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Exceptional preservation of tracheal rings in a glyptodont mammal from the Late Pleistocene of Argentina

MARTÍN ZAMORANO

Exceptionally well-preserved material from a fossil mammal is presented. For the first time, several fragments of tracheal rings and cricoid cartilage assigned to *Panochthus* sp. (Xenarthra; Glyptodontidae) from the Late Pleistocene of Argentina are described in detail and figured. In this contribution, in addition to a meticulous description, a tracheal ring was reconstructed and compared to tracheal rings of domestic and wild mammals. As a result, among domestic mammals it is similar to those of *Sus scrofa domestica* (domestic pig), and among wild mammals to those of *Zalophus californianus* (California sea lion). Tracheal rings of fossil vertebrates have been recognized in birds (Cariamiformes and Anseriformes) and other dinosaurs (Theropoda). This is likely the first report of tracheal rings in a fossil mammal; future comparisons with extant xenarthrans could provide information on the paleobiological implications of this structure in glyptodonts, and allow making inferences about other fossil mammals.

Introduction

The trachea of mammals is a relatively flexible cartilaginous and membranous tube that extends from the cricoid cartilage of the larynx to the middle mediastinum, where it bifurcates into the main bronchi (König and Liebich 2005). The framework of the trachea is formed by C-shaped plates of hyaline cartilage (“tracheal rings”). These vary in shape according to the species and in some cases according to the location on the trachea. The number also varies according to the species (Sisson and Grossman 1982). The cartilaginous rings provide the tube: (i) some rigidity, otherwise it would collapse as the lungs expand; (ii) some expansion, to be able to accommodate any increase in air volume, by means of the flexibility of the hyaline cartilage, and the dorsal incompleteness of the rings; and (iii) flexibility and extensibility, to be able to follow the movements of the head, neck and larynx (Sisson and Grossman 1982; Powell et al. 2010). Tracheal cartilages originate from the splanchnic mesoderm and form the true tracheal skeleton (Acuña Navas et al. 2010).

Xenarthrans are a particular group of mammals, characteristic of the Neotropical Region, widely represented in the South American fossil record, both in temporal extension and frequency of records (Scillato-Yané 1977; Paula Couto 1979). The family Glyptodontidae is a group of armored xenarthrans, whose representatives reached large to very large sizes (Scillato-Yané and Carlini 1998; Fariña 2001; Zamorano et al. 2014a), even exceeding 2300 kg (Soibelzon et al. 2012), and are recorded from the middle Eocene to the early Holocene (Fernicola 2008; Zamorano 2013; Zurita et al. 2016). From an evolutionary stand point, the evidence strongly suggests that glyptodonts are a monophyletic group (see Porpino et al. 2014; Zamorano 2019; among others).

Panochthus Burmeister, 1866 is one of the most abundant and diversified glyptodontids of the South American Pleistocene, as well as one of the largest Cingulata (see Fariña 2001; Zamorano et al. 2014a). Likewise, it is also among the most abundantly recorded groups in the Pampean region (Scillato-Yané et al. 1995; Cione et al. 1999; Zamorano 2012; Zamorano et al. 2014b). Together with *Glyptodon* Owen, 1839 they are the most widely distributed glyptodontids in South America, both latitudinally and altitudinally (Zurita et al. 2009, 2016; Zamorano 2012, 2019; Zamorano and Jara Almonte 2018; Zamorano and Oliva in press). In this contribution, several fragments of tracheal rings and the cricoid cartilage assigned to *Panochthus* sp. are described and figured. In this way, I intend to contribute to the understanding of these cartilages, which allow the indispensable entry of oxygen into a mammal body, an issue that is poorly studied in the extant mammals and seemingly never studied in extinct forms.

Institutional abbreviations.—MHM, Museo Histórico Municipal “Alfredo Enrique Múlgura”, General Belgrano, Province of B1uenos Aires, Argentina.

Geographic and stratigraphic setting

The fossil material was found on the right margin of the Salado River, near the city of General Belgrano, Buenos Aires, Argentina (35°45’5.52” S, 58°37’35.96” W; Fig. 1). The remains were collected in sediments of the Luján Formation dated between ca 14 and 12 ky (Late Pleistocene), in the transitional limit between La Chumbiada Member (ca 14 to 12 ky, Lujanian Stage/Age sensu Cione and Tonni 1999, 2001; Cione et al. 2015) and Gorch Member (ca 11.5 to 5 ky sensu Fucks et al. 2015), downstream the Paraje La Chumbiada, near Estancia La Invernada (Fig. 1). In Paraje La Chumbiada, Scanferla et al. (2013) recognized a gray to black clayey deposit interpreted as a

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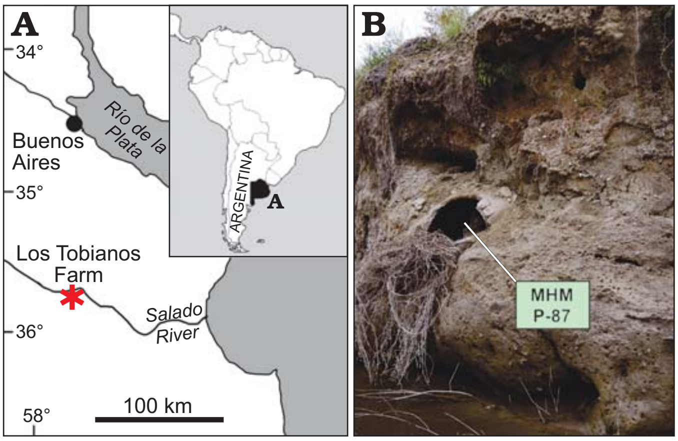

Fig. 1. **A**. Geographic location of studied area within Buenos Aires Province, Argentina (inset) near General Belgrano city, Los Tobianos Farm (35°45'5.52" S, 58°37'35.96" W), asterisk indicates where the studied specimen was discovered. **B**. Photo of the outcroup along the Salado River right bank, the site where *Panochthus* sp. (MHM-P 87) was found.

paleolagoon, in which several remains of fossil mammals were collected (*Hippidion principale* [Lund, 1842], *Smilodon populator* Lund, 1842, *Doedicurus clavicaudatus* [Owen, 1847], and *Megatherium americanum* Cuvier, 1796, among others), which corroborated the age of the level.

In general, the material recovered in the area where the remains studied here were collected are exceptionally preserved. Fossils of mammals recovered in this area contain large amounts of preserved collagen (Scanferla et al. 2013; Delsuc et al. 2016; Mitchell et al. 2016), and mummified exoskeletons of insects were found (Ramirez and Michat 2016). The high percentage of collagen preserved is a rare condition with respect to the rest of the Pleistocene deposits of the Pampas region (Scanferla et al. 2013), and this is probably what allowed the exceptional preservation of the cartilage studied here.

Material and methods

The fossil specimen described here was compared with tracheal rings and cricoid cartilage of domestic mammals, whose shape has been studied in detail, e.g., *Bos primigenius taurus* Linnaeus, 1758 (Artiodactyla, Bovidae), *Canis lupus familiaris* Linnaeus, 1758 (Carnivora, Canidae), *Capra aegagrus hircus* Linnaeus, 1758 (Artiodactyla, Bovidae), *Equus ferus caballus* (Linnaeus, 1758) (Perissodactyla, Equidae), *Felis silvestris catus* (Linnaeus, 1758) (Carnivora, Felidae), *Ovis orientalis aries* Linnaeus, 1758 (Artiodactyla, Bovidae), and *Sus scrofa domestica* Linnaeus, 1758 (Artiodactyla, Suidae) (Barone 1984; Dabanoğlu et al. 2001; Climent et al. 2005; König and Liebich 2005; Martínez and Salvador 2010; Powell et al. 2010). I also used those wild mammals for comparison, but only through literature, e.g., *Cerdocyon thous* (Linnaeus, 1766) (Carnivora, Canidae), *Didelphis* sp. (Didelphimorphia, Didelphidae), *Hydrochoerus hydrochaeris* Linnaeus, 1766 (Rodentia, Caviidae), *Mirounga angustirostris* Gill, 1866 (Carnivora, Phocidae), *Odobenus rosmarus* (Linnaeus, 1758) (Carnivora, Odobenidae), *Ursus maritimus* Phipps, 1744 (Carnivora, Ursidae), *Phoca vitulina* Linnaeus, 1758 (Carnivora, Phocidae), and *Zalophus californianus* Lesson, 1828 (Carnivora, Otariidae) (Sokolov et al. 1968; Harrison and Denny 1985; Bertassoli and Santos 2013; Moore et al. 2014; Junior et al. 2016; Moreto et al. 2017).

Systematic palaeontology

Family Glyptodontidae

Genus *Panochthus*

Type species: *Glyptodon tuberculatus* Owen, 1845; Middle Pleistocene–late Pleistocene) from the southern and center-northern areas of Argentina, Uruguay, south and central areas of Bolivia and southeastern region of Brazil.

Panochthus sp.

Material.—MHM-P 87, twenty-three fragments of tracheal rings, including fragments that probably belong to the crioid cartilage. The specimen consists of part of the skull (badly preserved), mandibular rami, postcranial bones (both humeri, radii-ulnae, both femurs, tibiae-fibulae, several elements of the carpus and tarsus, thoracic and lumbar vertebrae, cervical ribs) and the almost complete dorsal carapace. Because of the exceptional preservation of this material, fragments of tracheal rings, the crycoid cartilage and, some elements of the hyoid apparatus could be identified and were published by Zamorano et al. (2018). Late Pleistocene of General Belgrano, Buenos Aires, Argentina (35°45'5.52" S, 58°37'35.96" W) (Fig. 1). The remains were collected in sediments of the Luján Formation dated between ca 14 and 12 ky.

Description.—Tracheal cartilages are mostly small and fragile fragments; their thickness does not exceed 3 mm. Twenty-

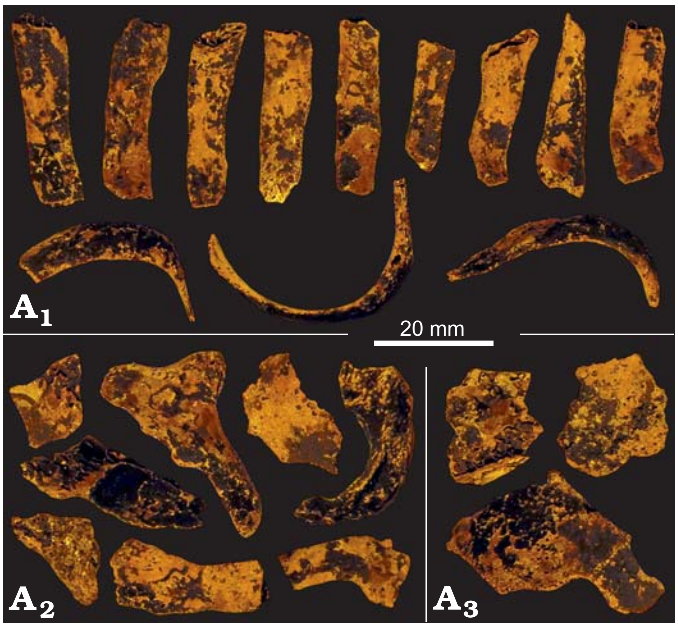

Fig. 2. Tracheal cartilages of glyptodont mammal *Panochthus* sp. (MHM-P 87) from the Late Pleistocene of General Belgrano, Argentina, in ventral views. Lateral (A$_1$), ventral and ventro-lateral (A$_2$) portions, fragment of cricoid cartilage (A$_3$) in ventral views.

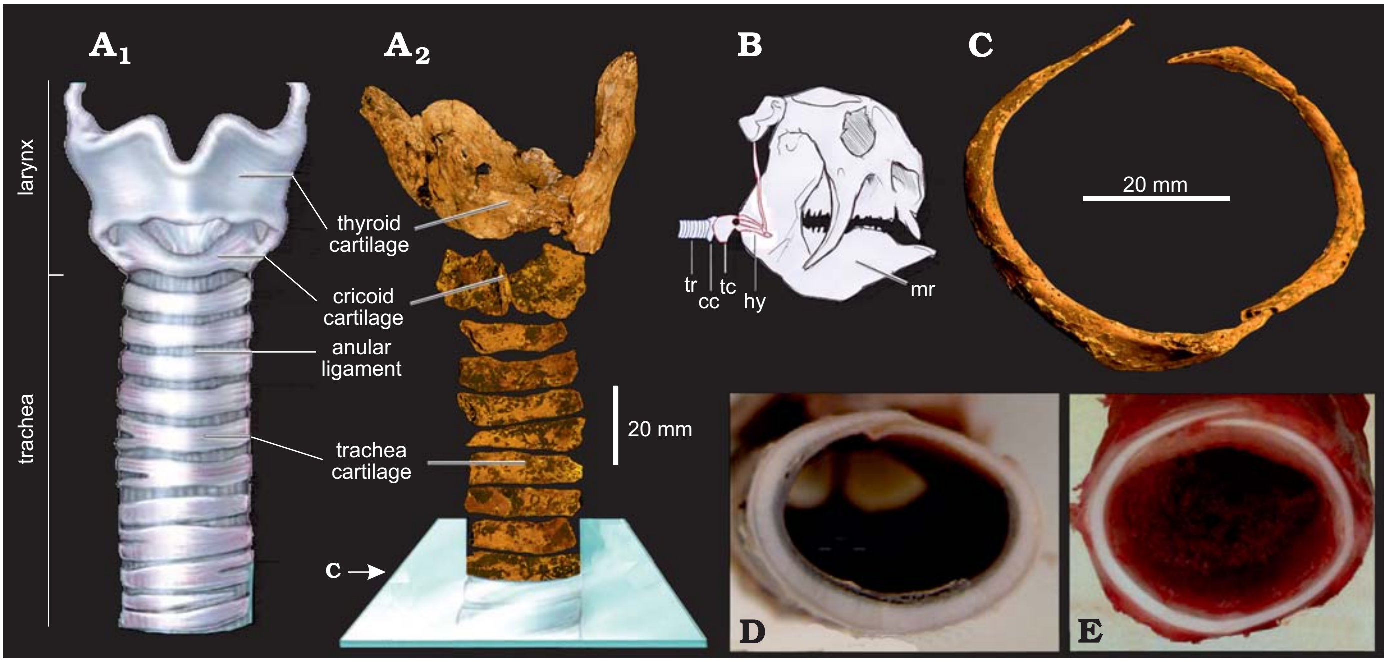

Fig. 3. Cartilages present in the neck of glyptodont mammal *Panochthus* sp. compared with Recent California sea lion and domestic pig. **A**. Thyroid, cricoid, and tracheal cartilages in ventral view; generalized mammal (A$_1$), *Panochthus* sp. (A$_2$). **B**. Explanatory drawing of the *Panochthus* sp. skull in lateral view, with hyoid apparatus and tracheal rings. **C–E**. Tracheal rings in anterior view. **C**. *Panochthus* sp. (MHM-P 87). **D**. California sea lion *Zalophus californianus* Lesson, 1828. **E**. Domestic pig *Sus scrofa domestica* Linnaeus, 1758. A, modified from Martínez and Turpín 2015; D, E, modified from Moore et al. 2014. Abbreviations: cc, cricoid cartilage; hy, hyoid apparatus; mr, mandibular rami; sk, skull; tc, thyroid cartilage; tr, tracheal rings.

three fragments of these tracheal rings were found, twelve of them belong exclusively to lateral sectors 19–54 mm in length and 6–8 mm in width. The three longest of these last fragments are fully curved (none of them cover the lateral sector completely), whereas the other nine are almost straight (Fig. 2A$_1$). Eight fragments belong to ventral portions of the rings; in this category are also included fragments of fused ventral and lateral portions (Fig. 2A$_2$), three of them, the largest ones, probably belong to the cricoid cartilage (this latter is similar in shape to a tracheal ring, although larger; Drake et al. 2010) (Fig. 2A$_3$). A tracheal ring was reconstructed; it is 80 mm high and 60 mm wide. Its diameter occupies approximately 15% of the skull height (without the mandible) (see Fig. 3B). The tracheal rings of *Panochthus* sp. would belong to a cylindrical trachea, slightly flattened on the dorsal and ventral sides, the free ends of each ring (that is, on its dorsal side) overlap, the left one above the right one (Fig. 3C).

Remarks.—Among domestic mammals, it is similar to those of *Sus scrofa domestica* (Fig. 3E), whereas among wild mammals it is similar to those of *Zalophus californianus* (Fig. 3D). Tracheal rings of *Sus scrofa scrofa*, a wild subspecies similar to its conspecific, are also similar, but those of *Zalophus californianus* resemble even more those of *Panochthus* sp., since these rings are flattened dorsally and ventrally, and not as in cross section as those of *S. scrofa scrofa*. Noteworthy, in *S. scrofa domestica* and *Z. californianus* the shape of the rings is constant along the entire trachea, as well as the overlapping of their free ends (Moreto et al. 2017). It has to be taken into account that the free ends of the tracheal cartilage of living mammals (in this case *S. scrofa domestica* and *Z. californianus*) are practically in contact, because the tracheal muscle holds them together, whereas in the fossils of *Panochthus* sp. these free ends are more widely separated.

Concluding remarks

During inspiration the air pressure is lower in the trachea than the atmospheric pressure, and without the tracheal rings, the trachea would collapse (Villee et al. 1971). For this reason the tracheal rings are totally indispensable for animals with lung breathing. In mammals these rings have the only basic and fundamental function of maintaining an open channel that allows the circulation of air from the larynx to the lungs and vice versa. Moore et al. (2014) studied the structure and rigidity of the tracheae of marine mammals and observed how the flow of air circulating through the tracheae behaved during diving. The rigidity of the trachea, deduced from the shape of the rings, is expressed in the capacity not to collapse. For some authors, this rigidity is an adaptation of marine mammals (Scholander 1940; Olsen et al. 1969; Kooyman and Sinnett 1979; Kooyman and Cornell 1981). However, Denison et al. (1971), Bostrom et al. (2008), and Moore et al. (2014) stated that it is similar to the rigidity of the tracheae of terrestrial mammals. In this sense, Moore et al. (2014) concluded that *Sus scrofa* (*S. scrofas crofa* and *S. scrofa domestica*) is the terrestrial mammal most similar to marine mammals. In turn, Harrison and Denny (1985) suggested that the influence of the shape and size of tracheal rings has to be taken into account on the running speed reached by mammals. To test this hypothesis, they used the relationship between the area occupied by the glottis lumen, the tracheal lumen (generated by the tracheal ring) and the body mass. In fossil mammals, these relationships cannot be calculated as a whole. Although the body mass has been estimated in several species of different groups (Fariña et al. 1998; Seebabher 2001; Reguero et al. 2010; Cassini et al. 2012; Toledo et al. 2014) the surface of the glottis lumen is unknown, and as for the lumen of the trachea, the present contribution is the first to report, figures and describes a tracheal ring of a fossil mammal. Tracheal rings have only been published in extinct birds: *Llallawavis scagliai* Degrange, Tambussi, Taglioretti, Dondas, and Scaglia, 2015 (Cariamiformes, Phorusrhacidae) (Degrange et al. 2015) and *Vegavis iaai* Clarke, Tambussi, Noriega, Erickson, and Ketcham, 2005 (Anseriformes, Vegaviidae) (Clarke et al. 2016); and other dinosaurs: *Scipionyx samniticus* Dal Sasso and Signore, 1998 (Theropoda, Coelurosauria) (Dal Sasso and Signore 1998).

In the literature, data on cricoid cartilage and tracheal rings of living xenarthrans are very scarce. Naples (1999) states that the cricoid cartilage is partially ossified in the skull of the giant anteater *Myrmecophaga tridactyla* Linnaeus, 1758, and that small movements between this and the back of the tracheal rings are likely; according to Borges et al. (2017), in *M. tridactyla* the trachea begins at the sixth cervical. For the folivores, Gilmore et al. (2008) report the differences in length of the trachea between the tree sloths, *Choloepus* Illiger, 1811, in which it is extremely short and *Bradypus* Linnaeus, 1758, in which it is very long (25–28 cm) and would be probably correlated with the wide range of movement between the neck and the head.

Thanks to exceptional preservation conditions, three cartilaginous structures of the neck of a glyptodontid referred to the genus *Panochthus* are preserved, corresponding to a first record in an extinct mammal. Two of these structures belong to the laryngeal zone, the thyroid cartilage described in Zamorano et al. (2018) and the cricoid cartilage, and the third originates in the tracheal zone, the cartilages of the tracheal rings; the last two structures are presented in this communication (Figs. 2, 3A_2).

In summary, the tracheal rings of *Panochthus* sp. corresponds to a cylindrical trachea, slightly flattened on the dorsal and ventral sides, the free ends of each ring overlap, the left one above the right one. Similar to those of *Sus scrofa domestica* and *Zalophus californianus*, but those of *Z. californianus* resemble even more those of *Panochthus* sp., since these rings are flattened dorsally and ventrally.

There are currently no other studies on tracheal rings in extinct mammals and in extant xenartrans; similar studies in extant xenartrans would provide valuable information on their adaptations. Future, more detailed analyses of the MHM-P 87, and possibly new findings of exceptionally preserved fossils could provide information on the paleobiological implications of this structure in glyptodonts. Likewise, these new data on the trachea and its adaptations in glyptodonts would allow to make inferences in other fossil mammals.

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Martín Zamorano [marzamorano@fcnym.unlp.edu.ar], División Paleontología de Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. CONICET. Paseo del Bosque s/n, (1900), La Plata, Buenos Aires, Argentina.

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