

## NEOGENE 'HORN SHARKS' *HETERODONTUS* (CHONDRICHTHYES: ELASMOBRANCHII) FROM THE SOUTHEASTERN PACIFIC AND THEIR PALEOENVIRONMENTAL SIGNIFICANCE

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**Abstract.** Horn sharks (Elasmobranchii: *Heterodontus* Blainville) correspond to a genus of chondrichthyan fishes, mostly distributed in warm-temperate to tropical regions of the Pacific and Indian Oceans. The fossil record shows that, in contrast to its current distribution, horn sharks were widely distributed both in the eastern Pacific and western Atlantic during the Neogene, being subsequently extirpated from some of these areas. In this contribution, we describe new *Heterodontus* teeth from three Pliocene localities in the Coquimbo Region, in north-central Chile, and make an extensive revision of the fossil record of the genus in the Americas, in order to specify the timing of their extirpation in the southeastern Pacific and discuss the possible causes of this event. The new specimens described herein belong to a species with a *Heterodontus francisci* type dentition. Our analysis suggest that the removal of horn sharks occurred in the context of a general faunal turnover in the transition from Pliocene to Pleistocene, and that it was probably controlled by an interplay between the oceanographic, tectono-eustatic and ecological changes occurred in the region at that time.

**Key words.** Miocene. Pliocene. Pleistocene. America. Chile. Fossil. Elasmobranchs. Extirpation.

**Resumen.** 'TIBURONES CORNUDOS' *HETERODONTUS* (CHONDRICHTHYES: ELASMOBRANCHII) NEÓGENOS DEL PACÍFICO SURORIENTAL Y SU SIGNIFICADO PALEOAMBIENTAL. Los tiburones cornudos (Elasmobranchii: *Heterodontus* Blainville) conforman un género de peces condricios, principalmente distribuidos en regiones templado-cálidas a tropicales de los océanos Pacífico e Índico. El registro fósil muestra que, en contraposición a su distribución actual, durante el Neógeno los tiburones cornudos se distribuyeron ampliamente tanto en el Pacífico oriental como en el Atlántico occidental, siendo posteriormente extirpados de algunas de estas áreas. En este trabajo, describimos nuevos dientes *Heterodontus* de tres localidades del Plioceno en la Región de Coquimbo, en el centro-norte de Chile, y realizamos una extensa revisión del registro fósil del género en las Américas, para precisar el momento en que se produjo su extirpación en el Pacífico suroriental y discutir las posibles causas de este acontecimiento. Los nuevos materiales aquí descritos pertenecen a una especie con dentición del tipo *Heterodontus francisci*. Nuestros análisis sugieren que la extirpación de los tiburones cornudos se produjo en el contexto de una renovación general de la fauna en la transición del Plioceno al Pleistoceno, y que fue probablemente controlada por una interacción entre los cambios oceanográficos, tectono-eustáticos y ecológicos ocurridos en la región durante aquellos tiempos.

**Palabras clave.** Mioceno. Plioceno. Pleistoceno. América. Chile. Fósil. Elasmobranchios. Extirpación.

*HETERODONTUS* Blainville, 1816 is a genus of elasmobranch fishes represented by nine living species that mainly inhabit warm-temperate to tropical regions of the Pacific and Indian oceans (Compagno *et al.*, 2005; Nelson, 2006). Three of these species occur in the eastern Pacific, namely: *Heterodontus francisci* (Girard, 1854), *Heterodontus mexicanus* Taylor and Castro-Aguirre, 1972 and *Heterodontus quoyi* (Frémin-

ville, 1840), with a distribution restricted to tropical and subtropical latitudes (Fig. 1), from the coasts of California to those of Ecuador and Peru (Compagno *et al.*, 2005; Kaschner *et al.*, 2016; Froese and Pauly, 2018; OBIS, 2018).

The fossil record suggests that horn sharks originated in the Jurassic and had a wide global distribution during the Mesozoic and Paleogene, being present in Europe, Central

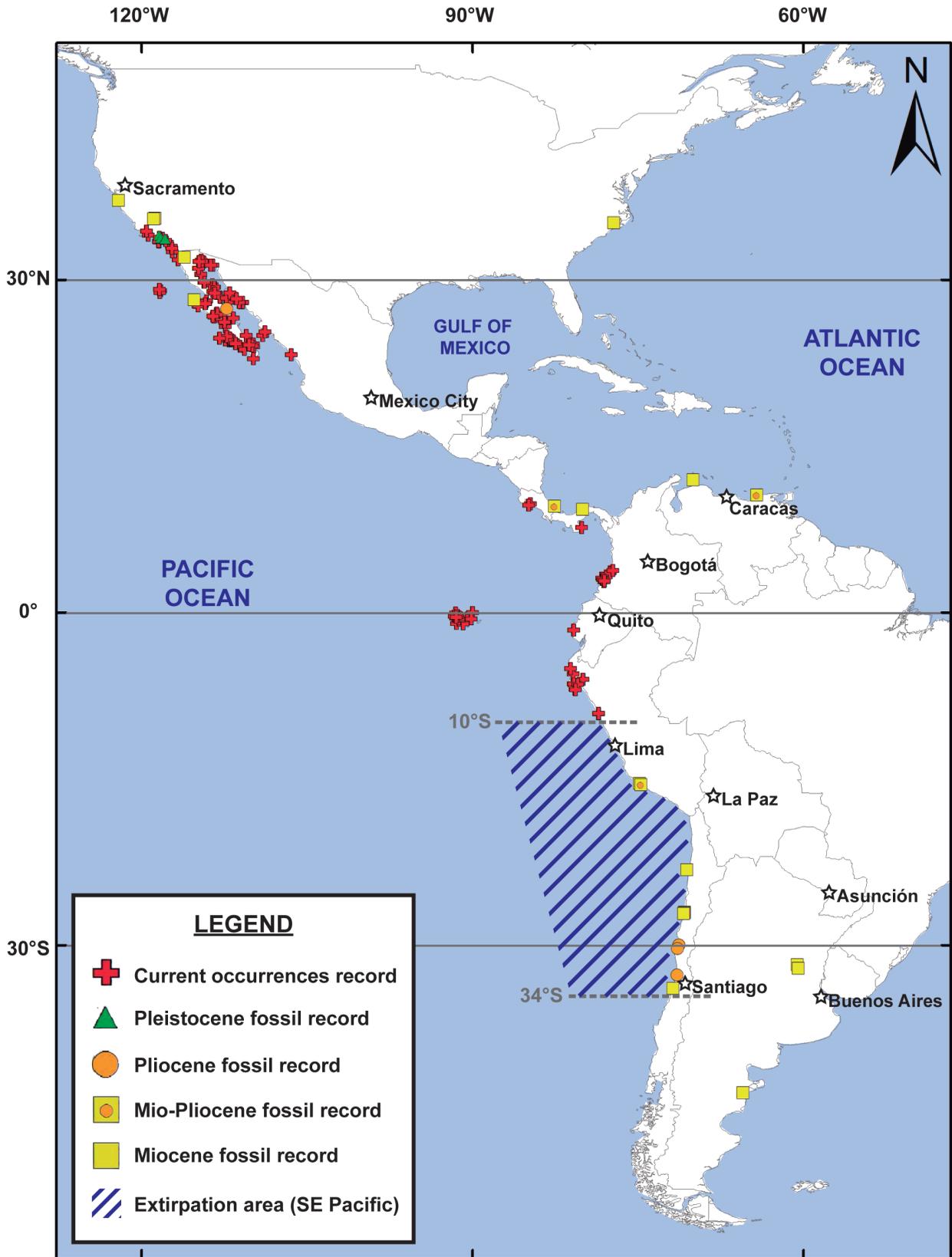


Figure 1. Distribution of *Heterodontus* in the Americas, from Neogene to Recent. Fossil records have been compiled from specialized literature (references in Table 1), while current occurrence records have been taken from the UNESCO's Ocean Biogeographic Information System database (OBIS, 2018). Note the existence of a large extirpation area, with no horn sharks occurrences at Recent times.

and Western Asia, northern Africa, South America, North America and Australia (Christiansen and Bonde, 2002; Fitzgerald, 2004; Kennedy *et al.*, 2008; Cappetta, 2012). In the Americas, their fossil record ranges from the Cretaceous to the Pleistocene (*e.g.*, Cappetta, 2012; Carrillo-Briceño *et al.*, 2018: tables S3-S4). Their current distribution, however, is very limited (Fig. 1). The Neogene fossil record of the Americas, for instance, indicates a wider distribution that included also the Western Atlantic coast, as far as Argentina (*e.g.*, Ameghino, 1906; Cione, 1978; Case, 1980; Laurito, 1999; Cione *et al.*, 2000, 2005, 2011; Aguilera, 2010; Carrillo-Briceño *et al.*, 2015, 2016, 2018). Likewise, for the eastern Pacific coast, the fossil record suggests that *Heterodontus* reached latitudes far as south as 34°S during the Neogene, thus inhabiting waters off the coast of north and central Chile (*e.g.*, Walsh, 2001; Suárez *et al.*, 2003, 2006; Carrillo-Briceño *et al.*, 2013; Suárez, 2015), where today it is absent. This region is nowadays affected by the upwelling of cold waters, brought from the sub-Antarctic region by the Humboldt Current (Marchant *et al.*, 2007; Montecino and Lange, 2009), which creates an environment that contrasts with the ecological preferences of horn sharks. Their ancient presence at mid-latitudes agrees well with the warmer water conditions suggested for this region during Miocene and Pliocene times (*e.g.*, Ibaraki, 1997; Tsuchi, 2002; Dekens *et al.*, 2007; Nielsen and Glodny, 2009; Le Roux, 2012). Therefore, the subsequent extirpation of *Heterodontus* from mid-latitudes in the southeastern Pacific is probably the consequence of deep paleoenvironmental changes and seems to be related to the oceanographic, tectonic and ecological changes that took place in that region during Plio–Pleistocene times. The reasons that explain the decline of horn sharks in the southeastern Pacific are possibly different from those for which they were extirpated from the western Atlantic, since these events occurred at different times and in dissimilar oceanographic and tectonic settings. In any case, to identify the controls that may have caused the extirpation of *Heterodontus*, it will be necessary to pinpoint the timing of its decline and disappearance in the fossil record.

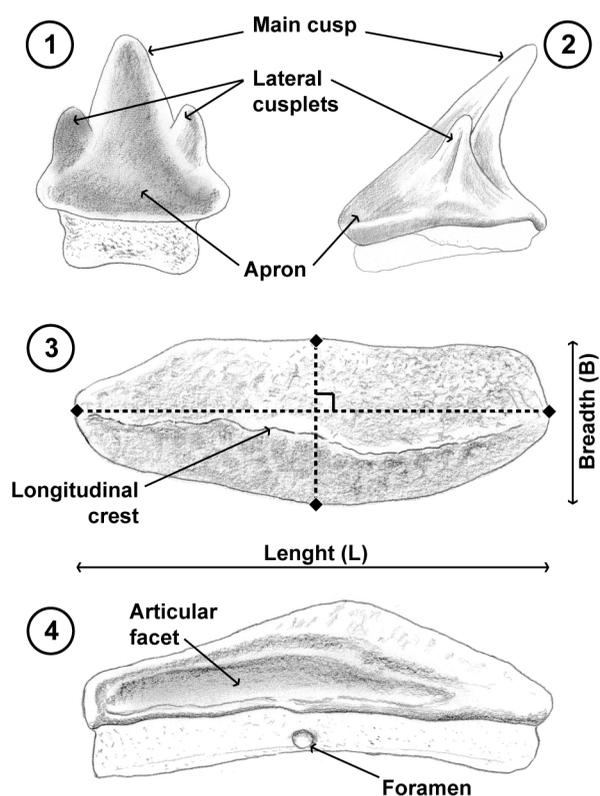
In this contribution, we report and describe an abundant occurrence of horn shark's fossil teeth collected from new localities in the Coquimbo Region (north-central Chile). We also analyze the *Heterodontus* fossil record in the Americas, reviewing the geographic and chronostratigraphic distribu-

tion of the source localities in order to discuss the paleobiogeographic evolution of the genus and the time and mode in which the extirpation of *Heterodontus* may have occurred.

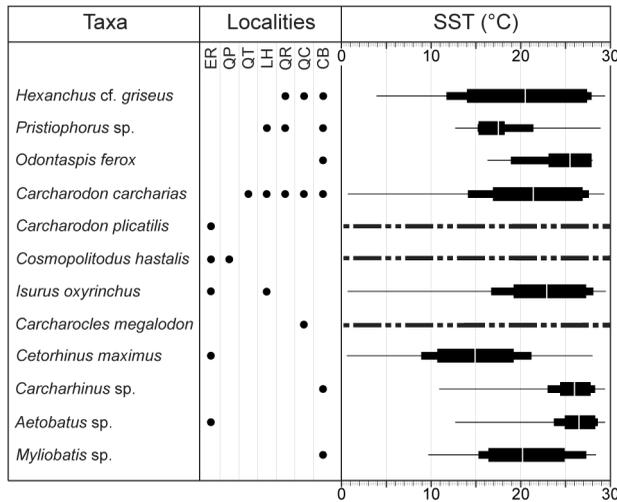
## MATERIALS AND METHODS

The specimens herein described were collected through sediment sampling at three fossiliferous sites—called 'Lomas del Sauce' (LdS), 'Los Clarines' (LCIV), and 'Quebrada Camarones' (QCT)—and subsequent sieving using meshes with 6, 3, and 2 mm openings. This allowed generating three rich collections of anterior and lateral teeth (89 from LdS, 46 from LCIV and 17 from QCT), most of which are complete and well-preserved. The specimens are housed at the Sala de Colecciones Biológicas of the Universidad Católica del Norte, Chile (SCBUCN).

Measurements and tooth terminology used in the text are illustrated in Figure 2. Taxonomic determination of the material were achieved by following the illustrated descriptions provided by Taylor (1972), Reif (1976), Herman *et al.*,



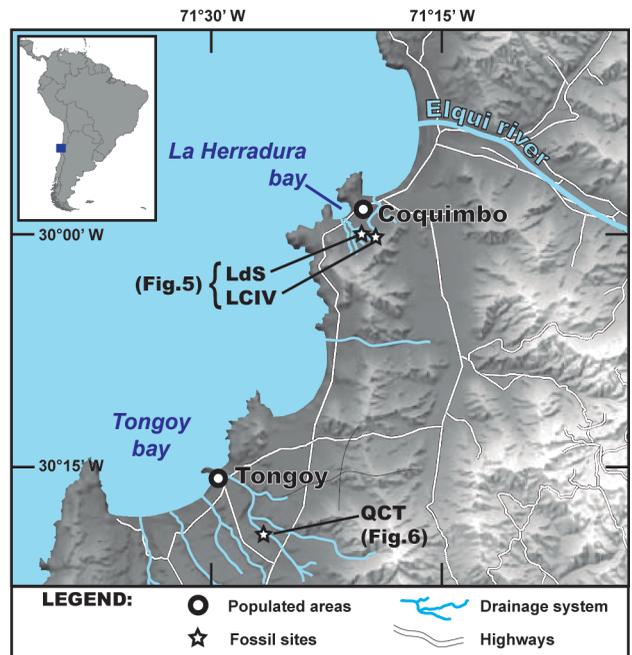
**Figure 2.** Tooth measurements and terminology used in this work. 1, anterior tooth, labial view; 2, anterior tooth, profile view; 3, lateral tooth, occlusal view; 4, lateral tooth, lingual view.



**Figure 3.** Chondrichthyan fossil record of the Coquimbo Formation. Source localities in the Tongoy area: ER, 'El Rincón'; QP, 'Quebrada Pachingo'; QT, 'Quebrada Tongoy' (Quebrada Camarones). Source localities in the Coquimbo area: LH, 'La Herradura'; QR, 'Quebrada Las Rosas'; QC, 'Quebrada El Culebrón'; and CB, 'Cantera Baja' (Long, 1993a; Suárez y Marquardt, 2003; Le Roux *et al.*, 2006; Staig *et al.*, 2015; Suárez, 2015). Sea surface temperatures (SST), are illustrated for the regions of occurrences of each taxon, based on the current records provided by Kaschner *et al.* (2016) in "Aquamaps" (datasets in Supplementary Online Material 1). For each taxon, it is shown: the temperature range for all the occurrences (thin bars), for the records located between the 10th and 90th percentiles (medium bars), and for those located between the 20th and 80th percentiles (thick bars). Mean temperature for each species is also shown (vertical white line inside the thick bars). For taxa with no SST data available, a dashed line is used.

(1993) and Cappetta (2012), as well as through comparative analyses with fossil and recent specimens from the following collections: Muséum National d'Histoire Naturelle (MNHN collection, Paris); Paläontologisches Institut und Museum at the Universität Zürich (PIMUZ collection, Zurich); Naturhistorisches Museum Basel (BNHM collection, Basel); Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas de la Universidad Nacional Experimental Francisco de Miranda (CIAAP-UNEFM collection, Coro) and René Kindlimann private collection with public access (RK collection, Uster).

Finally, an extensive data collection was made from the literature, in order to determine the chronostratigraphic and geographic distribution of the fossil records of *Heterodontus* in the Americas. Additionally, we collected information about current distributions and environmental preferences of horn sharks and other chondrichthyans from global information systems (Kaschner *et al.*, 2016; Froese and Pauly, 2018;



**Figure 4.** Location of the source localities, in the Coquimbo and Tongoy areas, Chile. Abbreviations: LCIV, Los Clarines; LdS, Lomas del Sauce; QCT, Quebrada Camarones.

OBIS, 2018). Sea surface temperatures (SST) in areas of occurrence of these taxa have been obtained by registering the mapping parameters provided by Kaschner *et al.* (2016) for each species; in particular, the information associated with the cells used for creating environmental envelope (see SST datasets in the Supplementary Online Material, 1–2). When available, improved versions of the distribution maps were used instead of the default computer-generated maps. The environmental data are derived from the United States National Centers for Environmental Prediction (NCEP) SST Climatology observations and from the Institut Pierre-Simon Laplace (IPSL) Climate model Special Report on Emissions Scenarios (SRES) A2 simulations, as explained in Kesner-Reyes *et al.* (2016). All this information served as input for analysis and discussion.

**GEOLOGICAL SETTING**

The collected material comes from three sites of the Neogene marine sediments of the Coquimbo Formation, in north-central Chile, and it is the first record of *Heterodontus* for this geological unit (Fig. 3). Both LdS and LCIV sites are placed in the city of Coquimbo, in front of La Herradura bay; while QCT site is located in the Tongoy bay area (Fig. 4).

**Coquimbo**

In the Coquimbo area (Fig. 4), the marine sediments include sandstones, siltstones, limestones, coquinas, and conglomerates. The whole set has been assigned to the Pliocene and Pleistocene on the basis of its fossil mollusk fauna (Herm, 1969; Emparan and Pineda, 2000). Different levels of marine terraces have been carved into these sediments. Both LdS (29° 59' 42" S; 71° 20' 02" W) and LCIV (29° 59' 51" S; 71° 19' 08" W) sites were excavated on the 'Serena II' terrace *sensu* Paskoff (1970), at about 60 m and 80 m above sea level, respectively (Fig. 5). This terrace is mostly composed by a succession of siltstones, sandstones and coquinaceous layers of Pliocene age

(Herm, 1969; Paskoff, 1970; Emparan and Pineda, 2000). Locally, some facies of sandstones and coquinaceous conglomerates of Pleistocene age appear, whose fauna and taphonomic and sedimentological characteristics are remarkably different. They are regression sediments that are distributed in some high areas of the terrace, resting on the Pliocene series in erosional discontinuity (Herm, 1969; Paskoff, 1970). Based on their litho- and biofacies, LdS can be entirely assigned to the Pliocene series, whereas in LCIV both Pliocene and Pleistocene series crop out (Fig. 5). At LdS, the Pliocene age is supported by the association of the gastropod *Chorus grandis*, the bivalve *Anadara chilensis* and the aquatic sloth *Thalassocnus carolomartini* in their fossiliferous

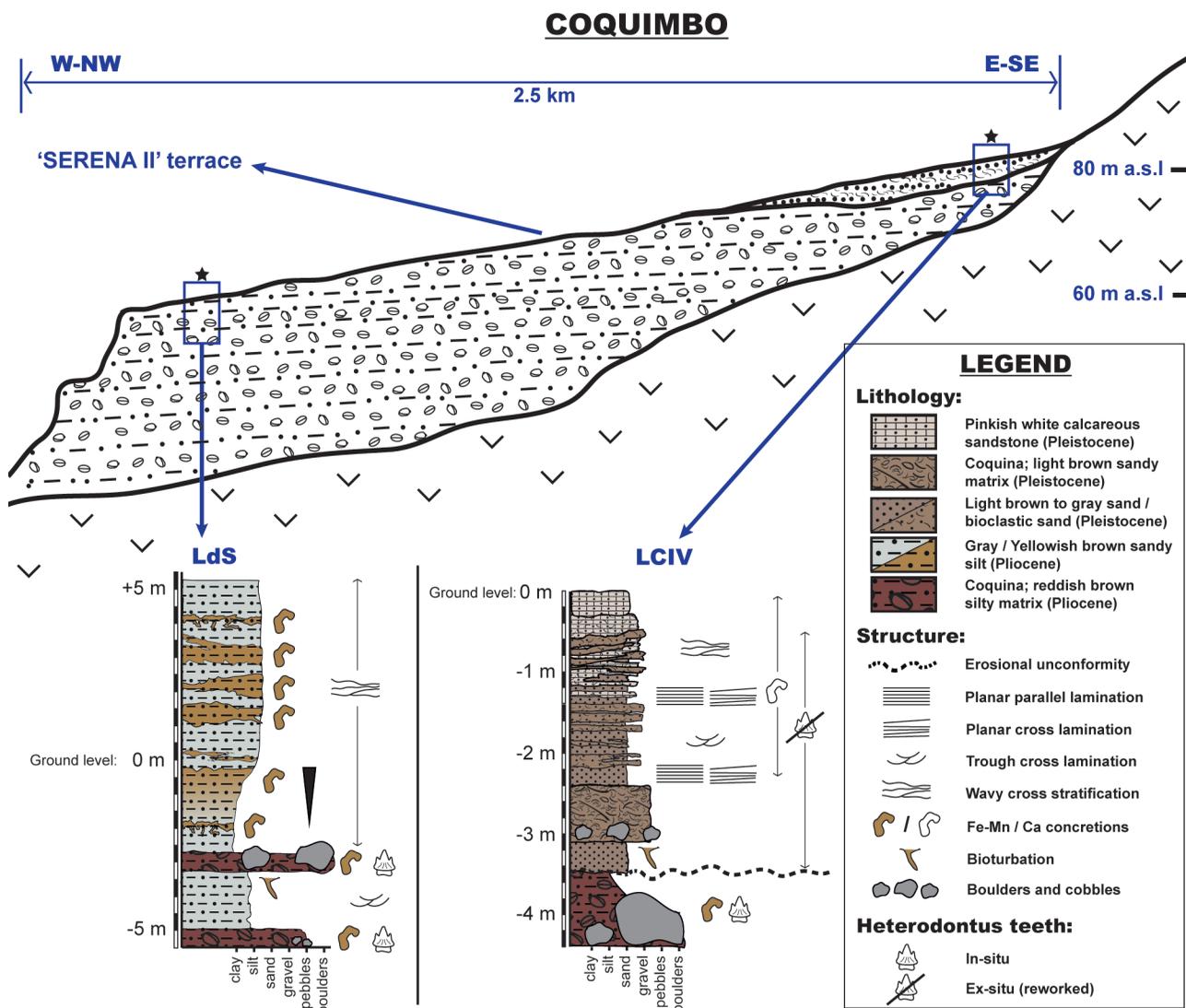


Figure 5. Stratigraphy of LdS and LCIV sites, in the Coquimbo Bay area.

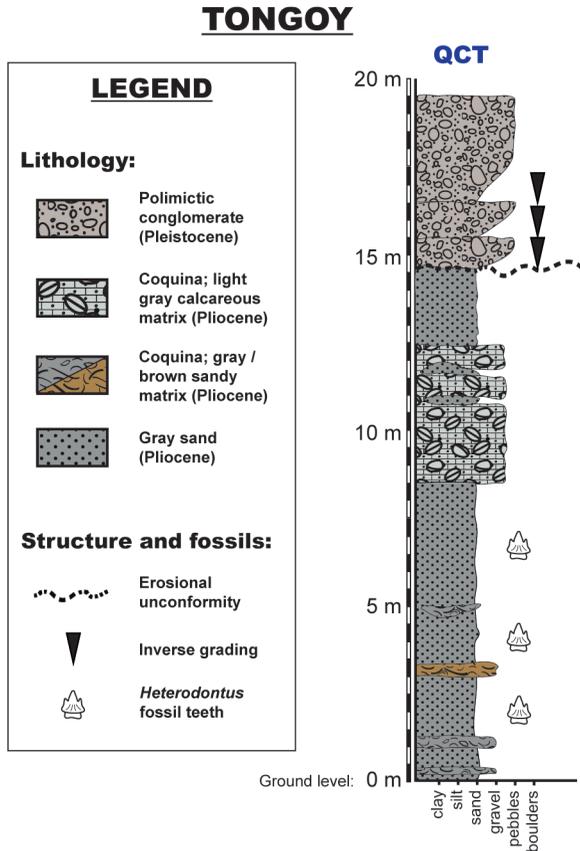


Figure 6. Stratigraphy of QCT site, in the Tongoy area.

layers (De Los Arcos *et al.*, 2017). At LCIV, the association of the gastropods *Hermineospina mirabilis*, *Hermineospina philippi*, *Chorus doliaris*, and *Chorus covacevichi* suggest a Pliocene age for the basal unit (DeVries, 1997; DeVries and Vermeij, 1997; Guzmán *et al.*, 2000; Nielsen, 2013). The upper member of LCIV is a succession of sand, limestones and coquinaeous layers that overlies the Pliocene sediments with an erosional disconformity. Their mollusk fossil content includes the bivalves *Argopecten purpuratus*, *Cyclocardia compressa*, *Mesodesma donacium*, and *Mulinia edulis*, as well as the gastropods *Incatella cingulata*, and *Concholepas concholepas*. This favors a Pleistocene age for the upper member, since all these species are forms which appeared or acquired massive development in the region during that epoch (Herm, 1969; DeVries, 1995; Guzmán *et al.*, 2000; Tsuchi, 2002).

**Quebrada Camarones, Tongoy**

In the Tongoy area (Fig. 4), the marine sediments appear

as a succession of muds, sands, coquinas and gravel infilling an extensive paleobay surrounded by topographic highs to the west and to the east (Le Roux *et al.*, 2006). The stratigraphic interval encompassed by the whole set is broad: while the basal layers date back to the early Miocene, the younger strata were deposited during the Pleistocene (Paskoff, 1970; Martínez-Pardo, 1979; Martínez-Pardo and Caro, 1980; Le Roux *et al.*, 2006). As in Coquimbo, they form marine terraces that have been affected by fluvial erosion, thus resulting in different ravines where the stratigraphy is exposed. One of them is Quebrada Camarones, next to the town of Tongoy. QCT site (30° 19' 14" S; 71° 26' 32" W; Fig. 4) is located on the north bank, where a 20 m-thick sedimentary succession crops out on a slope (Fig. 6). The strata where *Heterodontus* materials come from, overlies coquinaeous layers that contain the gastropods *Concholepas kieneri* and *Concholepas nodosa*, and underlies calcareous coquinaeous beds with the gastropods *Chorus grandis*, *Chorus giganteus*, and *C. doliaris*. Both assemblages support a Pliocene age for the source beds (DeVries, 1995, 1997; Nielsen, 2013).

**SYSTEMATIC PALEONTOLOGY**

- Class CHONDRICHTHYES Huxley, 1880
- Subclass ELASMOBRANCHII Bonaparte, 1838
- Order HETERODONTIFORMES Berg, 1937
- Family HETERODONTIDAE Gray, 1851
- Genus *Heterodontus* Blainville, 1816

**Type species.** *Squalus philippi* Schneider, 1801; original designation in Bloch and Schneider (1801). Recent.

?*Heterodontus francisci* (Girard, 1854)

Figure 7

**Locality and age.** Coquimbo (LdS, LCIV) and Tongoy (QCT), Pliocene.

**Referred material.** 22 anterior teeth (SCBUCN-6656 to SCBUCN-6661, and SCBUCN-6700 to SCBUCN-6703) and 130 lateral teeth (SCBUCN-6649 to SCBUCN-6655, SCBUCN-6687 to SCBUCN-6699, and SCBUCN-6704 to SCBUCN-6738).

**Anterior teeth (Fig. 7.1–3).** Anterior teeth are rather small,

and usually higher than wide. They range from 2.4 to 3.6 mm in height, and from 1.9 to 3.6 mm in width. Their crown is tricuspid, with a triangular and erect main cusp and two lateral cusplets, which are joined to the base of the main cusp and converge slightly towards it. The height of the main cusp is significantly greater than that of the lateral cusplets.

The crown expands over the root both labially and lingually, forming a wide apron (Fig. 2). On the lingual face the apron rests over the root, reaching the root edge. On the labial face, it extends beyond the root with a rectilinear basal outline. In profile view, the lingual face of the crown is strongly convex, whereas the labial face shows a more rectilinear outline.

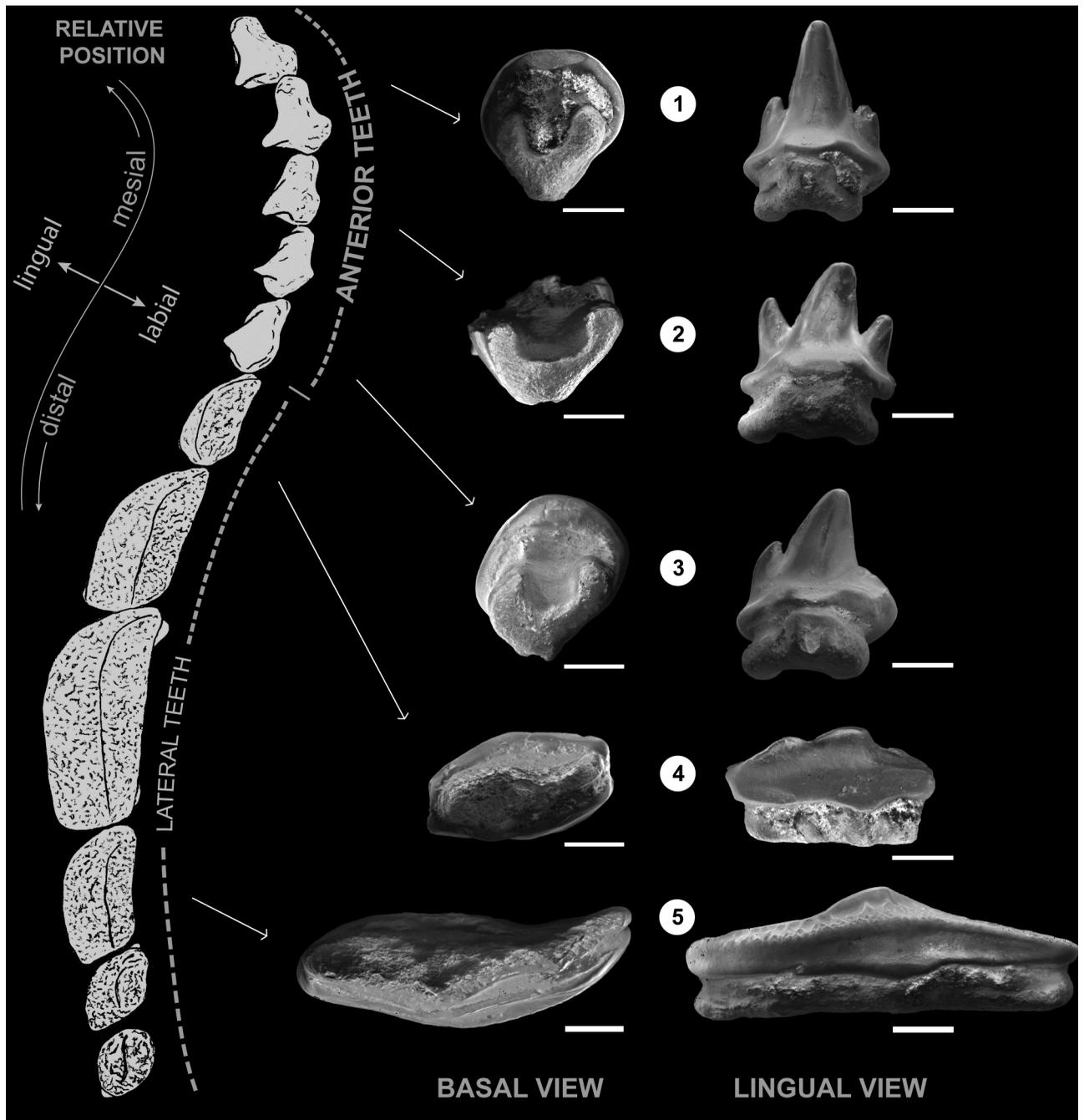


Figure 7. *Heterodontus* fossil teeth found in the Coquimbo Bay area, in basal and lingual view. 1, SCBUCN-6658; 2–3, SCBUCN-6660; 4, SCBUCN-6650; 5, SCBUCN-6655. This series partially shows the continuous morphological transition that exists from anterior to lateral teeth in *Heterodontus*. Their functional positions, within a *Heterodontus* jaw, are illustrated by means of the scheme on the left side. Scale bar = 1 mm.

The root is low and narrower than the crown. It is 'V'-shaped in basal view, showing two well-developed branches, which join towards the lingual side (Fig. 7). It also differentiates a lingual protuberance, which is partially covered by the apron of the crown. In many specimens this protuberance is pierced by a foramen, in the middle of the lingual root face. This medio-lingual foramen seems to be connected by a duct with a central foramen, which is located in the middle of the basal face.

**Lateral teeth (Fig. 7.4–5).** The lateral teeth are larger than the anterior ones and, in contrast to the latter, they are wider than high. They range from 1.4 to 4 mm in height, and from 3.6 to 11.6 mm in width. They are molariform-like teeth, which show a mesio-distally elongated and labio-lingually compressed shape. The crown extends beyond the root at all points in occlusal view, and it is slightly curved, showing an oval to sigmoidal shape. In lingual and profile view, it is cambered to nearly triangular, because of the presence of a keel-like longitudinal crest on its occlusal face (Figs. 2, 7).

The crown is strongly textured by folding of the enameloid. The longitudinal crest, mesio-distally oriented, runs through the whole occlusal face in a roughly medial position, following the outline of the lingual edge of the crown. From this crest arise numerous short ridges, which intertwine and extend towards both the lingual and labial edges of the crown, thus defining an ornamentation of enameloid ridges and alveoli. Towards its lingual edge, the crown also bears a medio-lingual articular facet (Figs. 2, 7), which is elongated in the mesio-distal direction.

The root is low and narrower than the crown and has a flat to slightly concave basal face. It bears a lingual protuberance pierced by a foramen, which appears to be connected with other two foramina, which are sometimes observed in the labial face of the root.

**Heterodonty.** Morphological transition between anterior and lateral teeth is continuous, and can be clearly appreciated in both basal and lingual views. This progressive change is partially illustrated in Figure 7.

In lingual view, while the symphyseal tooth is symmetrical, in more distal anterior teeth the main cusp of the crown is bent distally (Fig. 7.1–3). In the latter, there is also a difference in the size of the lateral cusplets, being smaller the distal one, towards which the main cusp bends. For the first

lateral tooth, both the main cusp and the mesial lateral cusplet have significantly reduced their heights, while the distal lateral cusplet is barely noticeable. So, at this point, the tooth is no longer tricuspid but it rather has a keel-like shape (Fig. 7.4). For lateral teeth in more distal positions, the keel acquires their characteristic triangular to cambered outline (Fig. 7.5).

In basal view, while the root of symphyseal teeth is symmetrical, with two wings of equal size arranged in 'V' form (Fig. 7.1), in the more distal anterior teeth the distal wing becomes smaller relative to the mesial wing (Fig. 7.2–3). For the first lateral teeth, the distal wing has become much reduced, and the rest of the base has broadened into a more rectangular form (Fig. 7.4). This trend continues in more distal lateral teeth, where the outline of the root gets to resemble that of the crown (Fig. 7.5).

## DISCUSSION

### *Taphonomic comments on Heterodontus teeth*

In contrast to all the teeth found in Pliocene outcrops from Tongoy and Coquimbo, many of the teeth found in the Pleistocene of LCIV exhibit intense abrasion, suggesting that they have undergone a significant reworking. Since the Pleistocene layers rest over fossiliferous Pliocene strata in erosional disconformity, these teeth could well have been remobilized from them. The addition of reworked Pliocene material within the Pleistocene layers can also be verified by: (1) the presence of fragments of the Pliocene coquina lithofacies, and (2) the inclusion of internal molds of mollusks, filled by the reddish brown silt which characterize the Pliocene lithofacies, rather than by the light brown to reddish gray sandy matrix of the Pleistocene units (compare in Figure 5). The intense dissolution observed in the calcareous mollusks from the Pliocene contrasts with the good preservation of the Pleistocene shells, indicating significant differences on the taphonomic processes that affected both fossil assemblages. Iron and manganese oxide mineralization, one of the most widespread features in Pliocene sediments and bioclasts, is also observed in the *Heterodontus* teeth found in Pleistocene layers. Altogether, these observations suggest an ex-situ condition for teeth found in Pleistocene sediments, so one should be cautious when making biostratigraphic and paleoecological interpretations of them.

### Taxonomic inferences

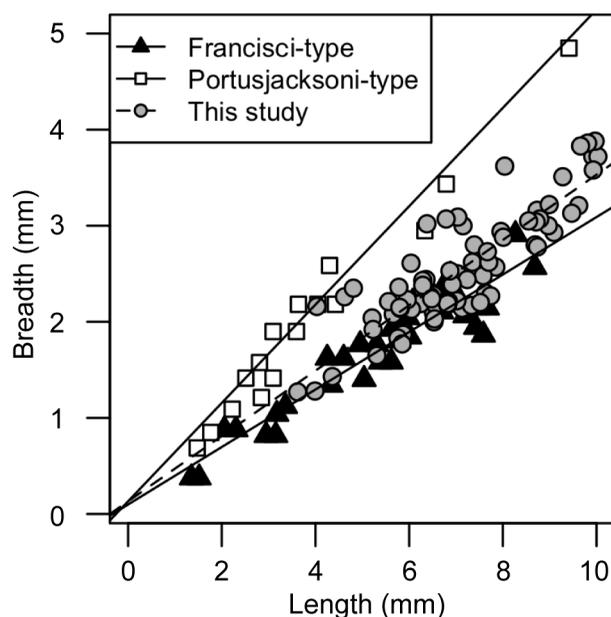
Taylor (1972), Reif (1976) and Herman *et al.* (1993) have studied the dentition of current horn sharks, noticing some variances among species. According to Reif (1976) there are two types of dentition in the living species of *Heterodontus*: a) the 'francisci-type' of dentition, in which the molariform-like teeth are slender and have a strong longitudinal crest, as in *H. francisci* (e.g., Reif, 1976: fig. 2; Herman *et al.*, 1993: pl. 23–30) or *H. quoyi* (e.g., Reif, 1976: fig. 4; Herman *et al.*, 1993: pl. 31–38); and b) the 'portusjacksoni-type' of dentition, with very broad molariform-like teeth that no longer looks like a keel, as in the case of *Heterodontus portusjacksoni* (Meyer, 1793) (e.g., Reif, 1976: fig. 5; Herman *et al.*, 1993: pl. 3–22). These two types are equivalent to the 'carinate molar' and the 'rounded molar' ones previously proposed by Taylor (1972). Although useful for morphological distinctions, it has not been proven that dentition types of Taylor (1972) and Reif (1976) have a systematic significance, so that the

groups derived from these distinctions may not represent monophyletic clades within the genus.

In the case of the lateral teeth from Coquimbo and Tongoy, most of them are slender (Fig. 8) and show a well-developed longitudinal crest, as in teeth of the *francisci*-type. They usually show a rather blunt keel. Some authors (e.g., Reif, 1976) have proposed the strength of the keel as an additional criterion that would help to distinguish among different species with *francisci*-type dentition. This criterion, however, cannot be evaluated straightforwardly on isolated teeth, since the shape and prominence of the keel can vary widely depending on the ontogenetic stage of the individual and the functional position of the tooth in the jaw (e.g., Herman *et al.*, 1993: pl. 23–38).

Regarding the anterior teeth, they are usually tricuspid in adults; except for *Heterodontus zebra* (Gray, 1831), whose anterior teeth can have 5 cusps; and *H. portusjacksoni*, whose anterior teeth can be both unicuspid and tricuspid (Taylor, 1972; Reif, 1976; Herman *et al.*, 1993). The anterior teeth described herein are all tricuspid. The lateral cusplets are poorly developed in some specimens, a feature that is observed in *H. francisci* and differentiates it from *H. quoyi* (Hermann *et al.*, 1993), but not from other species such as *H. mexicanus* or even *H. japonicus* (e.g., Reif, 1976: fig. 25).

In summary, all the traits observed in both lateral and anterior teeth agree well with those observed in *Heterodontus francisci*, so their attribution to this species is possible. However, we have used an open nomenclature (e.g., Matthews, 1973; Bengtson, 1988; Sigovini *et al.*, 2016), since it is not possible to discard the presence of some other species with *francisci*-type dentition among these specimens. According to Reif (1976), there are five species showing such a dentition: the three 'American' species (*H. francisci*, *H. quoyi*, and *H. mexicanus*), currently distributed along the eastern Pacific; and two other species, *Heterodontus galeatus* (Günther, 1870) and *Heterodontus ramalheira* (Smith, 1949), currently confined to the southwestern Pacific and the Indian Ocean, respectively (Compagno *et al.*, 2005). In addition to the current species, there are two Neogene extinct species that have been described in the Americas: *Heterodontus janefirdae* Case, 1980, from the early Miocene of North Carolina, USA, and *Heterodontus uscariensis* Laurito, 1999, from the late Miocene–Pliocene of Costa Rica. Future works dedicated to an exhaustive taxonomic review of the *Heterodontus* fossil



**Figure 8.** Relationship between breadth and length of lateral teeth from Coquimbo and Tongoy (regression equation, breadth =  $0.34 \times \text{length} + 0.13$ ,  $r^2 = 0.76$ ). These measurements exclude fragmented teeth. Grow behavior of main crushing teeth of the Portusjacksoni-type (breadth =  $0.51 \times \text{length} + 0.13$ ,  $r^2 = 0.96$ ) and the Francisci-type (breadth =  $0.30 \times \text{length} + 0.10$ ,  $r^2 = 0.89$ ) is also shown, as reported by Reif (1976). Lines show the fit of linear regression. Coquimbo and Tongoy teeth show a better correlation with *H. francisci* than with *H. portusjacksoni*; however, an analysis of co-variance revealed that still exist significant differences with both of them (intercepts,  $P < 0.0001$  in both cases).

specimens reported for the Neogene basins of Western Atlantic (Fig. 1), could support the taxonomic validity of both species, or by the contrary, a relationship with the extant species on the Pacific side.

### ***Late Cenozoic paleobiogeography of *Heterodontus* in eastern Pacific***

The fossil record of *Heterodontus* in the Americas shows that horn sharks were widespread in the eastern Pacific and western Atlantic during the Neogene (Fig. 1; Tab. 1). This Neogene distribution, in both the eastern Pacific and western Atlantic, contrasts markedly with the current distribution of the genus in the Americas, now restricted to the Pacific coast from California to Ecuador and Peru (Compagno *et al.*, 2005; Kaschner *et al.*, 2016; Froese and Pauly, 2018; OBIS, 2018). In the southeastern Pacific region, one of the most striking differences between fossil and current records is observed: there is a large region of more than 2,500 km of coastline (between 10°S and 34°S) where no horn sharks have been observed at Recent times (Compagno *et al.*, 2005; Lamilla and Bustamante, 2005; Kaschner *et al.*, 2016; Froese and Pauly, 2018; OBIS, 2018); nevertheless, there have been several paleontological finds of *Heterodontus* in Neogene sediments of the same area (Fig. 1; Tab. 1). So far, the genus has already been reported from the early Miocene of Navidad (Suárez and Encinas, 2002; Suárez *et al.*, 2006), the middle to late Miocene of Mejillones (Suárez *et al.*, 2003) and Caldera (Walsh, 2001; Suárez *et al.*, 2004; Gutstein *et al.*, 2008; Villafaña, 2015), the late Miocene to early Pliocene of Pisco (Muizon and DeVries, 1985; Kindlimann, 1990), the Pliocene of Tongoy and Coquimbo (this work), and the late Pliocene of Horcón (Carrillo-Briceño *et al.*, 2013). These records suggest that horn sharks inhabited the region during most of the Neogene and that, at some stage after; they have been extirpated from that area (Fig. 1).

For the Pleistocene, teeth of *Heterodontus* have been found in California (Kanakoff, 1956; Fitch, 1966, 1968; Long, 1993b) and Ecuador (pers. obs. JDCB; ongoing research). In all the extirpation area, there have not been records of the genus from Pleistocene strata so far. So it seems like the last occurrence of *Heterodontus* in this region is around the Pliocene/Pleistocene boundary. In any event, research on Pleistocene fossil fishes from the southeastern Pacific is

still scarce, so that the absence of horn sharks teeth in the Pleistocene could well be a sampling effect, produced by a reduced sample size in the fossil record. Systematic sampling through complete sections, at different Pliocene and Pleistocene locations along the Chilean and Peruvian coast, could contribute to addressing the information gaps still existing in the fish fossil record, thereby improving our understanding of the *Heterodontus* extirpation pattern.

### ***Environmental controls on *Heterodontus* extirpation***

The extirpation of horn sharks from the southeastern Pacific occurred in the context of a general faunal turnover that has been widely recognized in the transition from Pliocene to Pleistocene in the region (*e.g.*, Philippi, 1887; Möricke, 1896; Herm, 1969; Rivadeneira and Marquet, 2007; Kiel and Nielsen, 2010; Valenzuela-Toro *et al.*, 2013; Villafaña and Rivadeneira, 2014; Rivadeneira and Nielsen, 2017). Oceanographic, tectono-eustatic and ecological factors have been mentioned as mutually non-exclusive drivers of this turnover:

***Oceanographic changes.*** Temperature of sea water is known to affect physiological processes in ectothermic organisms, which may influence their movement and distribution patterns (*e.g.*, Fry and Hart, 1948; Brett, 1971; Di Santo and Bennett, 2011; Johansen and Jones, 2011; Luongo and Lowe, 2018). In the case of horn sharks living in temperate regions, temperature seems to be a major limiting factor: in north-eastern Pacific, *Heterodontus francisci* occurs off central California only in warmer-than-usual years, being otherwise restricted to the southern coast of California; while in south-western Pacific, *H. portusjacksoni* is known to conduct long migrations of up to 800 km from the southeastern coast of Australia to Tasmania in summer, and back to the north in winter (Compagno, 2001).

In the study region, along most of the extirpation area, prevailing conditions are marked by the presence of cool Subantarctic water masses, brought by the effect of the Humboldt Current; one of the most prominent eastern boundary currents in the world's oceans. There, dominant equatorward alongshore wind stress induces the upwelling of the cold waters nearshore (Marchant *et al.*, 2007). These conditions contrast with the environmental preferences of horn sharks, which mainly occur in warm-temperate to tropical shallow waters on continental shelves (Compagno

TABLE 1 – Heterodontus fossil record in the Americas and age of source beds.

ID	Region	Country	Locality	Age	Formation	Reference(s)
1	Pacific E	United States	California	late Miocene	Santa Margarita Sandstone	Domning (1978)
2	Pacific E	United States	Kern County, California	early Miocene	Jewett Sand Fm.	Mitchell and Tedford (1973)
3	Pacific E	United States	California	middle Miocene	Temblor Fm.	Mitchell (1965)
4	Pacific E	United States	LACMIP 59, Playa del Rey, California	Pleistocene	[unspecified]	Fitch (1966)
5	Pacific E	United States	San Pedro, California	Pleistocene	Timms Point Silt	Fitch (1968)
6	Pacific E	United States	Costa Mesa, California	late Pleistocene	Palos Verdes Sand Fm.	Long (1993b)
7	Pacific E	United States	Capistrano Beach Palisades, California	Pleistocene	San Pedro sand stratum	Kanakoff (1956)
8	Pacific E	Mexico	Baja California	middle Miocene	Playa Rosarito Fm./ San Ignacio Fm.	González-Rodríguez et al. (2013)
9	Pacific E	Mexico	Isla Cedros, Baja California	late Miocene	Almejas Fm.	Barnes (2008); González-Rodríguez et al. (2013)
10	Pacific E	Mexico	Loma del Tirabuzón, Baja California Sur	Pliocene	Tirabuzon Fm.	Applegate (1978); González-Rodríguez et al. (2013)
11	Pacific E	Peru	El Jahuay, Sacaco	late Miocene	Pisco Fm.	Muizon and DeVries (1985)
12	Pacific E	Peru	Sacaco	late Miocene to early Pliocene	Pisco Fm.	Kindlimann (1990)
13	Pacific E	Chile	Caleta Herradura de Mejillones	middle to late Miocene	La Portada Fm.	Suárez et al. (2003)
14	Pacific E	Chile	Cerro Ballena Norte, Caldera	late Miocene	Bahía Inglesa Fm.	Villafaña (2015)
15	Pacific E	Chile	Las Arenas, Caldera	middle to late Miocene	Bahía Inglesa Fm.	Suárez et al. (2004)
16	Pacific E	Chile	Mina Fosforita, Caldera	late Miocene	Bahía Inglesa Fm.	Walsh (2001); Gustin et al. (2008)
17	Pacific E	Chile	Lomas del Sauce, Coquimbo	Pliocene	Coquimbo Fm.	This work
18	Pacific E	Chile	Los Clarines, Coquimbo	Pliocene	Coquimbo Fm.	This work
19	Pacific E	Chile	Quebrada Camarones, Tongoy	Pliocene	Coquimbo Fm.	This work
20	Pacific E	Chile	Horcón-Maitencillo cliffs	late Pliocene	Horcón Fm.	Carrillo-Briceño et al. (2013)
21	Pacific E	Chile	La Boca, Navidad	early Miocene	Navidad Fm.	Suárez and Encinas (2002); Suárez et al. (2006)
22	Atlantic W	Argentina	Paraná river valley, Entre Ríos province	middle to late Miocene	Paraná Fm.	Cione (1978); Cione et al. (2000, 2005, 2011); Arratia and Cione (1996)
23	Atlantic W	Argentina	Arroyo Ensenada valley, Entre Ríos province	late Miocene	Paraná Fm.	Cione et al. (2005, 2011, 2012); Arratia and Cione (1996)
24	Atlantic W	Argentina	Trelew, Chubut province	late Oligocene to early Miocene	Gaiman Fm.	Cione (1978; 1986; 1988); Cione and Pandolfi (1984); Arratia and Cione (1996); Cione et al. (2011)
25	Atlantic W	Venezuela	Cerro Barrigón	late Miocene to early Pliocene	Cubagua Fm.	Aguilera and Rodrigues de Aguilera (2001); Aguilera (2010)
26	Atlantic W	Venezuela	Casa Cantaure, Paraguaná peninsula	early Miocene	Cantaure Fm.	Carrillo-Briceño et al. (2016)
27	Atlantic W	Panama	Piña, Colón province	late Miocene	Chagres Fm.	Carrillo-Briceño et al. (2015)
28	Atlantic W	Costa Rica	Alto Guayacán, Limón province	late Miocene to early Pliocene	Uscari Fm.	Laurito (1999)
29	Atlantic W	United States	Craven County, North Carolina	early Miocene	Trent Fm.	Case (1980)

*et al.*, 2005; Nelson, 2006). As seen in Figure 9, mean SST for each *Heterodontus* species varies from 19.2°C to 26.3°C. Most of the records of horn sharks worldwide have occurred in regions with SST between 17.9°C and 23.9°C; while for the eastern Pacific species only, they are concentrated between 19°C and 24.2°C (Kaschner *et al.*, 2016; Froese and Pauly, 2018).

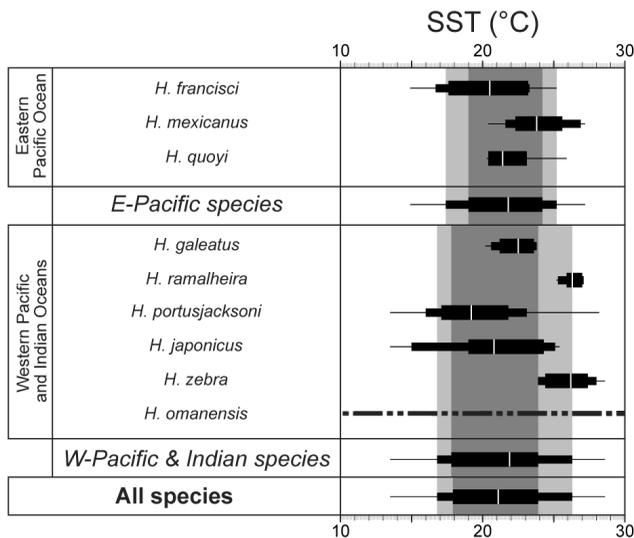
Although progressive cooling of the Humboldt Current System seems to have already begun by the end of Miocene (Covacevich and Frassinetti, 1990; Tsuchi, 2002; DeVries and Frassinetti, 2003; Le Roux, 2012), SST reconstructions show that conditions remained significantly warmer than today until about 3 Ma (Dekens *et al.*, 2007; Dowsett and Robinson, 2009; Dowsett *et al.*, 2013), collapsing afterwards towards colder temperatures. Warmer water conditions during Miocene and early Pliocene are also supported by the ecological preferences of microfossils (Ibaraki, 1990; Krebs *et al.*, 1992; Padilla and Elgueta, 1992; Marchant *et al.*, 2000; Tsuchi, 2002) and mollusk fauna (Herm, 1969; Covacevich and Frassinetti, 1980, 1983, 1986, 1990; Muizon and DeVries, 1985; DeVries and Frassinetti, 2003; Groves and

Nielsen, 2003) found in sediments from Chile and Peru.

The subsequent collapse of sea water temperature occurred at times of major global climatic and oceanographic changes (Zachos *et al.*, 2001; Ravelo *et al.*, 2004; Wara *et al.*, 2005; Lawrence *et al.*, 2006), being coeval with a major expansion of upwelling cells in the region (Ibaraki, 1997) and with the onset of modern oceanic conditions during late Pliocene (Le Roux, 2012). This cooling is thought to have exercised a control on the decrease in the diversity of mollusks (Herm, 1969; Covacevich and Frassinetti, 1990; DeVries, 2001; Rivadeneira and Marquet, 2007) and vertebrates (Cione *et al.*, 2007; Villafaña and Rivadeneira, 2014, 2018; Amson *et al.*, 2015) in the region.

**Tectonic activity and sea-level changes.** Many regions of the central Andes have experienced significant tectonic activity since late Pliocene (González *et al.*, 2003; Le Roux *et al.*, 2005, 2006, 2016; Clift and Hartley, 2007). In north-central Chile, facies changes observed in marine sediments reflects that the coastal area began to rise rapidly from 2.6 Ma, leading to the emergence of the platform during the Pleistocene (Le Roux *et al.*, 2005, 2006, 2016). This emergence, probably intensified by the coeval global sea level drop linked to the growth of polar ice caps (De Boer *et al.*, 2010), may have affected marine ecosystems by reducing living space on the platform, as proposed by Cione *et al.* (2007) for the extirpation of *Carcharias taurus*. Coastal uplift also imposed a physiographic uniformity (straight shorelines, small rivers, small embayments), which may have affected marine communities by destroying wave-sheltered environments and reducing habitat diversity (DeVries, 2001; Villafaña and Rivadeneira, 2014).

**Ecological feedbacks.** The effects that ocean cooling and reduction of habitats had on the faunal diversity may have triggered ecological feedbacks, that affected the ability of horn sharks to successfully adapt to these changes. DeVries (2001) mentioned a mass extinction event that, between 3 and 2 Ma ago, removed invertebrate taxa with warm-water affinities, as well as fauna from quiet-water, mixed substrate environments. Gastropods and bivalves, prey for larger vertebrates, experienced extremely elevated extinction rates at the species level (Rivadeneira and Marquet 2007; Kiel and Nielsen 2010), suggesting that trophic cascades may have also triggered vertebrate extinction during the faunal turnover (Villafaña and Rivadeneira, 2014). Then the loss of



**Figure 9.** Sea surface temperatures (SST) in areas of occurrence of *Heterodontus*, according to the records of Kaschner *et al.* (2016) in *Aquamaps* (datasets in Supplementary Online Material 2). For each taxa within the genus, the temperature range is shown for all the records (thin bars), for the records located between the 10th and 90th percentiles (medium bars), and for those located between the 20th and 80th percentiles (thick bars). Mean temperature for each species is also shown (vertical white line inside the thick bars). For *Heterodontus omanensis*, with no SST data available, a dashed line is used.

potential prey for sharks might have produced additional environmental stress for *Heterodontus*.

Therefore, all these controls (*i.e.*, oceanographic, through sea-water cooling; tectono-eustatic, through the reduction of habitats; and ecological, through the removal of prey) could have affected the distribution patterns of horn sharks in that time. In a recent analysis, Villafaña and Rivadeneira (2018) showed that both physiological tolerances (*e.g.*, salinity and thermal range) and life-history traits (*e.g.*, body size) were first-order modulators in the response of chondrichthyans to different environmental changes in the region. Regarding their body size, regional extirpation was more pronounced in small-sized forms (such as *Heterodontus*), being these forms more prone to experience strong range contractions related to different environmental changes. On the other hand, thermal tolerance may have represented an ecophysiological limit for horn sharks, since they cannot regulate its body temperature as do other species of the family Lamnidae, such as *Carcharodon carcharias*, *Isurus oxyrinchus*, and *Lamna nasus*. The expansion of the southern latitudinal range of these three genera (*Carcharodon*, *Isurus*, and *Lamna*) during the Neogene to the Recent, versus the contraction experimented concurrently by *Heterodontus*, brings support to this idea (Villafaña and Rivadeneira, 2018: tab. 3). However, it has also been found that *Heterodontus* can physiologically perform well in cooler conditions, being able to venture into deeper (and cooler) habitats for short periods of time (Luongo and Lowe, 2018). It appears thus that *Heterodontus* is able to live on those environments, either making incursions into higher latitudes or into cooler waters brought to low latitudes by the effect of currents. This capacity of horn sharks to perform in cooler waters would explain the fact that, despite their preference for tropical to subtropical environments, some of them have been found in areas with SST even lower than 17° C (Fig. 9). Then it seems that cooling by itself would not account for the extirpation of *Heterodontus*, so favoring the idea that tectono-eustatic and ecological drivers must have played an important role as well. Additionally, changes on other oceanographic variables, such as environmental oxygenation or salinity, could have also affect in the paleobiogeographic distribution of the genus. To evaluate this, further information on how these ecological variables evolved from Pliocene to Pleistocene in the region is needed.

## CONCLUSIONS

The fossil record of *Heterodontus* in Chile and Peru (between 10°S and 34°S) suggests that horn sharks inhabited the southeastern Pacific during most of the Neogene, and that they were extirpated from the region around the Pliocene/Pleistocene boundary. Oceanographic changes, such as sea water cooling; reduction of habitats, by tectonic activity and sea-level changes; and ecological feedbacks, such as trophic cascades; might have played a key role in this fate. Assessing the relative influence of these and other environmental factors in the extirpation of horn sharks from the region will require new data and research. Futures studies should be aimed at: (i) completing the fossil record by systematic sampling in Pliocene and Pleistocene marine sediments of Chile and Peru, (ii) refining the chronostratigraphy of the source localities, and (iii) unveiling additional imprints of climatic and tectonic changes within the Pliocene and Pleistocene marine sediments of the Chilean coast.

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