

## THE FIRST RECORD OF THE CHIMAEROID GENUS *EDAPHODON* (CHONDRICHTHYES, HOLOCEPHALI) FROM ANTARCTICA (SNOW HILL ISLAND FORMATION, LATE CRETACEOUS, JAMES ROSS ISLAND)

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**ABSTRACT**—A new species of an edaphodontid holocephalian, *Edaphodon snowhillensis*, sp. nov., is described based on a complete dentition collected in the late Campanian Herbert Sound Member of the Snow Hill Island Formation of James Ross Island, Antarctica. The dentition consists of paired vomerine, mandibular, and palatine tooth plates, which are almost completely preserved. The new species is characterized by a unique character combination out of which the presence of a subquadrangular vomerine tooth plate and a horse-hoof-shaped anterior outer tritor in the mandibular tooth plates appear to be unique characters among the edaphodontids. *Edaphodon snowhillensis*, sp. nov., represents the most complete dentition of a holocephalian fish from the Southern Hemisphere and the earliest record of the genus *Edaphodon* from the Antarctic continent and the Weddellian Biogeographic Province. Also, *E. snowhillensis*, sp. nov., is the southernmost specimen of this genus and according to the size of the tooth plates is one of the largest chimaeroid fish known.

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### INTRODUCTION

Holocephali is a relatively poorly diversified marine chondrichthyan clade that ranges from the Paleozoic to the Recent. It radiated during the Cretaceous, but its diversity diminished during the Cenozoic (Stahl, 1999). The most distinctive character of the group is its statodont dentition in which each tooth plate grows slowly throughout life and is not replaced (Patterson, 1992). Tooth plates can be distinguished from the teeth of sharks by their form, general morphology, and internal structure (Stahl, 1999). Within Holocephali, the suborder Chimaeroidei is the only holocephalian clade known since the Cretaceous. Presently, Chimaeroidei comprises three families: Callorhynchidae (*Callorhynchus* Lacepède, 1798), Rhinochimaeridae (*Rhinochimaera* Garman, 1901, *Neoharriotta* Bigelow and Schroeder, 1950, *Harriotta* Goode and Bean, 1895), and Chimaeridae (*Chimaera* (Collett, 1904), *Hydrolagus* Gill, 1862) (Didier, 1995; Stahl, 1999).

The dentition of chimaeroid fishes consists of two pairs of tooth plates in the upper jaw. The anterior ones are called vomerine tooth plates and the posterior ones palatine tooth plates. The lower jaw has only one pair of mandibular tooth plates (Stahl, 1999). The vomerine tooth plates are the smallest and have a reinforced cutting edge that often gives the tooth plate a beak-like profile (Stahl, 1999). Chimaeroid tooth plates show hypermineralized tissue concentrated in areas called tritors, which never spread over the entire occlusal surface like in other holocephalian fishes (Stahl, 1999). The tritors of chimaeroids do not arch outward over the labial margin of the jaw. On the contrary, they form massive broad pads, elongated ridges, or rows of column-like units over the occlusal surface of the tooth

plate. The patterns in which tritors are arranged as well as the shape of the tooth plate itself have been traditionally considered useful characters to differentiate chimaeroid genera and species. Moreover, many species were established on single, isolated tooth plates, for example, *Callorhynchus torresi* Otero et al., 2013; *Edaphodon bucklandi* Agassiz, 1843; and *Edaphodon mirificus* Leidy, 1856. However, this apparent taxonomic diversity could be due to ontogenetic variation or wear patterns (see Husakof, 1912; Ward and Grande, 1991; Stahl and Chatterjee, 2002).

Associated holocephalian dentitions are uncommon. Most finds consist of isolated complete tooth plates or fragmentary ones. Such was the case of the Antarctic chimaeroid record. The first mention of associated holocephalian dentitions was made by Grande and Eastman (1986), from putative late Eocene beds of the La Meseta Formation at Seymour Island (Marambio on Argentinian maps). The material consists of palatine and mandibular tooth plates and a dorsal spine that were assigned with doubts to the genus *Ischyodus* (see Grande and Eastman, 1986). Later, Ward and Grande (1991) described in detail part of the material illustrated by Grande and Eastman (1986), as well as new material, concluding that they might be assigned to *Ischyodus dolloi* Leriche, 1902. In the same paper, Ward and Grande (1991) described the new species, *Chimaera seymourensis*, from beds of the Acanitlados Allomember of the La Meseta Formation, which is presently considered to be early Eocene in age (Marensi, 2006).

The first Cretaceous Antarctic chimaeroid fish reported was *Chimaera zangerli* Stahl and Chatterjee, 1999. The species was based on an almost complete left palatine tooth plate, a right palatine tooth plate missing the mesial tip, two small tooth plate fragments, and a fragmentary chondrocranium. These materials

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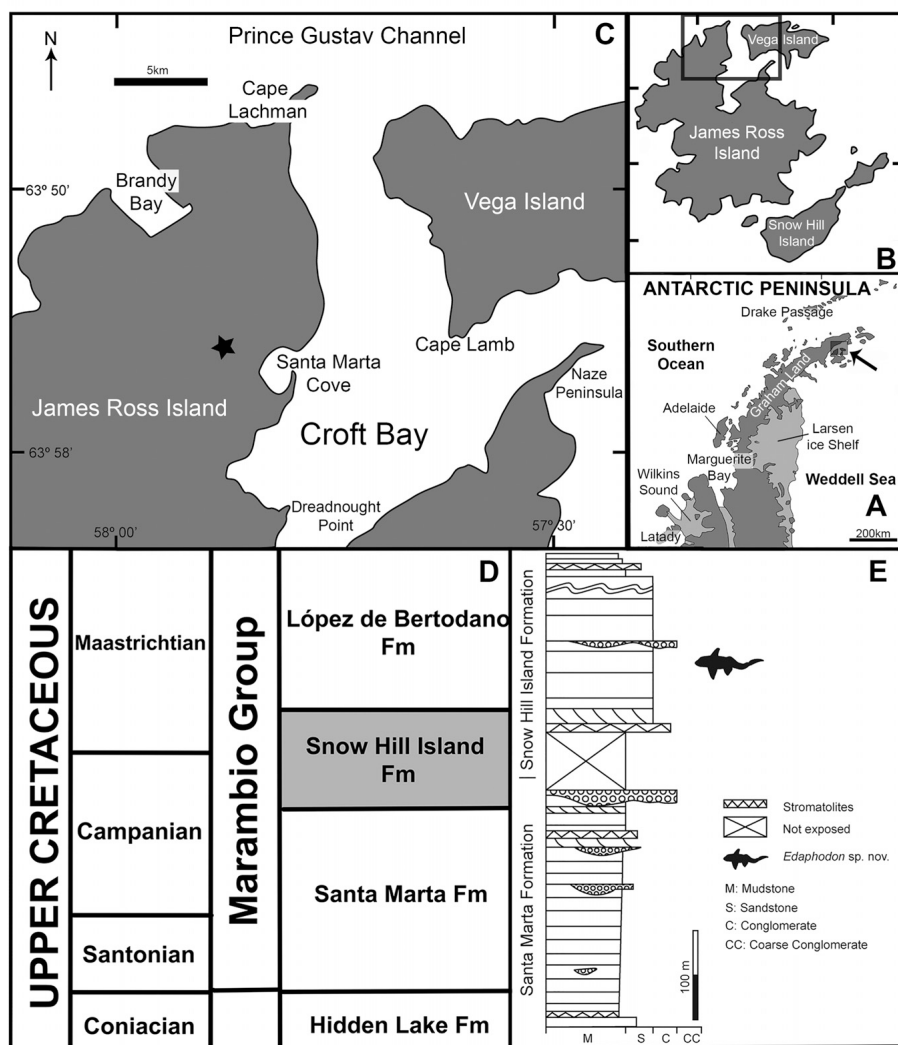


FIGURE 1. Map of collecting area (modified from Reguero et al., 2013). **A**, Antarctic Peninsula; **B**, James Ross Archipelago; **C**, detail of **B**, the star indicates the type locality (Santa Marta Cove, Snow Hill Island Formation; late Campanian); **D**, stratigraphic chart of the Marambio Group in the James Ross Basin, Antarctic Peninsula, in gray the Snow Hill Island Formation; **E**, simplified cross-section of the Snow Hill Island Formation at Santa Marta Cove showing the collecting point. Temporal and sedimentary units not to scale.

come from a single nodule found in Maastrichtian sediments of the López de Bertodano Formation on Seymour Island (Stahl and Chatterjee, 1999:982, figs. 1–7). Later, Stahl and Chatterjee (2002) reported and described the presence of *Ischyodus dolloi* in early Maastrichtian levels of the López de Bertodano Formation near Boardman Point, Seymour Island (see Stahl and Chatterjee, 2002:848). The material consists solely of a right mandibular tooth plate (see Stahl and Chatterjee, 2002:849, fig. 3). New chimaeroid remains, *Callorhynchus* sp. and an indeterminate rhinochimaerid, were recently reported (Otero et al., 2014:414–416). These authors mentioned that the material comes from the late Campanian Gamma Member of Santa Marta Formation. However, the Gamma Member corresponds to the lower part of the Snow Hill Island Formation (Olivero et al., 2008; Olivero, 2012).

Large tooth plates of an holocephalian fish were recovered during the 2013–2014 Antarctic Field Expedition supported by the Argentinian Antarctic Institute. These tooth plates come from the Upper Cretaceous levels of the Snow Hill Island Formation (Marambio Group) at James Ross Island (Fig. 1). Here, we describe these material and propose a new species of the genus *Edaphodon*, arguing the paleobiogeographic relevance of the new species. We also comment about possible fish-size, niche, and prey capabilities.

## MATERIALS AND METHODS

Most of the material was collected in 2013 by a team of scientists from La Plata Museum (J. P. O’Gorman, M. Fernández, and M. Reguero), Carmen Funes Museum (R. A. Coria), and Comahue National University (A. Iglesias). In a new expedition in March of 2014, R. A. Coria collected additional material: a right palatine tooth plate and fragments of the right mandibular tooth plate. The specimens are deposited at the La Plata Museum (MLP).

The tooth plates have been mechanically prepared by technical staff of the MLP and Carmen Funes Museum (MCF) to remove excess matrix. The tools used were a Microjack no. 5 and a Paleotool Aro. The specimen was studied under a Zeiss Stemi 2000-C stereomicroscope with different magnifications. Photographs of the specimen were taken with a Canon PowerShot G10 digital camera (under microscope) and a Canon Rebel T2i digital camera with a Canon EF 50 mm f/2.5 macro lens. Measures were taken with Vernier calipers directly on the material as well as with the free software ImageJ using high-resolution photographs.

**Tooth Plates Terminology**—The tritor terminology used here follows Stahl (1999) and Stahl and Parrish (2004) (see Fig. 2). Descriptive terminology follows Popov (2003) and Popov and

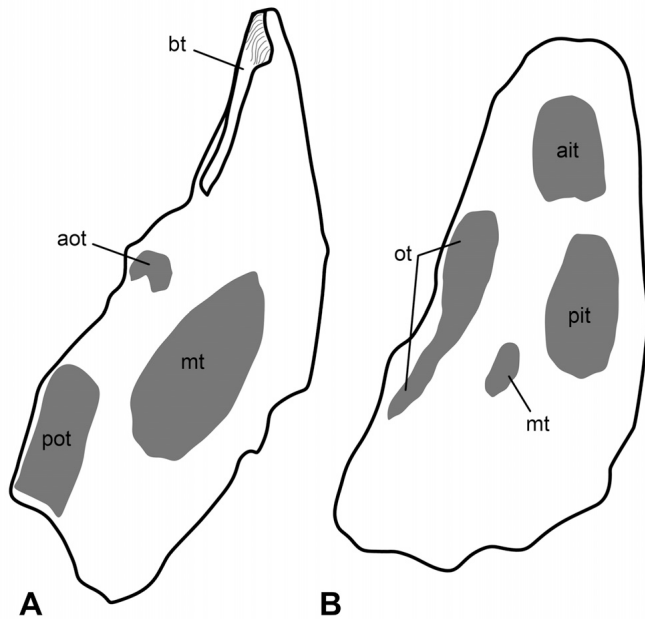


FIGURE 2. Schematic drawings (not to scale) of the mandibular and palatine tooth plates of *Edaphodon snowhillensis*, sp. nov., depicting the tritor terminology. **A**, mandibular tooth plate; **B**, palatine tooth plate.

Machalski (2014). The histological terminology follows Ørvig (1985). The measurement system is in part according to Popov and Machalski (2014) and Shin (2010).

**Institutional Abbreviations**—MCF, Museo Carmen Funes, Neuquén, Argentina; MLP, Museo de La Plata, La Plata, Argentina.

**Tooth Plates Terminology Abbreviations**—**ait**, anterior inner tritor; **aot**, anterior outer tritor; **bp**, basal pocket; **bt**, beak tritor (= symphyseal tritor of Popov and Machalski, 2014); **Km**, in mandibular tooth plates is the incomplete width of a dental plate measured perpendicular to the medial termination of the anterior outer tritor; **Kp**, in palatine tooth plates is the incomplete width of a dental plate measured perpendicular to the medial termination of the outer tritor; **mt**, median tritor; **ot**, outer tritor; **pit**, posterior inner tritor; **pot**, posterior outer tritor; **sm**, symphyseal margin; **str**, symphyseal tritorial rod; **tr**, tritorial rods.

### GEOLOGIC SETTING

The material was collected in beds of the Herbert Sound Member (Snow Hill Island Formation, Marambio Group) on James Ross Island (Fig. 1). The Marambio Group (Santonian–Danian) crops out mostly in the James Ross Archipelago (Marenssi et al., 2012). It is divided into the Santa Marta, Snow Hill Island, Haslum Crag, and López de Bertodano Formations (Olivero et al., 2008). The Herbert Sound Member (Gamma Member of Olivero et al., 1986), formerly part of the Santa Marta Formation, is presently considered to be the lower part of the Snow Hill Island Formation (Olivero et al., 2008). The Herbert Sound Member is characterized by quartz sandstone and mudstone beds, with a mudstone-dominated uppermost section (Olivero, 1992). It was deposited in a shallow marine environment (Crame et al., 1991; Olivero et al., 2008) and is considered late Campanian in age (Olivero and Medina, 2000).

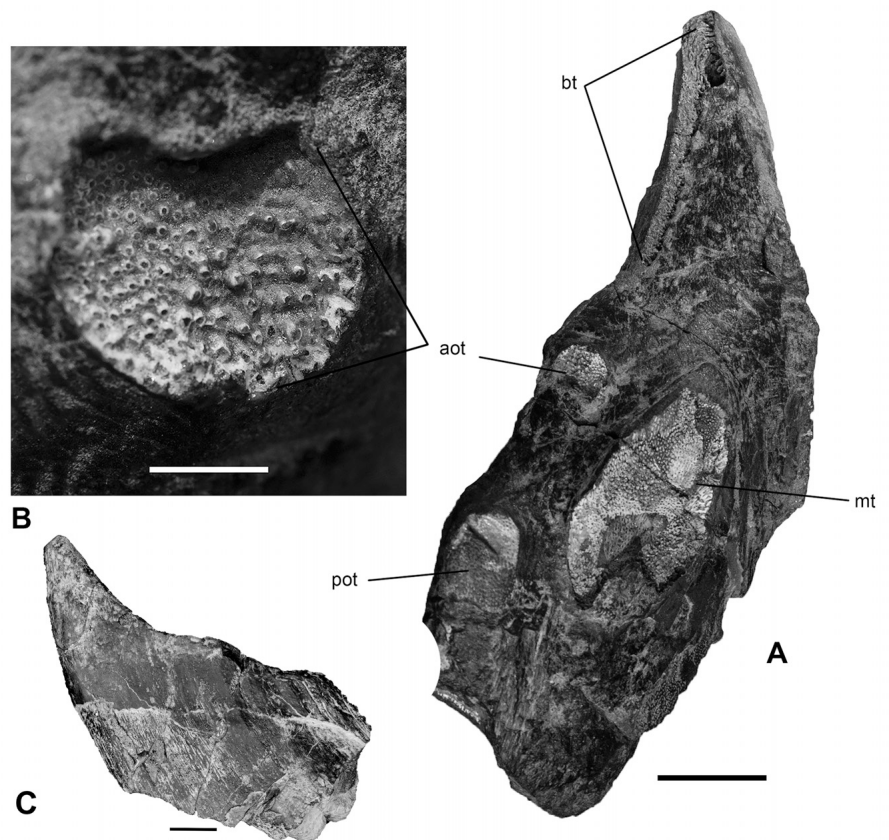


FIGURE 3. Left mandibular tooth plate of *Edaphodon snowhillensis*, sp. nov. (MLP 13-I-26-1). **A**, occlusal view; **B**, detail of the horse-hoof-shaped anterior outer tritor; **C**, basal view. Scale bars equal 20 mm (**A**, **C**) and 5 mm (**B**).

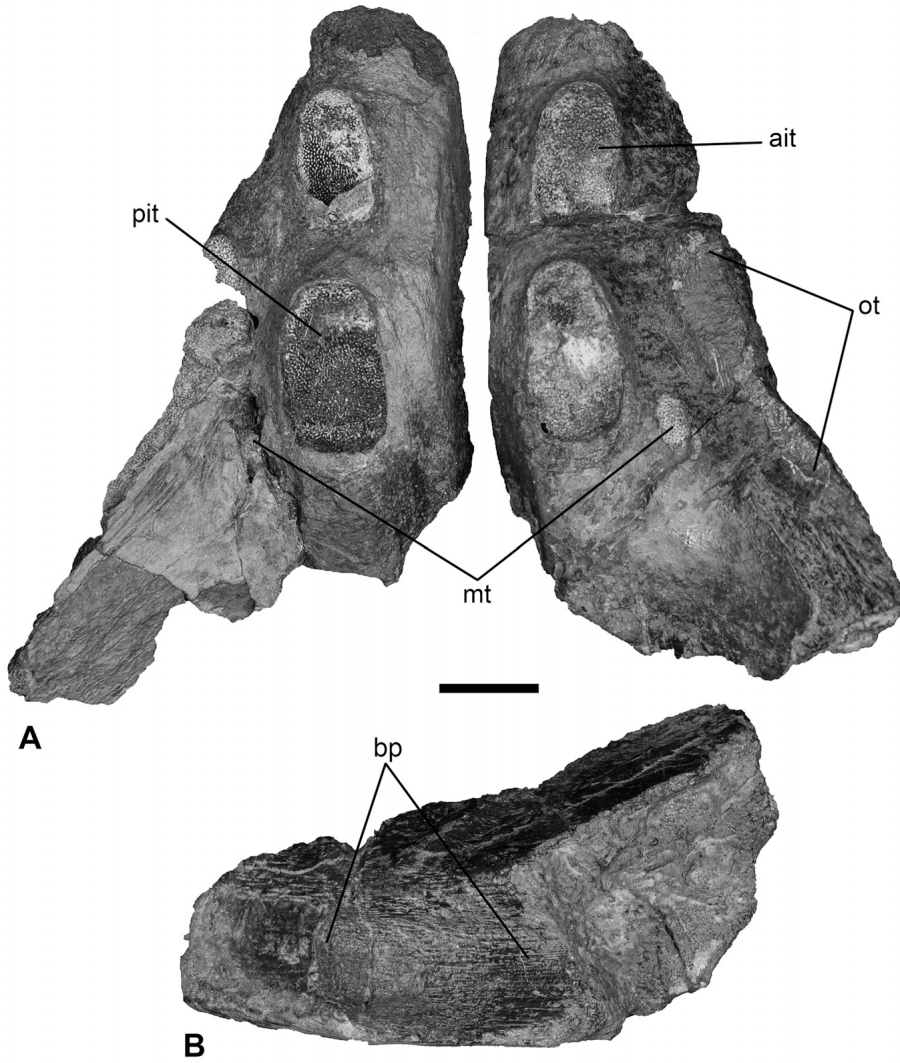


FIGURE 4. Palatine tooth plates of *Edaphodon snowhillensis*, sp. nov. (MLP 13-I-26-1). **A**, occlusal view; **B**, basal view. Scale bar equals 20 mm.

Several organisms have been reported from the Herbert Sound Member (see Table 1): among the invertebrates, bivalves and ammonites (Olivero and Medina, 2000; Olivero, 2012); among fishes, chondrichthyans and teleosts (Kriwet et al., 2006; Otero et al., 2014); among reptiles, mosasaurs (Novas et al., 2002; Martin and Fernández, 2007; Fernández and Gasparini, 2012), plesiosaurs (O’Gorman, 2012), and dinosaurs (Salgado and Gasparini, 2006; Cerda et al., 2012; Coria et al., 2013).

#### SYSTEMATIC PALEONTOLOGY

Higher-level taxonomy follows Nelson (2006). We here refer to the family ‘Edaphodontidae’ Owen, 1845, following Popov and Machalski (2014). We do not use the taxonomy of Stahl (1999) because the main characters used for grouping genera in the family Callorhynchidae Garman, 1901, were the presence and extent of reduction of the descending lamina and, as was mentioned by Popov (2003:510), “the reduction of the descending lamina is a character of general trend in the suborder evolution; this is associated with the transition of the chimaeroid dentition from crushing-breaking to breaking-cutting and cutting types, accompanied by the development of

numerous small tritoral pads or no tritors at all (*Rhinochimaera* Garman, 1901).”

CHONDRICHTHYES Huxley, 1880  
 HOLOCEPHALI Bonaparte, 1832  
 HOLOCEPHALOMORPHA Nelson, 2006  
 CHIMAERIFORMES Obruchev, 1953  
 CHIMAEROIDEI Patterson, 1965  
 CHIMAEROIDEA Bonaparte, 1832  
 ‘EDAPHODONTIDAE’ Owen, 1845  
*EDAPHODON* Buckland, 1838

**Type Species**—*Edaphodon bucklandi* Agassiz, 1843 (= *E. eurygnathus* Agassiz, 1843).

*EDAPHODON SNOWHILLENSIS*, sp. nov.  
 (Figs. 2–6)

**Etymology**—After the Snow Hill Island Formation.

**Diagnosis**—(Based on a character combination and characters unique to ‘Edaphodontidae,’ which are identified with an asterisk [\*]). ‘Edaphodontidae’ with a crushing-breaking dentition. Mandibular tooth plate with four tritors. Big, undivided, and

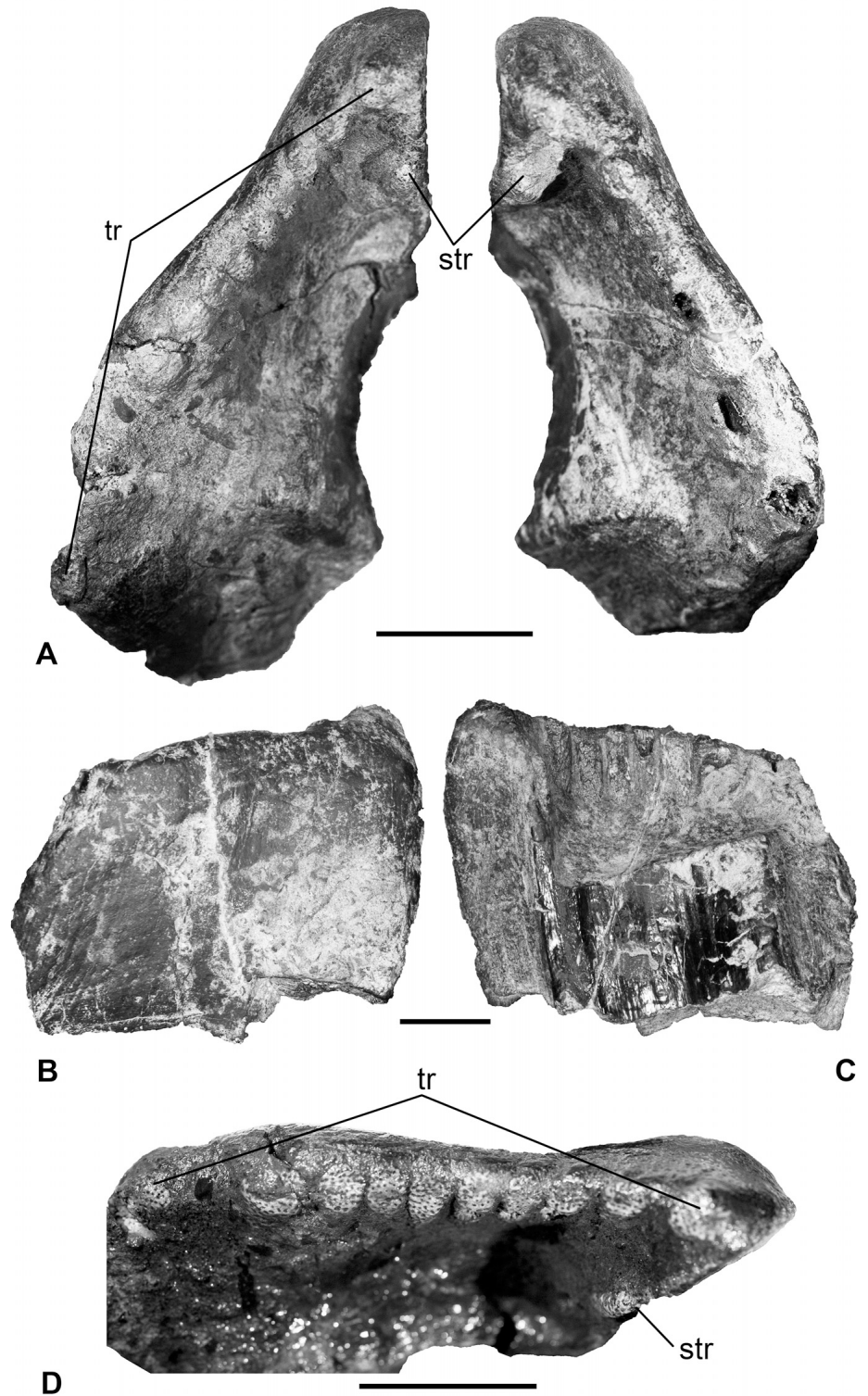


FIGURE 5. Vomerine tooth plates of *Edaphodon snowhillensis*, sp. nov. (MLP 13-I-26-1). **A**, symphyseal-occlusal view of right and left vomerine tooth plates; **B**, right vomerine tooth plate in basal view; **C**, right vomerine tooth plate in occlusal view; **D**, detail of the tritorial surface of the left vomerine tooth plate. All scale bars equal 20 mm.

oval median tritor. Two smaller unequal outer tritors. Horse-hoof-shaped anterior outer tritor [\*]. Extended posterior outer tritor relatively wider than the anterior outer tritor. Beak tritor exposed at the mesial tip and in a narrow strip along the labial margin of the beak. Beak tritor not extending downward in the symphyseal surface. Triangular palatine tooth plate with four tritors. Both inner tritors oblong (longer than wide) and almost

equal in size. Posterior inner tritor with a narrow anterior section and a wide posterior one. Small median tritor located distally to the inner posterior tritor. Elongated outer tritor, narrow at its distal end. Subquadrangular vomerine tooth plate [\*]. Tritorial series of the vomerine tooth plate composed of 10–12 tritorial rods. One inner symphyseal tritorial rod in the vomerine tooth plate. Vomerine mesial angle scarcely marked.

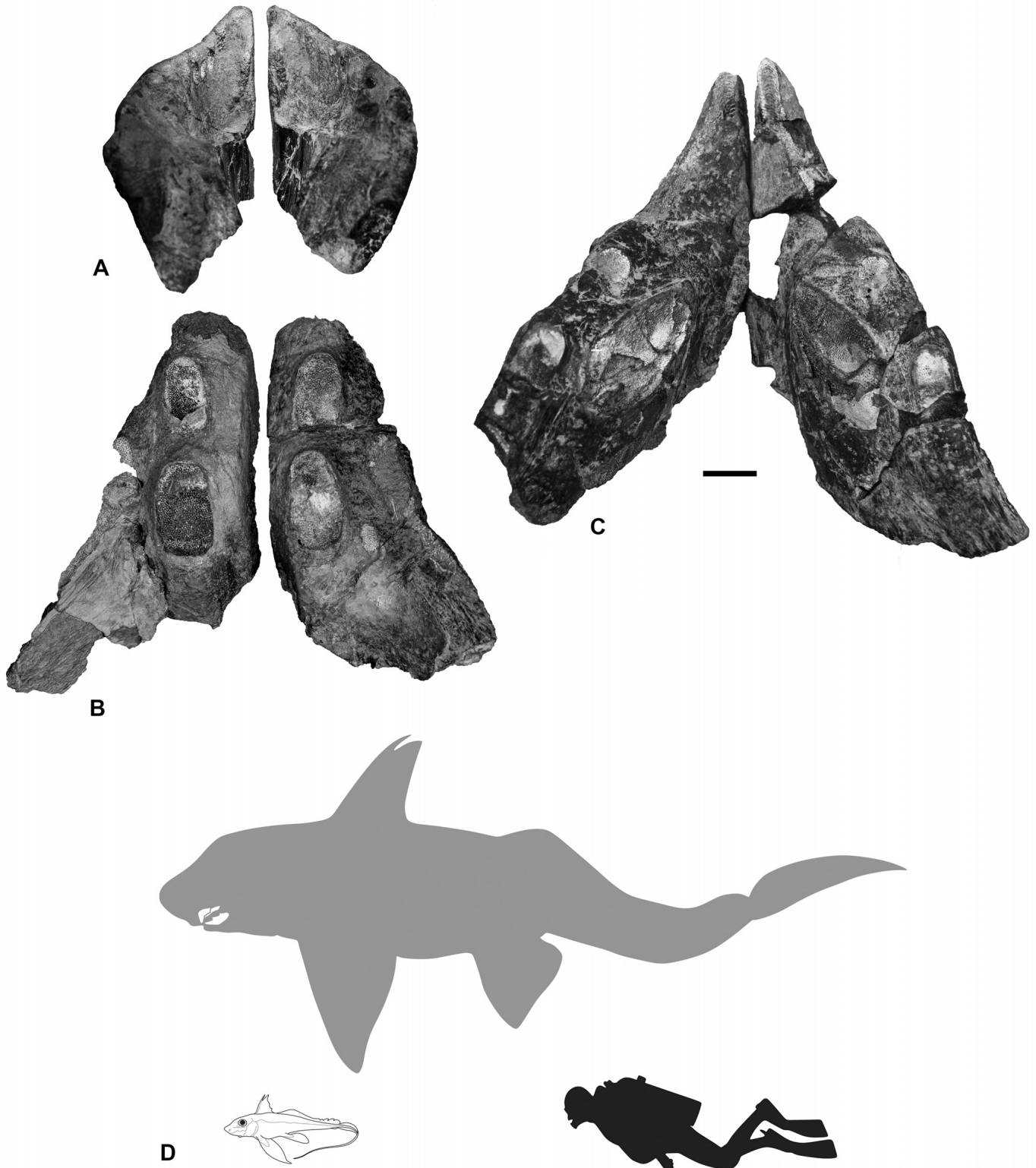


FIGURE 6. *Edaphodon snowhillensis*, sp. nov. (MLP 13-I-26-1). **A**, vomerine tooth plates; **B**, palatine tooth plates; **C**, mandibular tooth plates; **D**, Comparative reconstruction: *E. snowhillensis*, sp. nov., silhouette in gray above, *Chimaera monstrosa* line drawing below.

**Holotype**—MLP 13-I-26-1. The species is known only from the holotype, comprising a complete left and an almost complete right mandibular tooth plate, and two almost complete palatine and vomerine tooth plates. With the exception of the majority of vomerine tritorial rods and the mandibular posterior outer tritor, almost all tritorial pads show a high degree of post mortem disintegration (Figs. 3, 5, posterior outer tritor, tritorial rods; for comparison, see Stahl 1999:21, fig. 21).

**Geographical and Stratigraphical Provenance**—James Ross Island (S63°55'06.5", W57°53'20.1"); Herbert Sound Member of the Snow Hill Island Formation (late Campanian).

## DESCRIPTION

### Mandibular Tooth Plates

Large tooth plates (mesiodistal length = 180 mm, Km = 49.5 mm) laterally compressed and with a very well developed anterior beak (Fig. 3A). Both left and right tooth plates are almost completely preserved (Fig. 3). The mandibular tooth plates have four tritors: a large, undivided oval median tritor exposed on the oral surface and occupying most of the occlusal surface, two smaller outer tritors of almost equal width, and a long beak tritor (Fig. 3A). The beak tritor is composed of laminated pleromin in its rostral portion and vascular pleromin caudally. The other tritors are composed of vascular pleromin. No symphyseal tritor is present. The anterior outer tritor is horse-hoof-shaped and is located at the level of the mesial anterior third of the median tritor (Fig. 3B). The posterior outer tritor is oval and is located at the distal third of the median tritor (Fig. 3A). The labial margin of the tooth plate is reinforced by a beak tritor that is exposed at the mesial tip of the tooth plate and continues in a narrow strip along the labial margin. The beak tritor does not extend downward along the symphyseal surface. The tooth plates measure ca. 180 mm from the mesial tip to the distal preserved end. The left and right beaks seem to be in contact at the anterior portion of the symphyseal surface. There is a deep symphyseal surface that reaches a maximum depth of

32.2 mm. Caudally, the beak tritor ends at the deepest point of the symphyseal surface. The oral portion of the symphyseal margin has a well-developed ridge. The labial surface of the plates is smooth, and there is no descending lamina (sensu Patterson, 1992; see Fig. 3C). In basal view, the labial margin is raised by the prominence of the two outer tritors (Fig. 3C).

### Palatine Tooth Plates

Both palatine tooth plates are preserved (Fig. 4A). They are large (mesiodistal length ca. 130 mm, Kp = 35 mm), robust, and roughly triangular in occlusal view. They have four occlusal tritors. The tritors are composed of vascular pleromin. Left and right tooth plates have lost part of their oral surfaces in the caudal portion. The distal margin of the right plate is lacking part of its oral surface at the distal corner. The symphyseal margin is slightly curved towards the mesial tip. The tip of the mesial portion is ca. 30 mm wide, and the total length of the symphyseal margin is about 90 mm. In basal view, the labial margin slopes gradually outwards. The mesiodistal length (measured from the mesial end to the distal preserved angle) of the palatine tooth plates is between 131 and 150 mm. The lingual edge is about 65 mm wide. The oral surface bears four tritors: three large and one small. The elongate outer tritor follows the labial margin of the tooth plate; its mesial margin does not reach the posterior margin of the anterior inner tritor. The anterior and posterior inner tritors are almost equal in width. They are located near the symphyseal margin, but the posterior inner tritor is closer to the symphysis than the anterior one. A small oval median tritor is present. The median tritor is located between the outer and posterior inner tritors, near the distal end of the posterior inner tritor. The anterior inner tritor is 26 mm long and 17 mm wide; the posterior inner tritor is 33 mm long and 18 mm wide. The outer tritor is ca. 60 mm long and 8 mm wide in its anterior end and 4 mm in the posterior one. The median tritor is 14 mm long and 6 mm wide. The anterior third of the aboral (= basal) surface is slightly convex and almost smooth. The aboral surface has a

TABLE 1. List of the fossil fauna recovered from the Herbert Sound Member of the Snow Hill Island Formation at James Ross Island, Antarctica.

Taxa	Age	Stratigraphy	Locality	Author
Ammonites				
Kosmaticeratids	late Campanian	Snow Hill Island Fm.	James Ross Island	Olivero and Medina, 2000
Baculiitids	late Campanian	Snow Hill Island Fm.	James Ross Island	Olivero, 2012
Bivalvia				
Trigoniids	late Campanian	Snow Hill Island Fm.	James Ross Island	Olivero, 2012
Fishes				
Chondrichthyans <i>Notidanodon dentatus</i>	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
<i>Clamydoselachus thomsoni</i>	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
<i>Sphenodus</i> sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
<i>Squatina</i> sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
<i>Scapanorhynchus</i> sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
<i>Paraorthacodus</i> sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
<i>Centrophoroides</i> sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	Otero et al., 2014
<i>Cretalamna appendiculata</i>	late Campanian	Snow Hill Island Fm.	James Ross Island	Otero et al., 2014
Lamniformes indet.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
Actinopterygians <i>Enchodus</i> sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
? <i>Sphaeronodus</i> sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
<i>Apateodus</i> ? sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	2. 3. Kriwet et al., 2006
Albuliformes indet.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
Ichthyodectiformes indet.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
Teleostei indet.	late Campanian	Snow Hill Island Fm.	James Ross Island	Kriwet et al., 2006
Mosasauurs				
<i>Taniwasaurus antarcticus</i>	late Campanian	Snow Hill Island Fm.	James Ross Island	Novas et al., 2002; Martin and Fernández, 2007
Plesiosaurs				
Elasmosauridae indet.	late Campanian	Snow Hill Island Fm.	James Ross Island	O'Gorman, 2012
Dinosaurs				
<i>Antarctopelta oliveroi</i>	late Campanian	Snow Hill Island Fm.	James Ross Island	Salgado and Gasparini, 2006
<i>Trinisaura santamartaensis</i>	late Campanian	Snow Hill Island Fm.	James Ross Island	Coria et al., 2013
Lithostrotian sauropod indet.	late Campanian	Snow Hill Island Fm.	James Ross Island	Cerda et al., 2012

deep 'U'-shaped groove representing the basal pocket of the tooth plate (Fig. 4B). The surface of the basal pocket has marked parallel ridges (Fig. 4B).

### Vomerine Tooth Plates

Both vomerine tooth plates (Fig. 5) are preserved but lack their symphyseal projections. They are subquadrangular (Fig. 5B, C). To date, subquadrangular tooth plates have not been observed in other *Edaphodon* species, thus appearing to be unique for *E. snowhillensis*, sp. nov. Nevertheless, this is a common morphology present in the vomerine tooth plates of *Ischyodus*. The labial edge of the right tooth plate has a tritorial series composed of at least 12 closely arranged, tritorial rods. Each tritorial rod is roughly cylindrical in cross-section and is composed of vascular pleromin. The tritorial rods gradually increase in size distally. One medium-sized tritorial rod is developed at the symphyseal margin (= symphyseal tritorial rod), it is almost parallel to the symphyseal edge (Fig. 5C). In lingual view, the tritors are located in a slightly sigmoidal way (Fig. 5C, D). The mesial angle of the right vomerine tooth plate is blunt and attenuated. In basal view, the labial margin slightly slopes (with a midpoint blunt prominence) at the symphysis. The oral (= occlusal) surface is concave, and we can easily distinguish the unworn surface (which has glossy tissue on its surface) from the functional wear surface (which lacks this glossy tissue): at the limits of both areas, a central platform is developed (Fig. 5C). The glossy tissue present in the unworn surface of the tooth plate was referred to as vitrodentine or enameloid by Stahl (1999). In basal view, the labial surface of the tooth plate is almost smooth, slightly concave, and without a developed descending lamina. There are delicate growth lines present (Fig. 5B).

### SYSTEMATIC COMPARISON

The holotype of *Edaphodon snowhillensis*, sp. nov. (Fig. 6), is the most complete specimen of a fossil holocephalian fish found in the Southern Hemisphere. It has a dentition composed of massive tooth plates with deep symphyseal surfaces and broad tritorial pads. The absence of descending laminae and the presence of a broad symphyseal surface in the mandibular tooth plates identify it as a member of the family 'Edaphodontidae.'

The material is referred to the genus *Edaphodon* because it presents the following character combination: massive mandibular tooth plate with a developed anterior beak; symphyseal surface distally wide and narrowing mesially; laminated tritor extending along the labial margin of the beak, being exposed as a beak tritor at the tip of the tooth plate; anterior and posterior outer tritors appearing at the labial margin of the mandibular tooth plate; mandibular tooth plate with a large median tritor; palatine tooth plate massively built, long and triangular in occlusal view, with three large tritors (one outer and two inner) and one small median tritor; and vomerine tooth plate with tritorial series composed of tritorial rods on its oral surface (see Stahl, 1999).

Popov (2008) stressed that the validity of some species of edaphodontids should be examined because they are based on fragmentary material. In consideration of this, we compared the holotype of *Edaphodon snowhillensis*, sp. nov., only with some reasonably well-known species. The mandibular tooth plates of *Edaphodon snowhillensis*, sp. nov., shares with those of *E. bucklandi*, *E. sedgwickii* (Agassiz, 1843), and *E. hesperis* Shin, 2010, the typical overall morphology, which is laterally compressed, roughly triangular with a long and well-developed anterior beak and a large and centrally placed median tritor occupying most part of the occlusal surface. However, in occlusal view, the mandibular tooth plates of *E. snowhillensis*, sp. nov., differ from those of *E. sedgwickii* in having fewer tritorial pads (i.e., four tritorial pads in *E. snowhillensis*, sp. nov., versus six in *E. sedgwickii*; see Popov and Machalski, 2014:13), in lacking the

symphyseal branch of the beak tritor and the weakly defined bifurcation of the median tritor, and in having a horse-hoof-shaped anterior outer tritor (vs. oval anterior outer tritor in *E. sedgwickii*). Also, the mandibular tooth plates of *E. snowhillensis*, sp. nov., lack the inner tritor that is commonly present in, for example, *E. bucklandi* and *E. sedgwickii*. Popov and Machalski (2014) stressed that some of the specimens assigned to *E. sedgwickii* reveal a derived morphology of the mandibular median tritor and its systematic assignment is doubtful.

In occlusal view, the mandibular tooth plates of *Edaphodon snowhillensis*, sp. nov., share with those of *E. hesperis* the presence of four tritors, of which the median one is large and undivided. Also, both species have similar mesiodistal length. However, *E. snowhillensis*, sp. nov., differs from *E. hesperis* in having a large beak tritor composed of laminated pleromin in the mesial part and vascular pleromin distally (vs. small and mesial beak tritor composed of only laminated pleromin in *E. hesperis*), different length and morphology of the anterior and posterior outer tritors (vs. similar length and morphology of anterior and posterior outer tritors in *E. hesperis*); the beak of *E. snowhillensis*, sp. nov., is more pronounced and acute than that of *E. hesperis*; and the symphyseal margin is slightly curved in *E. snowhillensis*, sp. nov. (vs. straight in *E. hesperis*, *E. sedgwickii*, and *E. mirificus*).

In occlusal view, the mandibular tooth plate of *E. snowhillensis*, sp. nov., shares with *E. ubaghsi* Storms in Leriche, 1927, the presence of a median tritor extending forward over the anterior margin of the anterior outer tritor (see Duffin and Reynders, 1995:pl. 13B). However, *E. snowhillensis*, sp. nov., differs from *E. ubaghsi* in having a wider occlusal surface, a wider and shorter beak, and a smaller and morphologically different anterior outer tritor.

The palatine tooth plates of *Edaphodon snowhillensis*, sp. nov., have the typical overall morphology of the genus, which is roughly triangular and robust. The palatine tooth plates of *E. snowhillensis*, sp. nov., differ from *E. bucklandi*, *E. mirificus*, and *E. agassizi* in having the mesial margin of the outer tritor not projecting over the distal margin of the anterior inner tritor. However, this condition is present in *E. ubaghsi* (see Duffin and Reynders, 1995:pl. 13A). In *E. snowhillensis*, sp. nov., the outer tritor extends backward, projecting over the distal margin of the posterior inner tritor (vs. not projecting backward over the posterior inner tritor in *E. hesperis*).

The vomerine tooth plates of *Edaphodon snowhillensis*, sp. nov., differ from the genotype (*E. bucklandi*) and other species of the genus such as *E. eyrensis* Long, 1985, '*E. leptognathus*' Agassiz, 1843, *E. mirificus*, *E. sedgwickii*, *E. stenobryus* Cope, 1875, and *E. hesperis* in having a tritorial series with a large number of tritorial rods plus an inner symphyseal tritorial rod. Nevertheless, vomerine tooth plates are very conservative among chimaeroids, and differences in the number of tritorial rods could be due to ontogenetic or intraspecific variation more than to systematic features (see Johnson and Horton, 1972). It is noteworthy that *E. snowhillensis*, sp. nov., has subquadrate vomerine tooth plates, a remarkable character among *Edaphodon* species because in these species, the vomerine tooth plate is commonly triangular (Stahl, 1999).

### FINAL REMARKS

*Edaphodon snowhillensis*, sp. nov., differs from all other holocephalians in the following unique character combination: each mandibular tooth plate has an occlusal surface with an undivided large and oval median tritor, two smaller unequal outer tritors, and a beak tritor; the anterior outer tritor has a characteristic horse-hoof-shaped morphology; the beak tritor is exposed at the mesial tip and in a narrow strip along the labial margin of the beak, not extending downward to the symphyseal surface; triangular palatine tooth plate with four tritors; the inner tritors are

almost equal in size and longer than wide; the posterior inner tritor is narrow in its anterior section and posteriorly wide; the small median tritor is located distal to the inner posterior tritor; elongated, curved, and distally narrowed outer tritor; and subquadrangular vomerine tooth plate.

**Size**—The size of the fully grown tooth plates varies within each group of holocephalian fishes. Among chimaeroids, the length of the largest upper and lower plates ranges from 20 to 50 mm in *Callorhynchus*. The tooth plate size in some fossil chimaeroids is greater. For instance, *Ischyodus* Egerton, 1843, has mandibular plates of 50 mm or more (see Stahl, 1999). The largest tooth plates known belong to *Edaphodon sedgwickii*, in which the mandibular tooth plate reaches 225 mm in length. Remarkably, the mandibular tooth plate of *E. snowhillensis*, sp. nov., measures 180 mm in length, representing one of the largest chimaeroid fish known.

Ciccimurri et al. (2008) estimated the size of a fossil edaphodontin (*Eumylodus laqueatus* Leidy, 1873) based on the ratio between the palatine tooth plate length and the body length of extant analogues (the palatine tooth plate length represents approximately 4% of the body length of the fish). Taking into account that the mesiodistal length of the right palatine tooth plate (which is broken at its distal end) of *E. snowhillensis*, sp. nov., is at least 131 mm and the left one ca. 150 mm, we conclude that this new species was a very large fish that could have reached an estimated body length of at least 3 m (Fig. 6D).

**Niche and Prey Capability**—Extant holocephalians are entirely marine and are distributed all over the world except for the polar regions. They are grouped into three families: Callorhynchidae, Rhinochimaeridae, and Chimaeridae. Most species live in cool waters of the shelf or slope, although several species occur in shallow waters (Ebert and Sthemann, 2013). Several holocephalian fishes inhabit deep water, and their behavior is poorly known. However, it is well known that some species will form large aggregations, segregated by size and sex, whereas other species occupy different habitats depending on the stage in life (Ebert and Sthemann, 2013). Members of the family Callorhynchidae such as the extant elephant fish (*Callorhynchus* spp.) are predominantly benthic feeders (Ribbink, 1971) and display a variable habitat distribution, preferably cool temperate, inner-shelf waters, at a depth of 22–115 m (López et al., 2000; Kriwet and Gazdzicki, 2003). On the other hand, the members of Rhinochimaeridae and Chimaeridae inhabit marine deep tropical seas (Nelson, 2006).

Chimaeroids are predatory fishes and their hypermineralized tooth plates are assumed to be related to durophagy (Didier, 1995; Stahl, 1999). However, both soft-bodied and hard organisms are found in their digestive tract (Didier, 1995, and literature cited therein). Their diet primarily consists of benthic invertebrates (bivalves, gastropods, crustaceans, polychaetes, echinoderms) and other fishes, including chimaeroids. The chimaerid *Chimaera monstrosa* Linnaeus, 1758, is considered to

have an opportunistic feeding strategy (Moura et al., 2005). It has been shown to have a diet high in diversity and with differences in composition according to predator size groups. Moreover, differences in diet were observed between geographical areas and depths due to the predator size group and ontogenetic variation related to differences in spatial distribution (Moura et al., 2005).

Several holocephalians inhabited Southern Hemisphere seas at the end of the Mesozoic. Morphological evidence from the tooth plates indicates that they had different feeding modes. Stahl and Chatterjee (2002) hypothesized that chimaeroids having sectorial tritors scavenged on fish and even marine reptiles, whereas callorhynchids, possessing tritoral pads, could only crush their food. However, the callorhynchid '*Edaphodon kawai*' Consoli, 2006, has a long, robust beak armed with sectorial tritors along the symphyseal margin and a smaller anterior outer tritor pad. It is plausible that this particular disposition of tritorial elements enabled that species to employ both a cutting and a crushing action, optimizing the range of available prey.

To determine the feeding performance of *Edaphodon* and *Ischyodus*, Shin (2009) estimated its maximum theoretical bite force and compared with the bite force calculated for extant chimaeroids. Shin's study suggests that both fossil genera have a higher bite force than extant ones. Shin (2009) also analyzed the crushing performance of the tritors of *Edaphodon*. The crushing test showed that tritors not only provided a crushing surface but also held and stabilized the prey effectively. Bite force estimates suggest that *Ischyodus* and *Edaphodon* were capable of generating sufficient bite force to consume bivalves within gape size limitations, whereas crushing rigid gastropod shells was mechanically challenging.

*Edaphodon snowhillensis*, sp. nov., does not have the cutting blades of chimaerids. However, the vomerine tooth plate with a tritorial series composed of a large number of successive tritorial rods along with the cutting edge formed by the beak tritor of the mandibular plate could constitute a robust structure probably able to cut pieces of a larger organism. In addition, the presence of flat tritors in the palatine and mandibular tooth plates could have been useful for crushing prey items.

**Paleobiogeography**—Presently, there are no holocephalians living in the South Ocean surrounding the Antarctic continent (Nelson, 2006). Living Chimaeriformes are composed of three families, six genera, and 50 species (Roskov et al., 2014). They exhibited their highest diversity worldwide in the Late Cretaceous (Stahl and Chatterjee, 2002). However, the group is relatively poorly known from Cretaceous rocks of the Southern Hemisphere, in which it is represented by *Ptyktoptychion* Lees, 1986 (Albian, Australia), *Callorhynchus*, *Ischyodus*, *Elasmodes* Newton, 1878, *Harriotta* (Albian–Cenomanian, Australia), *Belgorodon* Nessov and Averianov, 1996 (Cenomanian–Coniacian, Australia), *Ischyodus* (Campanian–Maastrichtian, New Zealand, Antarctica), *Chimaera* (Maastrichtian, Antarctica),

TABLE 2. List of fossil holocephalian fishes found in Antarctica.

Taxa	Age	Stratigraphy	Locality	Author
<i>Chimaera seymourensis</i>	late Eocene	La Meseta Fm.	Marambio (Seymour) Island	Ward and Grande, 1991
<i>Ischyodus dolloi</i>	late Eocene	La Meseta Fm.	Marambio (Seymour) Island	Ward and Grande, 1991
<i>Callorhynchidae</i> indet.	early Eocene	La Meseta Fm.	Marambio (Seymour) Island	Kriwet and Gazdzicki, 2003
<i>Callorhynchus stahli</i>	early Eocene	La Meseta Fm.	Marambio (Seymour) Island	Kriwet and Gazdzicki, 2003
<i>Callorhynchus</i> sp.	late Maastrichtian	López de Bertodano Fm.	Marambio (Seymour) Island	Martin and Crame, 2006
<i>Callorhynchus torresi</i>	late Maastrichtian	López de Bertodano Fm.	Marambio (Seymour) Island	Otero et al., 2013
<i>Chimaera zangerli</i>	late Maastrichtian	López de Bertodano Fm.	Marambio (Seymour) Island	Stahl and Chatterjee, 1999
<i>Ischyodus dolloi</i>	early Maastrichtian	López de Bertodano Fm.	Marambio (Seymour) Island	Stahl and Chatterjee, 2002
Rhinochimaeridae indet.	late Campanian	Snow Hill Island Fm.	James Ross Island	Otero et al., 2014
<i>Callorhynchus</i> sp.	late Campanian	Snow Hill Island Fm.	James Ross Island	Otero et al., 2014
<i>Edaphodon snowhillensis</i> , sp. nov.	late Campanian	Snow Hill Island Fm.	James Ross Island	This contribution

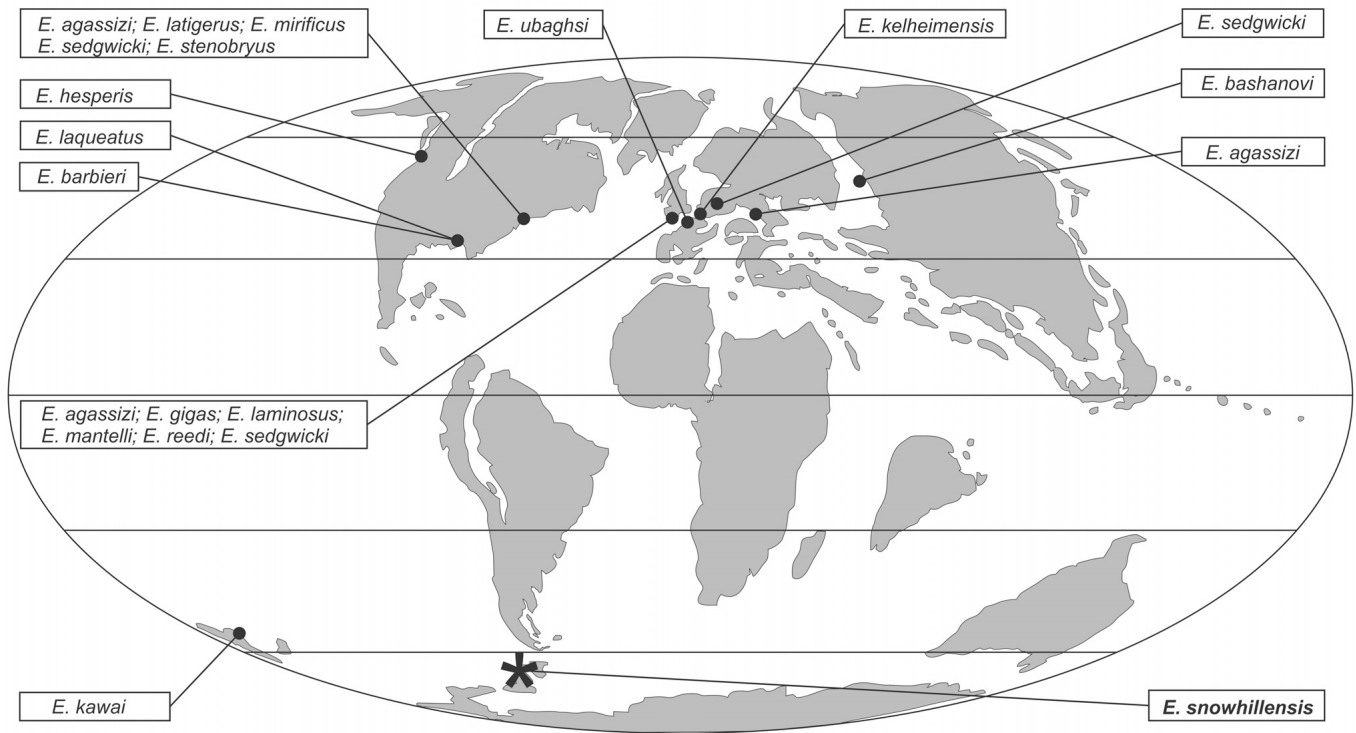


FIGURE 7. Simplified paleogeographic distribution of species of *Edaphodon* during the Late Cretaceous (modified from Blakey, 2013).

*Callorhynchus* (Cenomanian, New Zealand; late Campanian, Antarctica), indeterminate rhinochimaerid (late Campanian, Antarctica), and *Edaphodon* (late Campanian–lower Maastrichtian of Antarctica, Stahl and Chatterjee, 2002; middle Campanian–middle Danian of New Zealand, Consoli, 2006; upper Maastrichtian of Antarctica, Otero et al., 2013, 2014, this contribution). The scarce record from the Southern Hemisphere is probably due to more limited survey and a smaller continental surface than in the Northern Hemisphere.

Antarctic holocephalians are known from the Late Cretaceous to the early Eocene. *Edaphodon snowhillensis*, sp. nov., is the oldest ‘edaphodontid’ from Antarctica (see Table 2) and the southernmost record of the genus (Fig. 7). Moreover, among all the fishes recorded from Antarctica, the discovery of *Ischyodus dolloi* in Cretaceous and Eocene strata shows that this species is the sole Antarctic fish that persisted after the K–T extinction event.

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