



General Palaeontology, Systematics, and Evolution (Vertebrate palaeontology)

A Late Jurassic plesiosaur in Antarctica: Evidence of the dispersion of marine fauna through the Trans-Erythraean Seaway?



Un plésiosaure du Jurassique tardif en Antarctique : une preuve de la dispersion de la faune marine à travers la voie maritime Trans-Erythraean Seaway?

Jose P. O’Gorman^{a,b,*}, Soledad Gouiric-Cavalli^{a,b}, Roberto A. Scasso^c, Marcelo. Reguero^{a,d}, Juan J. Moly^a, Leonel Acosta-Burlaille^a

^a División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n., B1900FWA La Plata, Argentina

^b Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), C1425FQB Buenos Aires, Argentina

^c Instituto de Geociencias Básicas, Aplicadas y Ambientales de Buenos Aires (IGeBA – CONICET) Dto. de Cs.

Geológicas – FCEyN – Universidad de Buenos Aires Int. Guiraldes 2160, Ciudad Universitaria, Pab. II, C1428EHA Buenos Aires, Argentina

^d Instituto Antártico Argentino, 25 De Mayo 1143, San Martín, Buenos Aires, 1650 Argentina

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ABSTRACT

During the Jurassic two main marine pathways might act as dispersion routes for vertebrates and invertebrates between Laurasia and Gondwana: the Caribbean Seaway (between North and South America) and the Trans-Erythraean Seaway (splitting Africa from India, Madagascar). The former has proven to be of relevance as a dispersion route for marine vertebrates and invertebrates between the Tethys and Pacific margin of Gondwana. Nevertheless, little is known about the role of the Trans-Erythraean Seaway as a vertebrate dispersion pathway. The Trans-Erythraean Seaway divides the eastern and western South of Gondwana landmasses in the so-called break-up of Gondwana and connects the Tethys Sea with the Palaeo-Pacific. We describe a newly recovered plesiosaur specimen from the Ameghino (= Nordensköld) Formation, Antarctic Peninsula, the first Jurassic plesiosaur from

Abbreviations: **IAA**, Instituto Antártico Argentino, Buenos Aires Province, Argentina; **di**, diapophysis; **ns**, neural spine; **poz**, postzygapophysis; **prezygapophysis**; **dv**, dorsal vertebrae; **vf**, ventral foramina; **dr**, dorsal rib.

* Corresponding author. División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n., B1900FWA La Plata, Argentina.

E-mail addresses: joseogorman@fcnym.unlp.edu.ar (J.P. O’Gorman), sgouiric@fcnym.unlp.edu.ar (S. Gouiric-Cavalli), rscasso@gl.fcen.uba.ar (R.A. Scasso), mreguero@dna.gov.ar (Marcelo. Reguero), juanjomoly@fcnym.unlp.edu.ar (J.J. Moly), leoacosta@fcnym.unlp.edu.ar (L. Acosta-Burlaille).

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Antarctica. We discuss the importance of this record regarding the hypothesis of marine vertebrate dispersion through the Trans-Erythraean Seaway.

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R É S U M É

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Pendant le Jurassique, deux principales voies maritimes ont pu servir d’itinéraires de dispersion des vertébrés et invertébrés entre la Laurasia et le Gondwana : la mer des Caraïbes (entre l’Amérique du Nord et l’Amérique du Sud) et la voie Trans-Érythréenne séparant l’Afrique de l’Inde–Madagascar. Il a été prouvé de manière pertinente que la première a été un itinéraire de dispersion pour les vertébrés et invertébrés marins. Mais on connaît peu de chose du rôle qu’a pu jouer la Trans-Érythréenne en tant qu’itinéraire de dispersion des vertébrés. La voie Trans-Érythréenne divise les masses continentales des parties est et ouest du Sud-Gondwana en formant la fracture appelée gondwanienne, qui connecte la Téthys au Paléo-Pacifique. Nous décrivons ici un spécimen de plésiosaure nouvellement répertorié dans la formation Ameghino (= Nordensköld) de la péninsule Antarctique, le premier plésiosaure découvert en Antarctique. Nous discutons l’importance de cette découverte en ce qui concerne l’hypothèse d’une dispersion marine de vertébrés par la voie Trans-Érythréenne.

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1. Introduction

Plesiosauria was a successful clade of marine reptiles that achieved worldwide distribution from the Late Triassic until the end of the Cretaceous (Benson and Druckenmiller, 2014). Plesiosaurs show a great capability of dealing with different ecological settings such as freshwater, marine marginal (i.e., lagoons, estuaries, Benson et al., 2013; O’Gorman et al., 2013; Sato et al., 2003) up to open sea, and a wide latitudinal range (Kear, 2006; Knutsen et al., 2012; O’Gorman, 2012). In fact, plesiosaurs were present at high latitudes in both, the Northern and Southern Hemispheres at least since the Jurassic (Kear, 2012; Knutsen et al., 2012; Weems and Blodgett, 1996) and through the Cretaceous (Kear, 2006; O’Gorman, 2012; Vavrek et al., 2014). Therefore, they were capable of dealing with relatively low temperatures and high annual variation of photoperiods typical of high latitudes. The capability of inhabiting high latitudes was also inferred for other marine reptiles such as ichthyosaurs (Druckenmiller et al., 2012; Zverkov et al., 2015) and mosasaurs (Kear et al., 2005; Novas et al., 2002). This is probably related with the ability of regulate the body temperature inferred for these groups (Bernard et al., 2010).

The Late Jurassic marine reptile fauna of southwestern Gondwana is mainly known from the specimens of the Vaca Muerta Formation (Gasparini and Fernández, 1997; Gasparini et al., 2015). The palaeobiogeography of marine reptiles is explained by the opening of a marine pathway, which connected the European Tethys and the Paleo-Pacific, the so-called Caribbean Seaway (Gasparini and Iturralde-Vinent, 2006). However, an alternative dispersal route, the Trans-Erythraean Seaway, was also proposed (Gasparini, 1992, Fig. 1) as a dispersal route (Fernández, 1997; Gasparini, 1992; Gasparini and Fernández, 1997). However, the Antarctic material used as prove of it comprises only fragmentary ichthyosaurs teeth (Hikuroa, 2009;

Whitham and Doyle, 1989). So far, there has been no evidence of Antarctic Jurassic plesiosaurs mentioned in the literature.

During the Antarctic expedition supported by the Instituto Antártico Argentino and the Dirección Nacional del Antártico, CAV 2016, (January–February 2016), several plesiosaur dorsal vertebrae and ribs were collected at Longing Gap locality, Antarctic Peninsula (Fig. 2). The goal of this contribution is to describe the material and asses its palaeobiogeographic implications.

2. Geological setting

The Ameghino (= Nordenskjöld) Formation (Farquharson, 1982; Medina and Ramos, 1983) is a mudstone sequence that forms the basal sedimentary infill of the Larsen Basin, northeastern Antarctic Peninsula (del Valle et al., 1992; Mc Donald et al., 1988, Fig. 2a). Sediments were deposited during the thermal subsidence stage of the basin, which evolved from a continental rift in the Lower Jurassic to a back-arc basin in the Cretaceous (Hathway, 2000).

At Longing Gap locality (Fig. 2a), the Ameghino Formation consists of laminated or massive black mudstones and gray tuffs with abundant calcitic concretions (Kiesling et al., 1999). The tuff beds increase from the stratigraphically lower Longing Member to the overlying Ameghino Member (Whitham and Doyle, 1989, Fig. 2b, c) and reflects hemipelagic sedimentation close to an active volcanic arc (Kietzmann et al., 2009; Scasso, 2001). The complete sequence is about 580 m thick (Longing Member: 420 m and Ameghino Member: 160 m, according to Kiesling et al., 1999). Anoxic conditions prevailed during the accumulation of the Longing Member but changed to dysoxic conditions in the Ameghino Member (Doyle and Whitham, 1991; Whitham, 1993). The Ameghino Formation is Kimmeridgian to Berriasian in age (Kiesling and Scasso, 1996;

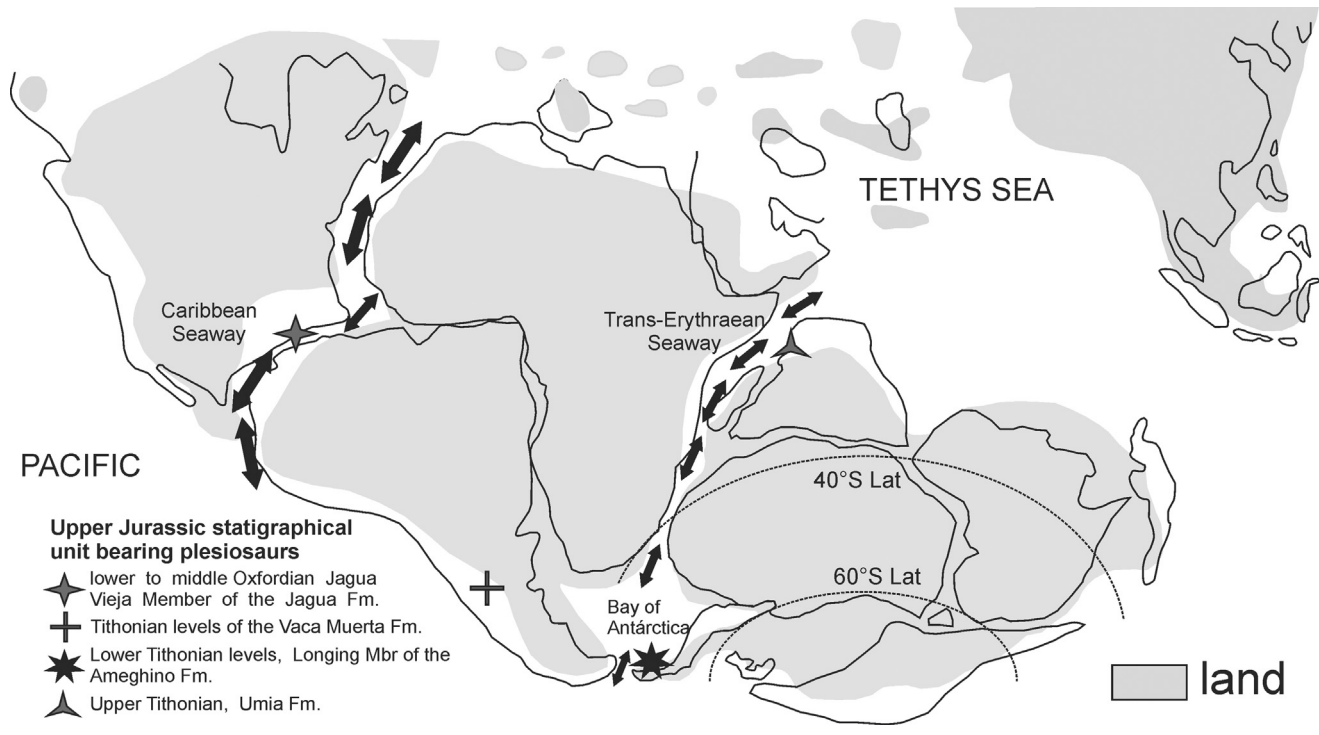


Fig. 1. Middle–Upper Jurassic palaeogeography and South Gondwana Oxfordian–Tithonian plesiosaur records (map modified from Stevens, 1997 and Challinor and Hikuroa, 2007 and plesiosaur records from Bardet et al., 1991; Gasparini and Iturralde-Vinent, 2006; Gasparini et al., 2015).
Fig. 1. Paléogéographie du Jurassique moyen–supérieur et enregistrements de plésiosaures de l’Oxfordien–Tithonien du Sud–Gondwana (carte modifiée d’après Stevens, 1997 et Challinor and Hikuroa, 2007 ; enregistrements de plésiosaures d’après Bardet et al., 1991; Gasparini and Iturralde-Vinent, 2006 ; Gasparini et al., 2015).

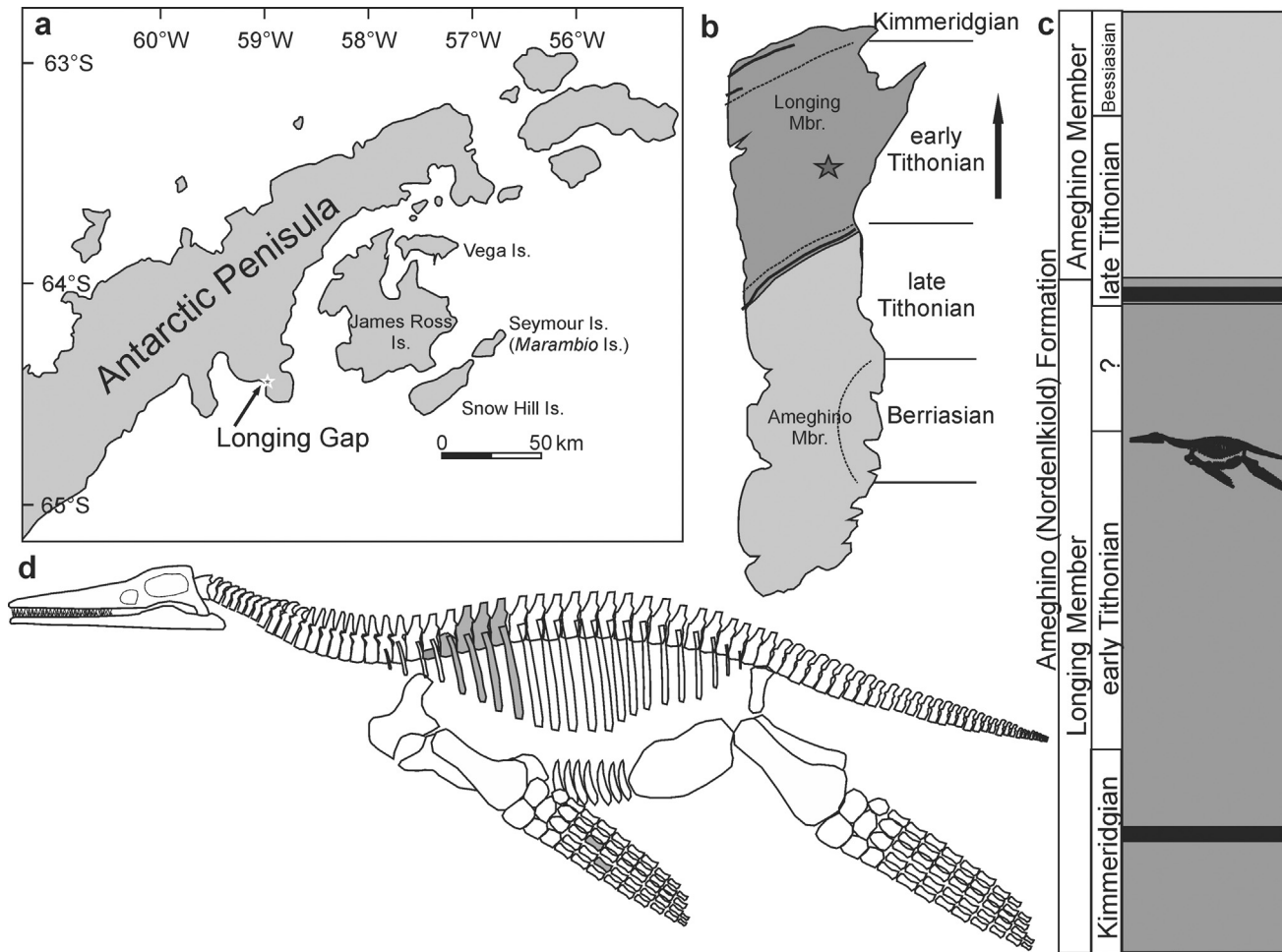


Fig. 2. **a**, Locality where IAA-PV 354 and IAA-PV 355 were collected; **b**, diagram of the stratigraphy and geochronology of the Longing Gap locality outcrops (modified from Kiessling et al., 1999); **c**, stratigraphical column of the Ameghino Formation (modified from Kiessling et al., 1999) with the position of IAA-Pv 354 and IAA-Pv 355; **d**, diagram showing the preserved elements of IAA-Pv 354 modified from Andrews, 1913.

Fig. 2. **a**, Localité où IAA-PV 354 et IAA-PV 355 ont été collectés ; **b**, diagramme stratigraphique et géochronologique des affleurements de la localité de Longing Gap (modifié d'après Kiessling et al., 1999) ; **c**, colonne stratigraphique de la formation Ameghino (modifiée d'après Kiessling et al., 1999) avec la position de IAA-Pv 354 et IAA-Pv 355 ; **d**, schéma montrant les éléments conservés de IAA-Pv 354, modifié d'après Andrews, 1913.

Kiessling et al., 1999). While the Longing Member of the Ameghino Formation is Kimmeridgian-early late Tithonian in age; the Ameghino Member is late Tithonian to Berriasian in age.

Palaeontological survey at the Ameghino Formation showed that it is a rich fossil-bearing unit (e.g., Whitham, 1993). It yields a rich invertebrate fauna composed of ammonoids, nautiloids, bivalves (Kiessling et al., 1999; Whitham and Doyle, 1989), and radiolarians (Kiessling and Scasso, 1996; Kiessling et al., 1999) and a rich vertebrate fauna composed of actinopterygian fishes (Arratia et al., 2004; Gouiric-Cavalli et al., 2016). Also, plant debris was reported (Medina and Ramos, 1983). The current study of the vertebrate fossil-bearing levels show that the actinopterygian fishes are the most commonly recovered material (Gouiric-Cavalli and Rasia, 2016; Gouiric-Cavalli et al., 2016).

3. Methods

Specimens were mechanically prepared by the senior author (J.P.O’G.). The tools used were a Micro Jack and ME 9100 jackhammers. The ontogenetic developmental categories of Brown (1981) — based on the fusion of the neural arch to the vertebral centrum — to differentiate ‘adult’ from the ‘juvenile’ growth stages are considered.

4. Systematic palaeontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Plesiosauria indet.

Material: IAA-Pv 354, five articulated dorsal vertebrae, fragments of at least two additional dorsal vertebrae, dorsal ribs and indeterminate fragments (Fig. 3a, b); IAA-PV 355; one dorsal vertebra, a fragment of dorsal rib and one indeterminate vertebral fragment (Fig. 3d).

Locality and horizon: Longing Gap locality, Antarctic Peninsula (64° 26′ 48.3″ S; 58° 58′ 06.5″ W). Longing Member of the Ameghino (=Nordenskjöld) Formation. Lower Tithonian (Fig. 2a, b, c).

5. Description

General features: Both IAA-Pv 354 and IAA-Pv 355 are strongly laterally compressed during taphonomic processes. IAA-Pv 354 was lying left side down. IAA-Pv 354 bears approximately parallel ribs and articulated vertebrae (Fig. 3a, b). IAA-Pv 355 was not collected in situ, thus, no information about its relative position or grade of articulation is known.

Axial skeleton: IAA-Pv 354 belongs to a section of the dorsal region and shows little inter-vertebral disarticulation. Four of the preserved dorsal ribs are displaced but the fifth rib remains near the diapophysis (Fig. 3a, b).

All the vertebral centra show strong lateral compression; as a consequence, part of the ventral surface is visible in lateral view, showing several ventral foramina. Additionally, the diapophyses are also laterally compressed and moved toward the sagittal plane, showing only the ventral

surfaces (Fig. 3c). Some of the foramina are located laterally, in a relatively high position (Fig. 3b). The vertebral centra are relatively short anteroposteriorly. Considering deformation, approximately values of length/height/width are 70 mm/90 mm/90 mm. The diapophyses are rectangular and strongly dorsoventrally compressed. Both postzygapophysis and prezygapophysis extend beyond the limit of the neural spine (Fig. 3a, b). Five ribs are preserved. The dorsal ribs show a concave lateral sulcus. However, the sulcus could be a feature produced by the lateral compression. IAA-PV 355 (Fig. 3d) vertebra is similar in shape and foramina disposition to the vertebrae in IAA-PV 354.

6. Discussion

6.1. Systematic affinities

Because IAA-Pv 354 and IAA-Pv 355 show neural arches fused with the vertebral centra, they are considered adults *sensu* Brown (1981). Some features of the specimen — shape, proportion of the vertebral centra, nearly flat articular faces and ventral foramina — indicate a clear plesiosaur affinity (Benson and Druckenmiller, 2014).

Similar vertebral centra that are relatively anteroposteriorly short, are recorded in other Jurassic plesiosaurs with “Pliosauromorph” morphotype *sensu* O’Keefe (2002), such as *Pliosaurus* (Knutsen et al., 2012) and *Marmornectes* (Ketchum and Benson, 2011). Unfortunately, the scarcity of material does not allow more comparisons. Based on these general features, the Antarctic specimens here reported were considered pliosauroids (Gouiric-Cavalli et al., 2016). However, the scarcity of material allows referring it as a Plesiosauria indet.

6.2. Taphonomy, Environmental setting and Palaeobiogeography

The scarce disarticulation observed in the IAA-Pv 354 is consistent with the low energy of the sedimentary environment where it was deposited (Doyle and Whitham, 1991). Also, it is consistent with the observed in the actinopterygian remains collected in levels immediately above and below (S. G-C pers. obs.), specimens usually articulated but in broken slabs.

Disarticulation by scavengers seems unlikely given the anoxic conditions and the virtually absence of ichnofossils and benthonic fossils (Arratia et al., 2004; Doyle and Whitham, 1991). These features and the absence of evidence of currents indicate that the final disarticulation was mostly due to decomposition (Lyman, 1994).

The palaeolatitude of the eastern margin of the Antarctic Peninsula at Longing Gap locality during the Late Jurassic was about 50° S (Stevens, 1997, Fig. 1). Thus, the plesiosaur remains reported here represent the southernmost record of the clade during that temporal framework. In contrast, in Laurasia Late Jurassic plesiosaur remains have been collected in localities at higher latitudes (~ 60° N, Hurum et al., 2012).

In spite of the relatively high latitude, palaeotemperatures seem to have ranged between 26°–30°C, as estimated for the sea surface at Falkland Plateau during the early

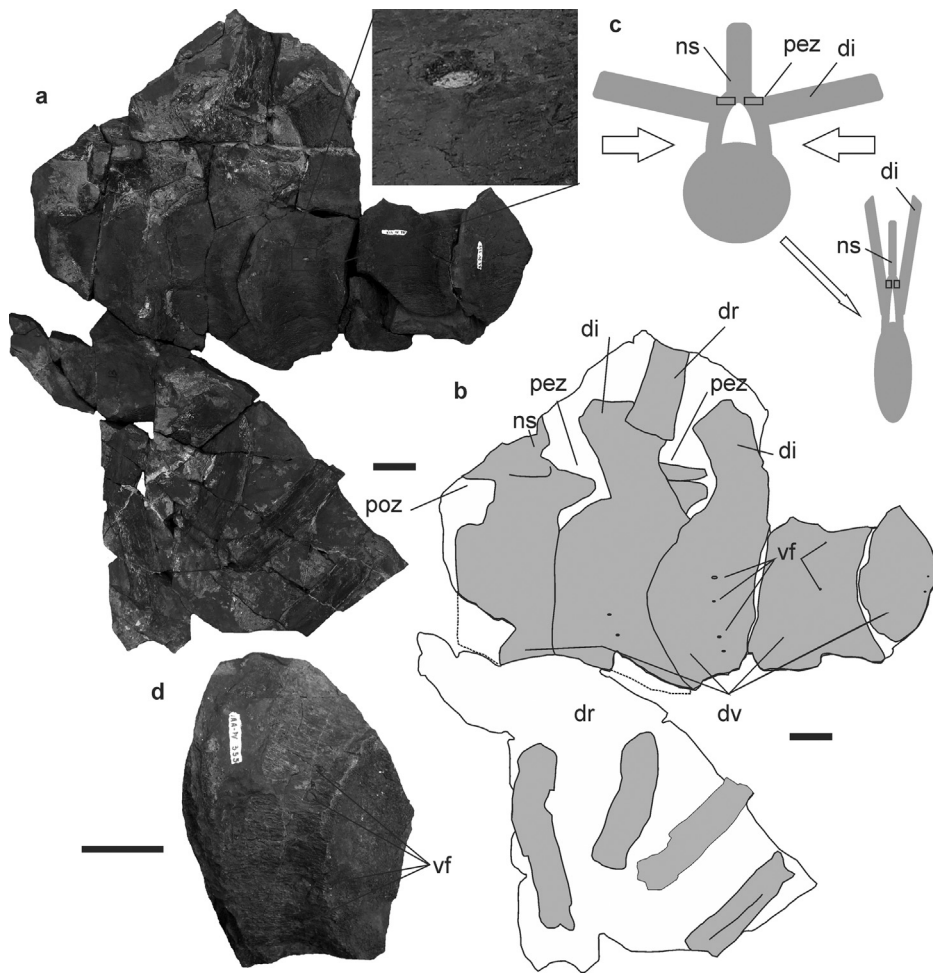


Fig. 3. Plesiosauria indet. IAA-Pv 354. a–b Articulated dorsal vertebrae in left lateral view and dorsal ribs: **a**, photo with detail of ventral foramen and **b**, diagram (scale bar = 40 mm); **c**, diagram showing the deformation suffered by the dorsal vertebrae; **d**, IAA-Pv 355 dorsal vertebra (scale bar = 40 mm).
Fig. 3. Plesiosauria indet. IAA-Pv 354. Vertèbres dorsales articulées en vue latérale gauche et côtes dorsales : **a**, photo avec détail du foramen ventral et **b**, diagramme (échelle = 40 mm) ; **c**, diagramme montrant la déformation subie par les vertèbres dorsales ; **d**, vertèbre dorsale (échelle = 40 mm).

Tithonian (Jenkyns et al., 2012). This palaeotemperature is relatively higher than that of the Maastrichtian sea surface, which was inferred for the Weddell Sea during the Campanian-Maastrichtian (16 °C to 8 °C, Huber et al., 2002). At that time, a rich plesiosaur fauna inhabited the area of the James Ross Archipelago located at ~64° S (O’Gorman et al., 2015, 2016; Otero et al., 2014; Poblete et al., 2011).

A palaeobiogeographic scenario, that includes the Trans-Erythraean Seaway, has been proposed as an explanation for the palaeobiogeographic distribution of some marine invertebrates. A Late Tithonian marine connection between Madagascar and South America was proposed based on ammonites palaeobiogeography (Riccardi, 1991), then the presence of the ammonite *Chigaroceras* in both, the western Tethys and the Andean region (Argentina) might be the prove of dispersion through the Trans-Erythraean Seaway (Leanza, 1996). The Tithonian distribution of the belemnoid *Produvalia* recorded in Antarctica and Madagascar is also an indicator of dispersion through the Trans-Erythraean Seaway (Mutterlose, 1986); similar

conclusion regarding dispersion of belemnoids through the Trans-Erythraean Seaway were reached by Challinor and Hikuroa (2007). The dispersion of the South Gondwana Ostracods Fauna (*sensu* Dingle, 1988) might be related with the opening of the Trans-Erythraean Seaway (Dingle, 1988). Piovesan et al. (2012) explain the palaeobiogeography of the ostracod *Majungaella* as a marine dispersion from East Africa to South America during the Late Jurassic. Late Jurassic bivalves’ distribution also is explained through a marine connection by the Trans-Erythraean (Gardner and Campbell, 2002).

The palaeobiogeographical implication of this new plesiosaur record represents to be the link between the Late Jurassic (Tithonian) plesiosaurs from Neuquén Basin, Argentina (Gasparini and O’Gorman, 2014; Gasparini et al., 1997) and the Late Jurassic (Tithonian) plesiosaur records from India (Bardet et al., 1991). Therefore the new Antarctic record is an evidence that support the possibility of plesiosaur dispersion – and probably of other large motile forms such ichthyosaurs – between the Antarctic Bay and

the Eastern Tethys through the Trans-Erythraean Seaway, during the Late Jurassic as was previously hypothesized (Fernández, 1997; Gasparini, 1992; Gasparini and Fernández, 1997; Prasad et al., 2017).

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