odontaspidae taxa of the early Paleogene, inhabiting a wide range of latitudes of the Northern and Southern Hemisphere, which is also consistent with high vagility and a circum-global distribution as observed in living odontaspidae (Musick et al. 2004).

The Danian marks the first occurrences of *Brachycarcharias*, with at least three species (*B. lerichei*, *B. atlasi*, and *B. mississippiensis*) occurring in deposits of the Northern Hemisphere (see Fig. 4). Mannerling & Hiller (2008) reported an indeterminate species of *Brachycarcharias* from the Paleocene of the Southern Hemisphere (New Zealand). However, the occurrence from the Paleocene of New Zealand appears, in our opinion, controversial. Teeth figured by Mannerling & Hiller (2008, fig. 11L–N) as low-

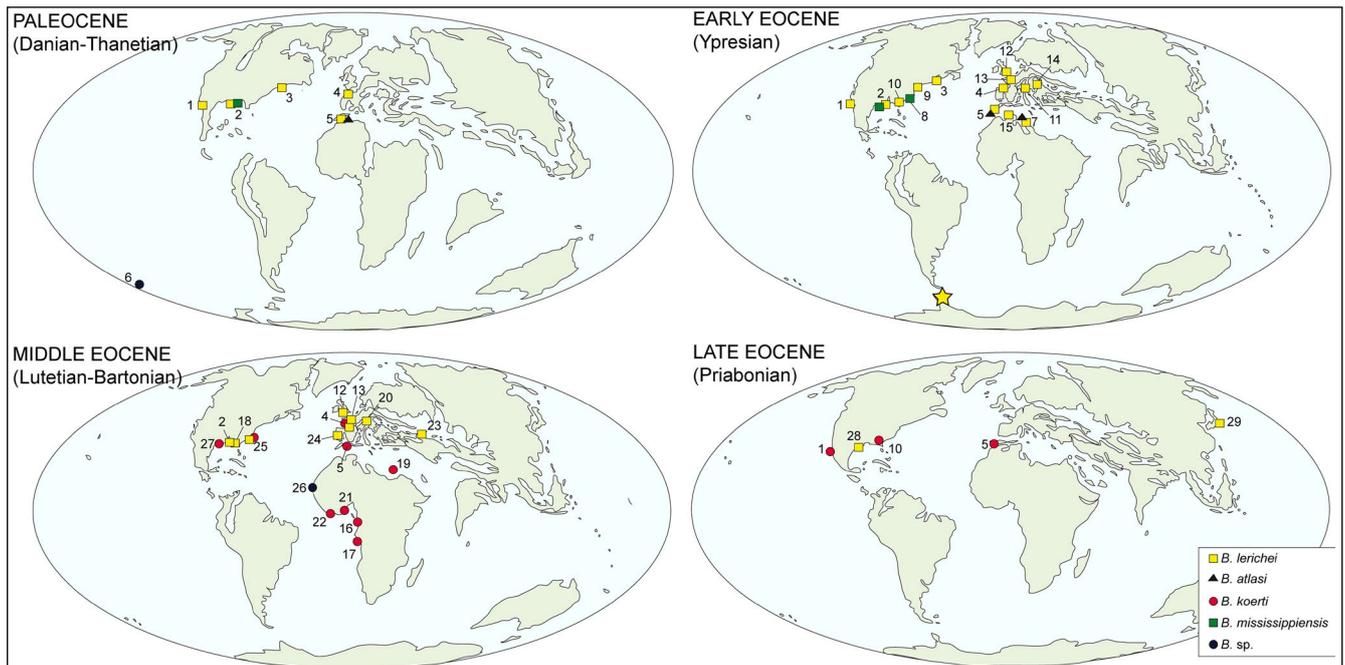


Fig. 4 - Schematic simplified maps showing the paleobiogeographic distribution of *Brachycarcharias* Cappetta & Nolf, 2005. Localities: 1 Mexico, 2 Mississippi, 3 Maryland, 4 France, 5 Morocco, 6 New Zealand, 7 Tunisia, 8 South Carolina, 9 Virginia, 10 Georgia, 11 Italy, 12 England, 13 Belgium, 14 Austria, 15 Algeria, 16 Congo, 17 Angola, 18 Alabama, 19 Egypt, 20 Germany, 21 Nigeria, 22 Togo, 23 Uzbekistan, 24 Spain, 25 North Carolina, 26 Senegal, 27 Texas, 28 Louisiana, 29 Japan. The yellow star marks the Ypresian occurrence of *B. lerichei* in the La Meseta Fm of Seymour Island, Antarctica. Data from Marramà et al. (2017b). Maps modified from Scotese (2002).

er laterals of *Brachycarcharias* sp. possess only small, narrow and not very high lateral cusplets, a very sigmoidal main cusp in profile view, and strongly bent distally. Conversely, lower lateral teeth of *Brachycarcharias* always possess robust, high and upright cusplets and a main cusp that is only slightly sigmoidal and which is not (or only slightly) bent distally in lower teeth (Cappetta & Nolf 2005; Van Den Eeckhaut & De Schutter 2009; Cappetta & Case 2016). Moreover, teeth of *Brachycarcharias* sp. figured as upper anteriors by Mannering & Hiller (2008, fig. 11I–K) possess very small, low lateral cusplets, a low root with robust and very divergent lobes, a very robust and wide main cusp base. In comparison, upper anterior teeth of *Brachycarcharias* show very large and upright lateral cusplets, a comparably higher root with more tapered lobes forming a smaller angle, and a crown decreasing regularly in width apically (see Van Den Eeckhaut & De Schutter 2009; Marramà et al. 2017b). The exclusion of *Brachycarcharias* from the Paleocene of New Zealand might be also supported by biogeographic reasons, since the high clustering of *Brachycarcharias* occurrences in the Paleocene of the Northern Hemisphere suggests that the centre of origin of this taxon would have taken place between North America and the

Tethys realm. If we exclude the doubtful *Brachycarcharias* teeth from the Paleocene of New Zealand, the Ypresian occurrence of *B. lerichei* in Antarctica, beside representing the southernmost occurrence of the genus, also implies that this species reached the Southern Hemisphere in concomitance with its maximum geographic distribution (see also Marramà et al. 2017b) via a dispersal corridor along the continental margins of the western Atlantic Ocean, as suggested for other elasmobranchs (Long 1994). The widespread Ypresian distribution of *B. lerichei* (well-before the maximum expansion of the genus with *B. koerti* in the Lutetian of southwestern Africa) was probably due to the concomitance of its opportunistic strategy, eurytherm adaptation, high vagility, and favourable global high temperatures in the context of the early Eocene Climatic Optimum.

Brachycarcharias disappeared at the end of the Eocene, with the last occurrences from Priabonian deposits of Georgia, USA (as '*Carcharias*' *koerti* in Parmley et al. 2003), Mexico (González-Barba 2003), Morocco (Gajić et al. 2014), Japan (Tanaka et al. 2006) and Louisiana, U.S.A. (Breard & Stringer 1995). The absence of *Brachycarcharias* in TELMs 6 (Lutetian) and 7 (Priabonian) of the La Meseta Formation on Seymour Island is consistent with the

reduction and disappearance of cartilaginous fishes during the latest phase of the Eocene in this region that was related to the progressive cooling, reduction of shelf areas, and establishment of Antarctic ice sheets (Grande & Eastman 1986; Kriwet et al. 2016). In this perspective, the gradual disappearance and extinction of *Brachycarcharias*, as well as other odontaspids such as *Striatolamia* and *Palaeohypotodus* at the end of the Eocene, might be related, at least in part, to a major wave of biotic turnovers that took place at the E–O boundary and that particularly involved marine top predators (Prothero et al. 2003; Marramà et al. 2017b). This turnover of taxa at the Eocene-Oligocene transition was the most severe extinction event in the Cenozoic and was likely related to significant temperature declines and sea level falls (e.g., Zachos et al. 2001; Liu et al. 2009; Harnik et al. 2012). It has also been suggested that Eocene odontaspids were partly replaced by other odontaspids in the Oligocene (e.g., *Aralose-lachus*, new *Carcharias* species) and predominantly by lamnids (e.g., *Carcharoides*, *Isurus*, *Lethenia*) that might have been better adapted to cooler environments (Marramà et al. 2017b).

CONCLUSIONS

Eocene shallow marine sediments of the La Meseta Fm on Seymour Island yielded the most diverse Paleogene ichthyofauna from the Southern Hemisphere to date. This fauna provides important insights into diversity and distribution patterns of both cartilaginous and bony fishes during crucial time intervals in global climatic developments such as the early Eocene climatic optimum (ca. 53–49 Ma) resulting in extensive greenhouse conditions. The first report of the extinct sand tiger shark *Brachycarcharias* from Ypresian strata of the La Meseta Formation, Seymour Island, Antarctica, helps to better understand the paleobiology and paleobiogeography of this Paleogene taxon. Teeth of *Brachycarcharias lerichei* were recovered from TELMs 2 (early Ypresian), 4 and 5 (late Ypresian) and an increase in raw numbers from 4 teeth in the early Ypresian to 45 teeth in the late Ypresian is recognizable. The rather high abundance and increase of *B. lerichei* teeth in the La Meseta Fm agrees well with the general pattern of taxonomic diversity increase of chondrichthyans postulated for this assemblage.

The wide habitat and geographic distribution of this species, ranging from deep-waters to shallow water environments and from tropical to cool-temperate climates, indicate that *B. lerichei* was a rather opportunistic, cosmopolitan, highly vagile, and eurytherm top predator in marine food-webs, which might have been the reasons for its success during the Paleocene and Eocene. At the end of the Eocene, however, this species vanished, which correlates with decreasing global temperatures and the appearance of new, probably better adapted lamniform sharks.

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