Bridging the southern gap: First definitive evidence of Late Jurassic ichthyosaurs from Antarctica and their dispersion routes

L. Campos [a,f,*], M.S. Fernández [a,f], Y. Herrera [a,f], M. Talevi [b,f], A. Concheyro [c,e,f], S. Gouiric-Cavalli [d,f], J.P. O'Gorman [d,f], S.N. Santillana [e], L. Acosta-Burlaille [d], J.J. Moly [d], M. A. Reguero [d,e,f]

[a] *División Paleontología Vertebrados, Unidades de Investigación Anexo Museo, Facultad de Ciencias, Naturales y Museo, UNLP, Av. 60 y 122, B1900, La Plata, Argentina*
[b] *Universidad Nacional de Río Negro, Instituto de Investigación en Paleobiología y Geología, Av. Roca 1242, (R8332EXZ), General Roca, Río Negro, Argentina*
[c] *Instituto de Estudios Andinos Don Pablo Groeber, CONICET and Universidad de Buenos Aires, Ciudad Universitaria, Pabellón 2, 1428, CABA, Argentina*
[d] *División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, UNLP, Paseo de Bosque s/n, B1900, La Plata, Argentina*
[e] *Instituto Antártico Argentino, Campus Miguelete, 25 de Mayo 1151, 3er piso, B1650HMK, San Martín, Buenos Aires, Argentina*
[f] *Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina*

ARTICLE INFO

ABSTRACT

New ichthyosaur remains from the Upper Jurassic of Antarctica, recovered from the Ameghino (=Nordenskjöld) Formation are described. These three new specimens represent the first unambiguous records of ichthyosaurs in this continent. Based on the morphology of the humerus, we refer one of the specimens to Ophthalmosauridae, the dominant ichthyosaur forms from the Middle Jurassic until the extinction of the group during the Late Cretaceous. In addition to the new Antarctic records, we re-evaluate ichthyosaur remains of two individuals from the Upper Jurassic of Madagascar and describe a third new specimen, which is the most complete ichthyosaur from this region of Gondwanaland. These findings provide new insights into the role of the seaways opened during the Jurassic in the dispersion of ichthyosaurs, particularly ophthalmosaurids. Antarctic and Malagasian ichthyosaurs bring additional support to the hypothesis of the Mozambique Corridor acting as a dispersal route connecting the Tethys Sea and the southern Pacific margins of Gondwana, at least since the Late Jurassic.

1. Introduction

Ichthyopterygians were a successful clade of diapsid that inhabits the marine environment during most of the Mesozoic. From basal Early Triassic shallow marine and probably suction feeder forms, they diversified into obligatory marine ones (Motani et al., 2015). Early in their evolution during the Jurassic, parvipelvian ichthyosaurs evolved a fish-shaped body plan characterized by a reduced pelvic girdle and an increment of the tail length, traits that enabled them to cruise as in living tunas (Motani 2005). Such deep body plan modification, unique among reptiles, and inferred swimming capabilities as cruising forms allowed them to achieve a wide geographic distribution (Motani 2005). One of the most important episodes in the history of the group is represented by the rise of the ophthalmosaurids, which evolutionary history comprises almost all Bajocian–Cenomanian ichthyosaurs (Fischer et al., 2016). Their fossil records indicate that this group also achieved a widespread distribution soon after their first appearance. Thus, the oldest ophthalmosaurids have been recovered from the Aalenian–Bajocian boundary of Mendoza (Argentina) and the early Bajocian of Alaska (Fernández 2003; Druckenmiller and Maxwell 2014). In recent years there have been abundant and diverse discoveries of Upper Jurassic ichthyosaurs from Arctic high-latitude regions ranging between 60° and 70° N palaeolatitudes, such as northern Canada (Maxwell 2010), Svalbard Archipelago (*e.g.* Roberts et al., 2014; Delsett et al., 2017, 2018,
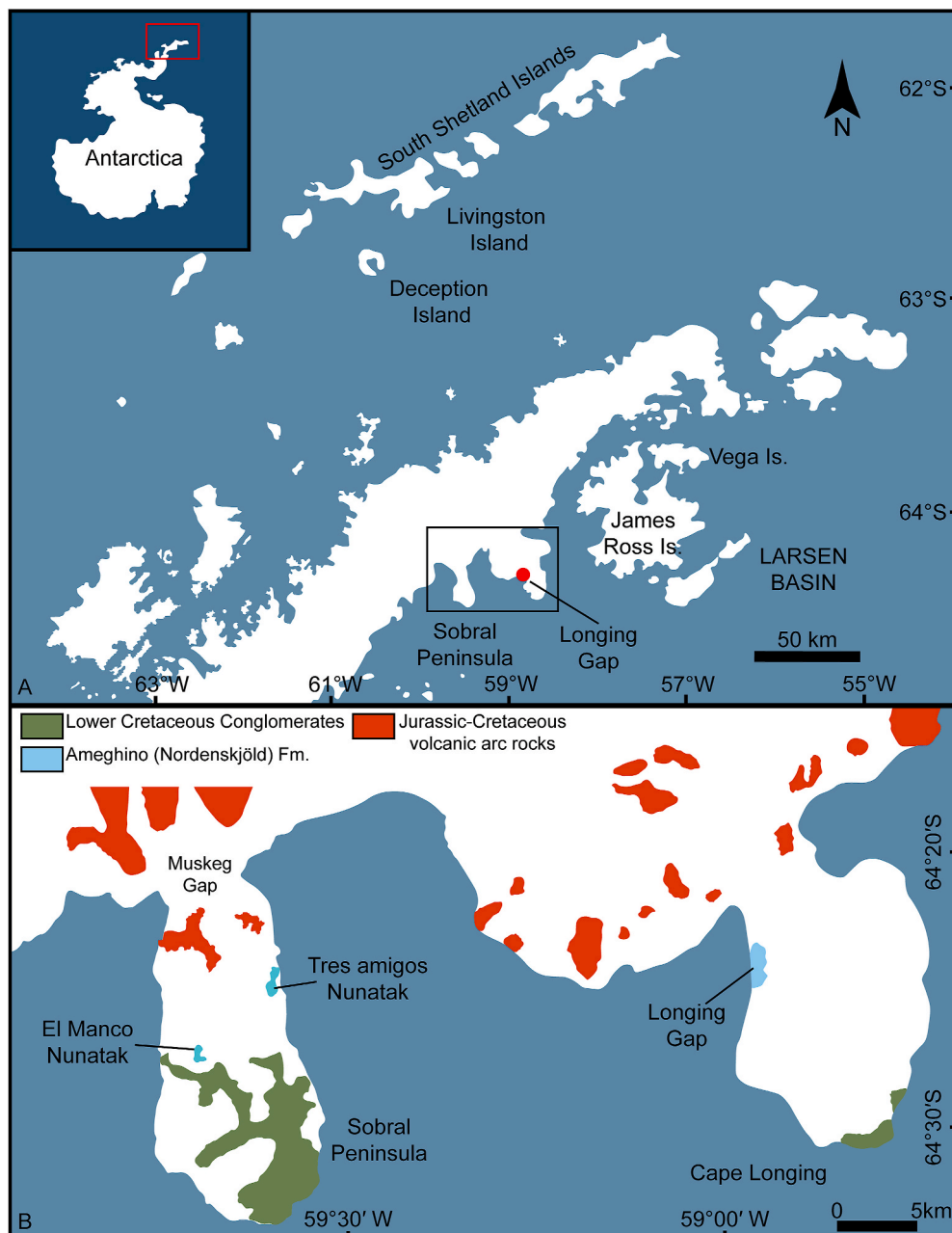
Fig. 1. Antarctic Peninsula location map. Red dot indicates the locality (Longing Gap) where ichthyosaur specimens were found. Modified from del Valle and Núñez (1988). **B**. Sketch geological map of Cape Longing. Modified from Whitham and Storey (1989).

2019), and northern Russia (Zverkov et al., 2015).

Mainly due to uneven sampling, it is still unclear if Late Jurassic ichthyosaurs occurrences (in terms of diversity and abundance) at high latitudes in the northern hemisphere are equivalent in the southern hemisphere. In particular, marine Jurassic deposits of several regions of Gondwana, such as Antarctica and Madagascar, are extremely under-sampled compared to Upper Jurassic northern high localities, such as the Slottsmøya member of the Agardhfjellet Formation of Svalbard (Delsett et al., 2016).

1.1. Historical background of ichthyosaurs from Antarctic and Madagascar

The first mention of an Antarctic ichthyosaur corresponds to Whitham and Doyle (1989). In this contribution and the framework of the stratigraphic description of the Ameghino (=Nordenskjöld)

Formation, the authors mentioned: "*Ammonites are the most common members of a predominantly nekto-pelagic fauna that also includes several species of fish, an ichthyosaurid, belemnites, and pseudoplanktonic bivalves*" (Whitham and Doyle 1989: 375). This is the only phrase in which marine reptiles are mentioned without further references and/or photos. Years later, Doyle and Whitham (1991) mentioned that an ichthyosaur mandible was recovered from the Longing Member of Ameghino Formation. Unfortunately, no further details from this specimen are given in that contribution. Hikuroa (2009) described a cast of a partial lingual surface of a tooth crown recovered from Tithonian beds of the Hauberg Mountains Formation in the Bean Peaks, Ellsworth Land, Antarctic Peninsula. In this case, there is a photo of the material (Hikuroa 2009: fig.2); however, the fragmented nature of the material leaves some doubts on its systematic determination as it is discussed in the present contribution.

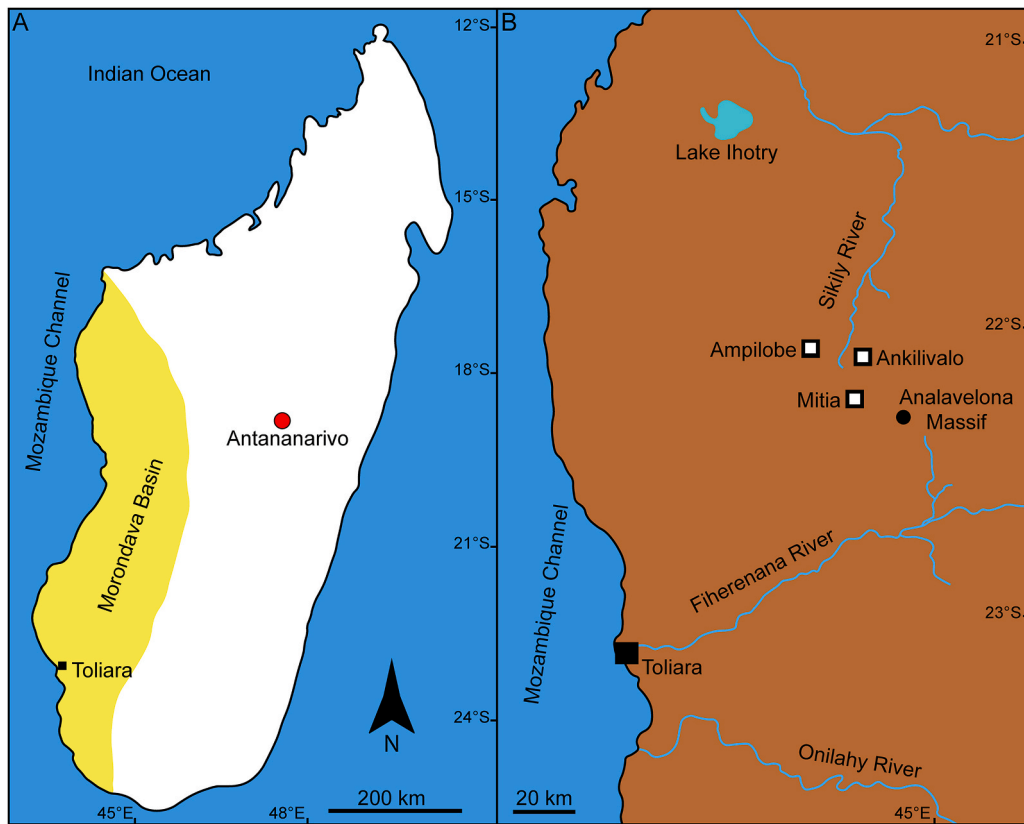The material from Antarctica studied herein was recovered as part of

Fig. 2. A. Morondava Basin location map. **B.** Map of the localities where ichthyosaur specimens were collected. Modified from Geiger and Schweigert (2006).

the Vertebrate Paleontology Research Program of the Instituto Antártico Argentino (led by MR), in which researchers of the Museo de La Plata as well as from several academic institutions are invited to participate. Antarctic fieldworks on Jurassic fossil-bearing units have been in development since 2015/2016 led by one of the authors (SGC), with the main focus of recovering fish material. The summer field Antarctic seasons in 2016 and 2018 provided the ichthyosaur material described herein. These findings are important as they represent the first ichthyosaurs from the Upper Jurassic of Antarctica and collaborate to improve marine vertebrate records from this region of Gondwana, which are extremely scarce and correspond mainly to fishes (*e.g.* Arratia et al., 2004; Gouiric-Cavalli et al., 2019).

Also poorly known are Late Jurassic ichthyosaurs from Madagascar. To date, only two very incomplete ichthyosaur specimens have been reported from marine Upper Jurassic deposits of Toliara, south-western Madagascar (Fernández 1997a). Here we identify a new and previously undescribed specimen from the same region.

Antarctic and Malagasian materials provide an excellent opportunity to explore the distribution patterns of Late Jurassic ichthyosaurs following the break-up of Gondwana. A Hispanic (= Caribbean) Corridor has been pointed out as the main seaway connecting Tethyan and Palaeopacific herpetofaunas during the Late Jurassic (*e.g.* Gasparini and Iturralde-Vinent 2006). However, by the Late Jurassic, other seaways, such as the Mozambique Corridor, could be acting as alternative dispersion routes (*e.g.* Fernández 1997a; Bardet et al., 2014; O'Gorman et al., 2018). On this basis and taking into account that the specimens presented herein were found at both, eastern and western extremes of the Mozambique Corridor, the aims of this contribution are to describe the new specimens from Antarctica and compare them with those of Madagascar; and to explore the palaeobiogeographical implications of these findings.

Institutional abbreviations: **CM** Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; **IAA-Pv** Instituto Antártico

Argentino, San Martín, Buenos Aires, Argentina; **KGMV** Kachchh Geological Museum, Kachchh, India.

2. Geological setting and age of the Antarctic specimens

The Ameghino Formation is represented by radiolarian-rich black mudstones and gray tuffs sequence corresponding to a basal infill of the Larsen Basin (Farquharson 1982; Medina and Ramos 1983; Kiessling et al., 1999), northeastern Antarctic Peninsula. As in James Ross Island, both members of the Ameghino Formation are exposed in Longing Gap locality (Fig. 1) (Whitham and Doyle 1989). The lower Longing Member (Kimmeridgian–early late Tithonian) exhibits anoxic conditions of deposition due to the presence of high levels of amorphous organic matter and the absence of bioturbation. The overlying Ameghino Member (late Tithonian–Berriasian) is composed of thinly bedded, intercalated, massive or laminated mudstones, tuffs, and volcaniclastic sandstones, with several ichnofossils (*Chondrites*, *Planolites*, and *Zoophycos*) (Whitham 1993). It depicts a change in the oxygen conditions, reflecting a dysaerobic deposition environment inferred from horizons with epibenthic bivalves (Doyle and Whitham 1991).

The fauna reported in the Ameghino Formation is mainly represented by invertebrates such as ammonoids (Medina and Ramos 1983) and bivalves (Crame 1982). Microfossils are represented by calcareous nannofossils recovered from laminated mudstones (Concheyro and Scasso 1999). They exhibit low richness, are scarce, and constitute an early–late Tithonian poor preserved association. The presence of *Polycostella beckmanii* Thierstein confirms its age and suggests Tethyan affinities (Leanza et al., 2020). Vertebrate records are dominated by osteichthyan fishes like aspidorhynchiforms, pachycormiforms, ichthyodectiforms (*e.g.* Arratia et al., 2004; Gouiric-Cavalli et al., 2019), dapediids, halecomorph, and several indeterminate actinopterygians (Gouiric-Cavalli, pers. obs 2020). Also, remains of a plesiosaur were recently reported (O'Gorman et al., 2018).
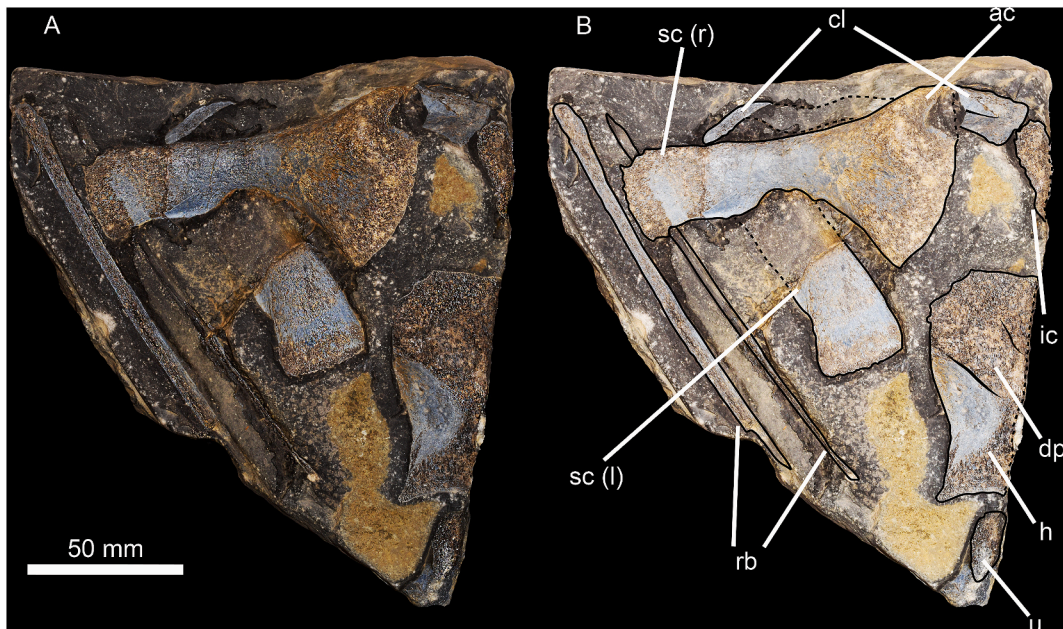
Fig. 3. Postcranial elements of Ophthalmosauridae cf. Platypterygiinae (IAA-Pv 712). **A.** Photograph. **B.** Interpretation. Abbreviations: ac, acromion; cl, clavicle; dp, dorsal process; h, humerus; ic, interclavicle; rb, rib; sc, scapula; u, ulna.

The ichthyosaur specimens described herein were found *ex-situ*. However, the presence of scarce and very resistant to dissolution calcareous nanofossils as *Watznaueria britannica* (Stradner) Reinhardt and *Crepidolithus crassus* (Deflandre) Nöel, found in the matrix surrounding the bony elements, suggests that ichthyosaur specimens come from the Longing Member of the Ameghino Formation, confirming an early– late Tithonian age.

3. Material and methods

The specimens IAA-Pv 358 and IAA-Pv 359 were found *ex-situ* (i.e. as a result of surface collection) in the lowermost section of the Longing Member (Kimmeridgian–early late Tithonian) of the Ameghino Formation, in the Longing Gap locality (Fig. 1). A third specimen (IAA-Pv 712) was found in a moraine. The samples for calcareous nannofossils study were taken directly from the sediment surrounding the bones. Samples were processed with standard processing techniques.

The ichthyosaur specimens from Madagascar were found in three different localities of the Tulear Province in the southern Morondava Basin (Fig. 2A): Ampibole and Ankilivalo in the high valley of the Sikily, and Mitia, northern Analavelona Massif (Fig. 2B). In these localities, discontinuous Tithonian (Upper Jurassic) sandstones crop out and, in past decades, have proven to be a rich fount of marine invertebrate fauna (Besairie 1972; Charbonnier et al., 2012).

Geographic location of the specimens discussed in the present contribution is based on GPS coordinates information taken, when possible, from the original papers. When not available in published literature, coordinates were obtained from Google Earth and Google maps by searching the localities from where the fossils were extracted. Palaeolatitudinal data was obtained by implementing the Palaeolatitude calculator online v.2.1 (van Hinsbergen et al., 2015) and the palaeomagnetic frame presented in Torsvic et al. (2012).

3.1. Palaeohistological analysis

Palaeohistological samples were taken from one vertebra of IAA-Pv 359 and a rib of IAA-Pv 712. Three thin sections were prepared using standard palaeohistological techniques (Chinsamy and Raath 1992) and examined with light microscopy at the laboratory of the Instituto de

Investigación en Paleobiología y Geología of Universidad Nacional de Río Negro (Argentina). In the specimen IAA-Pv 359 a centrum was selected for histological exploration, and it was sectioned sagitally and transversely, whereas in the specimen IAA-Pv 712 a rib was sectioned transversely.

4. Results

SYSTEMATIC PALAEONTOLOGY
Ichthyosauria de Blainville, 1835
Baracromia Fischer et al., 2013a.
Ophthalmosauridae Baur, 1887.
cf. Platypterygiinae Arkhangelsky, 2001 (*sensu* Fischer et al., 2012)

Material: IAA-Pv 712 (Fig. 3). Postcranial remains including scapulae and fragmentary right clavicle, fragmentary ribs, and partially preserved humerus and ulna.

Locality and age: Longing Gap locality (64° 26′S, 58° 59′W; palaeolatitude: 48°S), Antarctic Peninsula. Early–late Tithonian.

Comparative description: All the bones were found included on a single block and present no signs of deformation. The right clavicle is partially preserved on its anterior and lateral aspects and is overlapped by the right scapula. The anterior surface is convex as in *Mollesaurus periallus*, *Ophthalmosaurus icenicus*, and *Brachypterygius extremus* (Fernández and Talevi 2013; Moon and Kirton 2016, 2018) and becomes flat towards the medial margin suggesting that the preserved medial portion of the clavicle is near to the area of contact with its left contralateral. Judging by this, the medial portion of the clavicles would have been dorsoventrally low and lacking the medial digitiform processes present in *O. icenicus*, *Aegirosaurus leptospondylus*, and *Janusaurus lundi* and resembles that of *Keilhauia* (Moon and Kirton 2016; Delsett et al., 2019).

The right scapula is completely preserved and exposed in lateral (external) view. As in "*Platypterygius*" *sachicarum* and "*Platypterygius*" *americanus*, the scapular shaft is strap-like in lateral view (Maxwell and Kear 2010; Maxwell et al., 2019) and possesses a tear-like outline in cross-section. The distal end of the scapula is slightly anteroposteriorly expanded and its edge is weakly convex. Proximately, the scapula broadens in a fan-shaped fashion due to the presence of the acromion
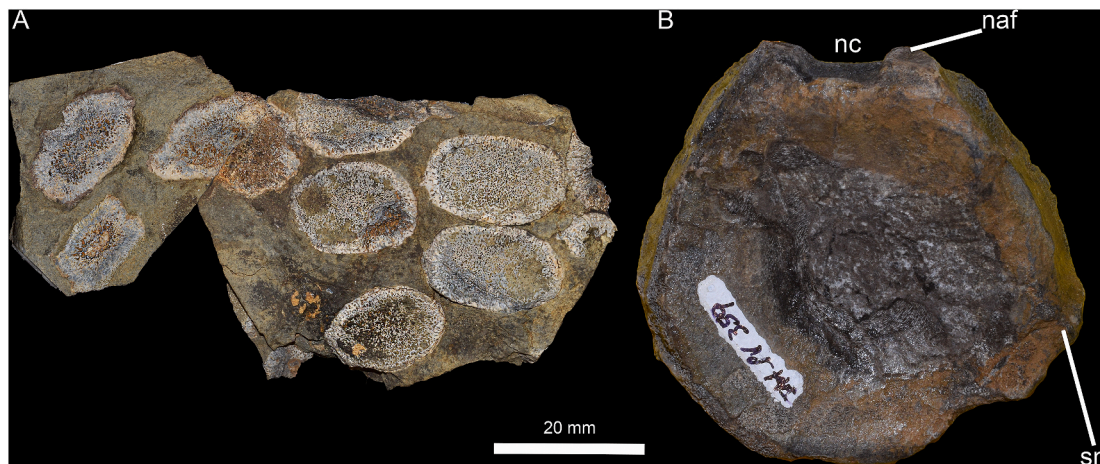
Fig. 4. A. Appendicular elements of Ichthyosauria indet. (IAA-Pv 358) in dorsal/ventral view. **B**. Anterior caudal centrum of Ichthyosauria indet. (IAA-Pv 359) in anterior view. Abbreviations: naf, neural arch facet; nc, neural canal; sn, synapophysis.

and the scapular contribution to the glenoid fossa. The morphology of the acromion resembles that of *Keilhauia nui, Brachypterygius extremus, Undorosaurus? kristiansenae*, and *Undorosaurus? kielane* in which this is discretely developed (Tyborowski 2016; Delsett et al. 2017, 2019; Moon and Kirton 2018) thus differing from the prominent process of *Svelto-nectes* and *Acamptonectes* (Fischer et al. 2011, 2012).

The right humerus is partially preserved and based on the presence of the proximal portion of the dorsal process it is interpreted to be exposed in dorsal view (Fig. 3). This process originates near the proximo-posterior area of the humerus as in *Keilhauia* (Delsett et al., 2019). The proximal end is nearly flat, and the surface of the bone is sandpaper-like, suggesting that IAA-PV 712 was probably a juvenile (Johnson 1977). Distally, the ulnar facet is slightly concave, differing from the deeply concave ulnar facet present in *Arthropterygius* spp. (Maxwell 2010; Zverkov and Prilepskaya 2019; Campos et al., 2020). As in many ophthalmosaurids like *Gengasaurus nicosiai, Palvennia hoy-bergeti*, and the Indian ophthalmosaurid specimen (KGMV 0501), the ulnar facet is not posteriorly deflected in a way that the proximal edge of the humerus and this facet are nearly parallel ((Paparella et al., 2016); Prasad et al., 2017; Delsett et al., 2018). The posterior margin of the bone is nearly straight as in KGMV 0501 (Prasad et al., 2017). Distal to the ulnar facet is a fragmentary bone that is interpreted as the right ulna due to the closeness with the humerus.

Microanatomical and histological organization: Macroscopically the structure shows a compact cortical region without a free medullar cavity (Supplementary Data 1G). This area is occupied by a cancellous tissue of secondary origin with intertrabecular spaces separated by thick trabeculae of lamellar bone (Supplementary Data 1H). A compact cortical region is differentiated from the spongy core region; this transition is gradual with an increase in the size of the resorption spaces from the cortical to the medullary region. The cortical bone is completely invaded by thick bundles of fibers. Embedded in the fibrous matrix numerous longitudinal vascular canals and some secondary osteons are observed (Supplementary Data 1I). Although in ichthyosaurs ribs the degree of bone remodeling is a difference observed between juvenile and adult individuals (Talevi et al., 2012(Talevi et al., 2021)), in this case, the high degree of remodeling and the presence of a large number of bundles of fibers would indicate a muscle insertion area.

Remarks: The specimen IAA-Pv 712 can be confidently referred to Ophthalmosauridae given the presence of a plate-like dorsal process on the dorsal surface of the right humerus. The presence of an ulnar facet that is not posteriorly deflected suggests that this specimen could represent a platypterygiine ophthalmosaurid (Fischer et al., 2012), due to date, there is no record of a non-platypterygiine featuring this morphology on the humerus. IAA-PV 712 most likely represents a

juvenile individual based on the small size and proximal shape of the humerus (Johnson 1977).

Ichthyosauria indet.

Material: IAA-Pv 358 (Fig. 4A). Fragments of an articulated fin.
Locality and age: Longing Gap locality (64° 26′S, 58° 59′W; palaeolatitude: 48°S), Antarctic Peninsula. Lower section of the Longing Member of the Ameghino Formation. Early–late Tithonian.
Comparative description: The fin fragments consist of twelve articulated elements, five of which are complete. None of the bones present signs of deformation. These elements are dorsoventrally thick as anteroposteriorly long. This feature characterized the proximal phalanges of *Chacaicosaurus cayi*, some *Stenopterygius* species such as *S. quadriscissus* and *S. aaleniensis* (Maxwell et al., 2012), and *Oph-thalmosaurus icenicus*, and differ from those of *Brachypterygius extremus* in which these are square-shaped (Moon and Kirton 2016, 2018). All the fin elements depict a sandpaper and unfinished texture of their external surfaces, suggesting that the specimen could correspond to a juvenile (Johnson 1977). The articular facets of all the elements, except for the most proximal one, are predominating rounded. The most proximal element is larger than the others, and its distal edge bears three almost straight facets for articulation with distal elements. This articulation pattern (i.e. one element distally in close articulation with other three fin elements) occurs commonly in the zeugopodial-basipodial articulations or as a consequence of a digital bifurcation. The fragmentary nature of the material does not permit to determine with confidence if it corresponds to a zeugopodial fragment or if it is a more distal part of the fin.

Remarks: IAA-PV358 presents very similar morphology and proportions typically found in derived ichthyosaurs forms, in which phalangeal identities are lost, the elements suffer dorso-ventral flattening and acquire nodular shape (Caldwell 1997a, 1997b; Maxwell et al., 2014). All ichthyosaur taxa from the Late Jurassic onwards until the extinction of the group during the Cenomanian–Turonian (Fischer et al., 2016) belong to Ophthalmosauridae, with the Hauter-ivian–Barremian taxa *Malawania anachronus*, recovered from the Chia Gara Formation (Iraq) as a unique exception (Fischer et al., 2013a). This taxon presents hexagonal phalanges with a tightly packed pattern on its forefin (Fischer et al., 2013a). Such morphology quite differs from that of the specimen IAA-PV 358; thus, it seems very unlikely that it belonged to that basal ichthyosaur lineage.
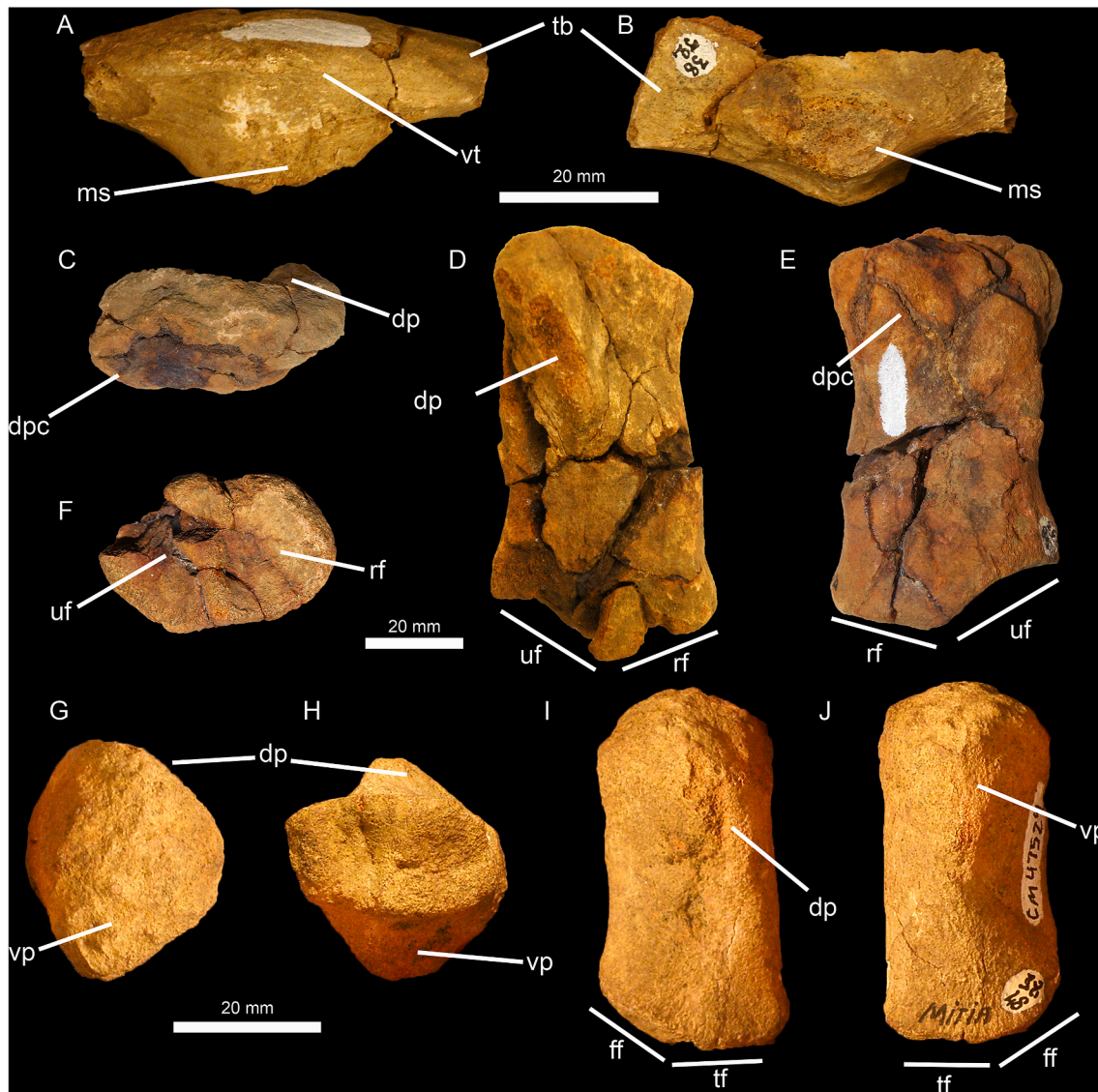
Ichthyosauria indet.

Fig. 5. Postcranial elements of Ophthalmosauridae (CM 47524). **A-B.** Interclavicle in ventral (**A**) and posterior (**B**) views. **C–F.** Right humerus in proximal (**C**), dorsal (**D**), ventral (**E**), and distal (**F**) views. **G-J.** Right femur in proximal (**G**), distal (**H**), dorsal (**I**), and ventral (**J**) views. Abbreviations: dp, dorsal process; dpc, delto-pectoral crest; ff, fibular facet; ms, medial stem; rf, radial facet; tb, transverse bar; tf, tibial facet; uf, ulnar facet; vp, ventral process.

Material: IAA-Pv 359 (Fig. 4B). Eight partially preserved vertebrae.

Locality and age: Longing Gap locality (64° 26′S, 58° 59′W; palaeolatitude: 48°S), Antarctic Peninsula. Lower section of the Longing Member of the Ameghino Formation. Early–late Tithonian.

Description: The remains correspond to eight incomplete vertebral centra, three of which are relatively complete and were found in articulation. The surface of the bones presents no sign of erosion or deformation. The dorsal surface presents a pair of facets flanking the floor of the neural channel for articulation with the neural arches (Fig. 4B). Based on the complete fusion of the apophyses and its position on the ventral half of the lateral surfaces of the centra, these can be assigned to the anterior caudal region of the vertebral column.

Microanatomical and histological organization: As is typical of advanced ichthyosaurus and *Cymbospondylus* (microtype 2, Houssaye et al., 2018), the microanatomical pattern of the IAA-Pv 359 is characterized by organized spongiosa, and trabeculae are essentially oriented along the sagittal plane. Sagittal sections are hourglass-shaped with conspicuous periosteal and endochondral territories (Supplementary Data 1A). The two cones of periosteal bone extend from the center of growth dorsally and ventrally, whereas the two cones of endochondral

bone extend anteriorly and posteriorly (Supplementary Data 1A). Both areas are spongious and lack compact bone. The transverse sections correspond to the periosteal area and are observed paired cone-shaped territories spread from the centrum core towards the facets for articulation with the neural arch (Supplementary Data 1B). At the histological level in the sagittal section of the endochondral territory, the centrum anterior and posterior borders exhibit calcified cartilage cells, and it is continued with a primary spongy tissue without signs of remodeling (Supplementary Data 1C, D). The intertrabecular spaces are much smaller, giving the tissue a more compact appearance (Supplementary Data 1C). Numerous Sharpey fibers are seen in the anterior and posterior areas (Supplementary Data 1E). In the periosteal area, the spongiosa is homogeneous with relatively small intertrabecular spaces. The trabeculae are thin, oriented mostly perpendicular to the sagittal plane, and are regularly spaced (Supplementary Data 1C). These bone trabeculae consist of pseudolamellar bone with little presence of osteons. Limited remodeling occurs, and some secondary osteons are observed (Supplementary Data 1F). Houssaye et al. (2018) observed that during ontogeny, the microtype 2 type presents a strong increase in the number of trabeculae and reduction of the size of the intertrabecular spaces. On

Fig. 6. Cranial and postcranial elements of Ophthalmosauridae (CM 47525). **A-D.** Basioccipital in anterior (**A**), dorsal (**B**), left lateral (**C**), and posterior (**D**) views. **E-F.** Caudal centrum in anterior (**E**) and left lateral (**F**) views. **G-I.** Right scapula in medial (**G**), lateral (**H**), and ventral (**I**) views. Abbreviations: ac, acromion; bsf, basisphenoid facet; cf, coracoid facet; eca, extracondylar area; ef, exoccipital facet; fm, foramen magnum; gc, glenoid contribution of the scapula; icd, impressions of the cochlear duct; lmf, lateral margin of the foramen magnum; oc, occipital condyle; of, opistothic facet; sn, synapophysis; stf, stapedial facet.

this basis, the pattern observed on the IAA-Pv 359 is compatible with a juvenile specimen.

Remarks: Due to the vertebral morphology of the specimen IAA-PV 359 is strongly amphicoelous, with unfused neural arches and dorsoventrally taller than anteroposteriorly longer, these elements can be confidently assigned to Ichthyosauria. Unfortunately, and even though there is a high degree of overlap between the materials represented by vertebrae and appendicular remains with those of the ophthalmosaurids, there is currently no formal and unified criterion for assigning this type of isolated remains to Ophthalmosauridae. This specimen most likely represents a juvenile individual based on its small proportions and the microanatomical structure.

Description and comparison of Malagasian ichthyosaurs

The specimens were collected by the geologist Claude Germain, in the Tulear Province, south Madagascar. Part of Germain's private collection was acquired in 1987 by the Carnegie Museum of Natural History and is currently housed in this institution. CM 47525 and CM 47526 were briefly described by Fernández (1997a), and here we

provide a reassessment of such material together with the description of CM 47524.

Ichthyosauria de Blainville, 1835
Baracromia Fischer et al., 2013a.
Ophthalmosauridae Baur, 1887.
Ophthalmosauridae indet.

Referred material: CM47524 (Fig. 5, Supplementary Data 2). Postcranial skeleton including atlas-axis complex, postero/dorsal-sacral centra, interclavicle, right humerus, and femur.

Locality and horizon: Mitia, Tulear Province, Madagascar. Upper Jurassic. Palaeolatitude: 34°S.

Comparative description: The atlas-axis complex is entirely preserved except for the right dorsal portion. Anteriorly, it is roughly heart-shaped, and the surface is deeply concave for the reception of the basioccipital condyle (Supplementary Data 2). A small keel is present on the ventral surface but less developed than those in *Acamptonectes*, *O. icenicus*, and several "*Platypterygius*" spp. (Kolb and Sander 2009; Maxwell and Kear 2010; Fischer et al., 2012; Moon and Kirton 2016).

Laterally, there is no trace of suture between the atlas and axis, and the parapophyses are located at the same height, although the atlantal parapophysis is slightly dorsoventrally taller. The posterior surface of the axis is also concave but to a lesser degree than the anterior atlantal surface (Supplementary Data 2).

Based on the overall morphology, the remaining vertebrae can be identified as belonging to the presacral portion of the column, probably corresponding to the region where the presacral-caudal transition occurs. All centra are strongly amphicoelous and present thickened peripheral margins on their anterior and posterior faces (Supplementary Data 2). In lateral view, the apophyses are very close to each other over the ventrolateral region of the centra, showing a rounded outline. Despite the closeness of the structures mentioned above, these are not completely fused but connected by their proximal portions (Supplementary Data 2). Anterior to the parapophysis, a shallow ridge connects it to the anterior thickened margin of the centrum (Supplementary Data 2).

A small portion of the interclavicle is preserved and consists of the medial region of both the transverse bar and the medial stem. On the ventral surface, there is a small tuberosity in the area of the union of the transverse bar and the neck of the medial stem as in *O. icenicus* and *U. gorodischensis* (Moon and Kirton 2016; Zverkov and Efimov 2019) (Fig. 5A). In posterior view, the medial stem is D-shaped with a convex ventral surface (Fig. 5B).

The humerus is a short element with proximal and distal ends equally anteroposteriorly developed (Fig. 5C–F). This element is about 0.55 times proximodistally longer than the femur, following the common trend reported by Delsett et al. (2017), in which the femur becomes gradually shorter relative to the humerus through the Early/Middle Jurassic–Cretaceous interval. The proximal epiphysis is roughly rectangular in proximal view and its surface densely pitted for the application of cartilage (Fig. 5C). On the dorsal aspect, the dorsal process originates over the proximo-posterior region and extends anterodistally (Fig. 5D). The process is proximodistally short, not reaching the midpoint of the shaft as in *Aegirosaurus leptospondylus* and *Keilhauia nui* (Delsett et al., 2017). Ventrally, the deltopectoral crest appears much less prominent than the dorsal process and originates from the anterior-most part of the proximal half of the humerus like in *Arthropterygius* (Maxwell 2010; Zverkov and Prilepskaya 2019; Campos et al., 2020) (Fig. 5E). Like *Keilhauia*, the deltopectoral crest is restricted to the proximal half of the element (Delsett et al., 2019). Contrasting with most ophthalmosaurids, the distal epiphysis bears only two articular facets for the radius and ulna, like in *Undorosaurus? kristiansenae*, *Undorosaurus? kielanae*, and *Nannopterygius enthekiodon* (Druckenmiller et al., 2012; Tyborowski 2016; Moon and Kirton 2018) (Fig. 5F). Both facets are equal in anteroposterior length and separated by a dorsoventral ridge. The radial facet is slightly dorsoventrally shorter than the ulnar and presents a D-shaped outline with a convex anterior edge. In ventral view, the ulnar facet appears posteriorly deflected and forms an acute angle of ~35° (Fig. 4E).

The right femur presents a similar morphology to that of the humerus, with its proximal and distal ends equally developed (Fig. 5G–J). In proximal view, the surface is pitted and D-shaped, with a dorsoventrally broad anterior edge due to the presence of the dorsal and ventral processes (Fig. 5G). The distal surface of the femur presents two articular facets for the tibia and fibula, unlike "*Pl.*" *hercynicus*, "*Pl.*" *americanus*, "*Pl.*" *australis*, and *Maiaspondylus lindoei*, which present three (Kolb and Sander 2009; Maxwell and Kear 2010; Zammit et al., 2010; Zverkov and Grigoriev 2020). These facets are equal in anteroposterior length as in *Sveltonectes* and contrast with *Ar. chrisorum* that presents a much more developed tibial facet (Maxwell 2010; Fischer et al., 2011) (Fig. 5H). Similar to *Janusaurus*, the dorsal process is anteriorly located over the dorsal surface of the femur, whereas the ventral process is placed in a relatively more posterior position (Roberts et al., 2014) (Fig. 5I). The anterior and posterior margins of the femur run parallel in proximodistal direction, and together with the lack of expansion of the epiphyses, they

give a rectangular outline to the bone in both dorsal and ventral views (Fig. 5I–J).

Remarks: CM 47524 is assigned to Ophthalmosauridae based on the presence of a well-developed plate-like process on the dorsal surface of the humerus. The morphology of the distal region of the humerus is shared with some ophthalmosaurids (see above), but the incompleteness of the material makes CM 47524 not amenable to generic referral.

Ophthalmosauridae indet.

1997a *Brachypterygius extremus* Fernández p. 752, fig.1.

Referred material: CM47525 (Fig. 6). Isolated basioccipital, partial scapula, and caudal centra.

Locality and age: Ankilivalo, Tulear Province, Madagascar. Late Jurassic. Palaeolatitude: 34°S.

Comparative description: The basioccipital is a massive and roughly spherical element. In anterior view, the surface is flattened and densely pitted for cartilage covering (Fig. 6A). This surface is divided into two specular halves given the presence of a vertical groove that widens ventrally and separates a pair of protuberances that mark the area of contact with the basisphenoid (Fig. 6A). The presence of these anteroventral bosses is also reported in *O. icenicus* (Moon and Kirton 2016). Dorsally, two ovoid concavities representing the exoccipital facets flank the ventral surface of the foramen magnum, which presents an "hour-glass" outline (Fig. 6B). The floor of the foramen magnum forms a simple furrow with a pitted surface differing from the anteriorly bilobed form of *Acamptonectes* (Fischer et al., 2012) (Fig. 6B). Like *Br. extremus*, the floor of the foramen magnum is only slightly raised (Moon and Kirton 2018), contrasting with *O. icenicus*, which presents a more elevated surface (Moon and Kirton 2016), and with *Sveltonectes*, *Palvennia*, and *Ar. thalassonotus* that feature an almost flat surface (Campos et al., 2020) (Fig. 6C). In lateral view, the facets for the opisthotic and stapes occupy the anterior half of the lateral surface of the basioccipital, unlike *Br. extremus* in which these facets take up much of the lateral surface (Moon and Kirton 2018) (Fig. 6C). Contrary to *Ar. thalassonotus*, *Palvennia*, and *Janusaurus*, these facets are not anteriorly shifted (Campos et al., 2020) but seen in lateral view. The occipital condyle is strongly rounded in posterior view (ratio height/width = 0.9), unlike the much wider condyle present in *Sveltonectes* and *Leninia* (Fischer et al. 2011, 2013b) (Fig. 6D). Also, in posterior view, the bone surrounding the occipital condyle (extracondylar area) is ventrally reduced, and only its lateral portions are visible, as in *Br. extremus* (Moon and Kirton 2018) (Fig. 6D).

The preserved centra have a rounded outline and are weakly amphicoelous in both, anterior and posterior views (Fig. 6E). On the lateral surface of the vertebrae, the apophyses appear completely fused, forming a stout synapophysis that is located over the ventral half of the bones (Fig. 6F). Due to this fusion and the total lack of contact between the synapophysis and the anterior and posterior margins of the centra, these elements are judged to belong to the anterior portion of the caudal region.

The right scapula is incompletely preserved and consists of the proximal portion of the bone. In medial and lateral views, the element is anteroposteriorly expanded (Fig. 6G–H), and its anterior half is laterally recurved, forming a shallow concavity on the lateral surface and the acromion process anteriorly. On the ventral articular surface, the facet for the coracoid appears slightly more anteroposteriorly developed than the glenoid contribution of the scapula, which is square-shaped and slightly deflected in posterior direction (Fig. 6I).

Remarks: CM 47525 is an ophthalmosaurid based on the morphology of the basioccipital. The degree of reduction of the extracondylar area of this element is only present in some Jurassic ophthalmosaurids and most Cretaceous taxa, whereas in non-ophthalmosaurids, this structure is well-developed both ventrally and laterally (*e.g.* McGowan 1973; Miedema and Maxwell 2019; Maxwell and Cortés 2020; Swaby and Lomax 2020). On the other hand, the strong
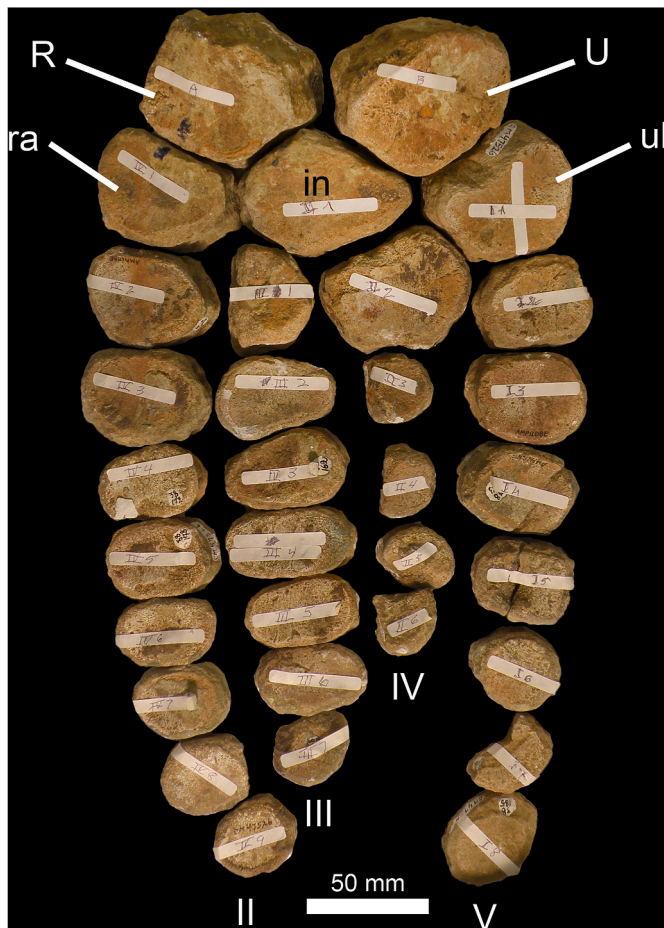
Fig. 7. Forefin of Ophthalmosauridae (CM 47526). Abbreviations: in, intermedium; R, radius; ra, radiale; U, ulna; ul, ulnare; II–V, indicate digits.

sphericity of the occipital condyle indicates that the specimen was an osteologically mature individual at the moment of its death (Druckenmiller and Maxwell 2010; Kear and Zammit 2014).

cf. Ophthalmosauridae

1997a Ichthyosauria *incertae sedis* Fernández p. 752, fig.2.

Referred material: CM 47526 (Fig. 7). Partial forefin, including zeugopodial and autopodial elements.

Locality and age: Ampilobe, Tulear Province, Madagascar. Late Jurassic. Palaeolatitude: 34°S.

Comparative description: The fin seems to be narrow, showing only four incomplete digits that directly articulate with the basipodium, although the exact number of digits and the contacts among the elements from the basipodial row onwards, could not be determined with total confidence. The radius is pentagonal in dorsal view with a straight and thickened anterior edge and the posterior one forming a point. It articulates with the intermedium and radiale distally and the ulna posteriorly, which is anteroposteriorly longer than the radius. Similar to *Palvennia* the facet for the radiale is the longest, followed by that for the intermedium, and the ulnar facet is the smallest (Delsett et al., 2018). In proximal view, it presents a trapezoidal outline with a posterior margin dorsoventrally taller than the anterior. Anteriorly, the radial surface is considerably thicker proximally than distally as in *Ar. chrisorum* (Maxwell 2010). The ulna is roughly rectangular in dorsal and ventral views and is anteroposteriorly longer than proximodistally (Fig. 7). The dorsal surface is rounded in outline with an anterior edge slightly dorsoventrally ticker than the posterior edge contrasting with *Ar.*

thalassonotus in which the posterior margin of the ulna is about a quarter of the dorsoventral length of the anterior margin (Campos et al., 2020). As the ulna, the intermedium is anteroposteriorly longer than proximodistaly and possesses a rhomboidal outline (Fig. 7).

From the proximal phalangeal row onwards, all the elements tend to acquire a brick-like shape and decrease in size similar but in a lesser degree to "*Platypterygius*", *Sveltonectes*, and *Br. extremus* (Fernández and Aguirre-Urreta 2005; ; Kolb and Sander 2009; Maxwell and Kear 2010; Zammit et al., 2010; Fischer et al., 2011; Moon and Kirton 2018), although their anterior and posterior margins are still more or less rounded and convex. A major difference is observed in the disposition of the phalanges of CM 47526 concerning the examples mentioned before since, in all those taxa, the phalanges are tightly packed. The arrangement of CM 47526 is more similar to that of *O. icenicus*, with bigger spatial gaps among the phalanges (Moon and Kirton 2016). Finally, the distal-most elements lose their rectangular aspect and become strongly oval.

Remarks: CM 47526 is far the most problematic specimen regarding its taxonomic affinities. The morphology and arrangement of the preserved zeugopodial elements and more distal elements preclude its identification as a member of the lineage of *Malawania*. This morphology is similar to that of the ophthalmosaurids, being the lack of the pre-axial accessory element (PAE) the only difference to the typical ophthalmosaurid forefin. However, this is interpreted as caused by a lack of preservation rather than a real feature. Considering the present evidence and the temporal range attributed to the Malagasian specimens, it is most likely that CM 47526 represents an ophthalmosaurid.

5. Discussion

5.1. Palaeobiogeographical implications

Middle to Late Jurassic ichthyosaur records are mainly represented by specimens from the Northern Hemisphere, especially those of the western Tethys (Sander 2000), Russia (Zverkov and Prilepskaya 2019), and Svalbard (Norway) (Druckenmiller et al., 2012; Roberts et al., 2014; Delsett et al. 2017, 2018, 2019). On the other hand, Southern Hemisphere records were predominantly found in Argentina (Fernández, 1994, 1997b, Fernández, 1999; Fernández et al., 2019; Campos et al., 2020). Besides Argentinian records, only two ophthalmosaurids were reported during the Middle to Late Jurassic of Gondwana, in Madagascar (Fernández 1997a) and India (Prasad et al., 2017). The remaining occurrences of ichthyosaurs in the Jurassic of Gondwana to date correspond to very fragmentary and non-diagnostic material from Antarctica. This material consists of a partial cast of the lingual surface of a tooth crown, which is slightly curved in postero-lingual direction with an oval cross-section and presents faint longitudinal striae on the enamel surface (Hikuroa 2009). These traits are also present in many Late Jurassic marine reptiles such as metriorhynchids and plesiosaurs (Massare 1987; Foffa et al., 2018) and, coupled with the absence of the root and crown tip, prevent a secure assignment of the material.

Baracromian ichthyosaurs were primarily represented by the ophthalmosaurids, which had a widespread distribution during Middle Jurassic to early Late Cretaceous. The presence of common ophthalmosaurid genera like *Arthropterygius* in the Upper Jurassic deposits of Canada, Russia, and Argentina (Maxwell 2010; Zverkov and Prilepskaya 2019; Campos et al., 2020) highlights the great dispersal potential of these forms. Moreover, some recent phylogenetic analyses (*e.g.* Campos et al., 2020; Jacobs and Martill 2020; Zverkov and Grigoriev 2020) have pointed out potential close relationships among the Patagonian species *Ar. thalassonotus* with several Late Jurassic boreal realm forms such as *Ar. chrisorum*, *Ar. volgensis*, *Janusaurus lundi*, and *Keilhauia*. This relationship supports the idea of at least one ophthalmosaurid lineage dispersing across northern high latitude regions and the south-western margins of the Paleopacific.

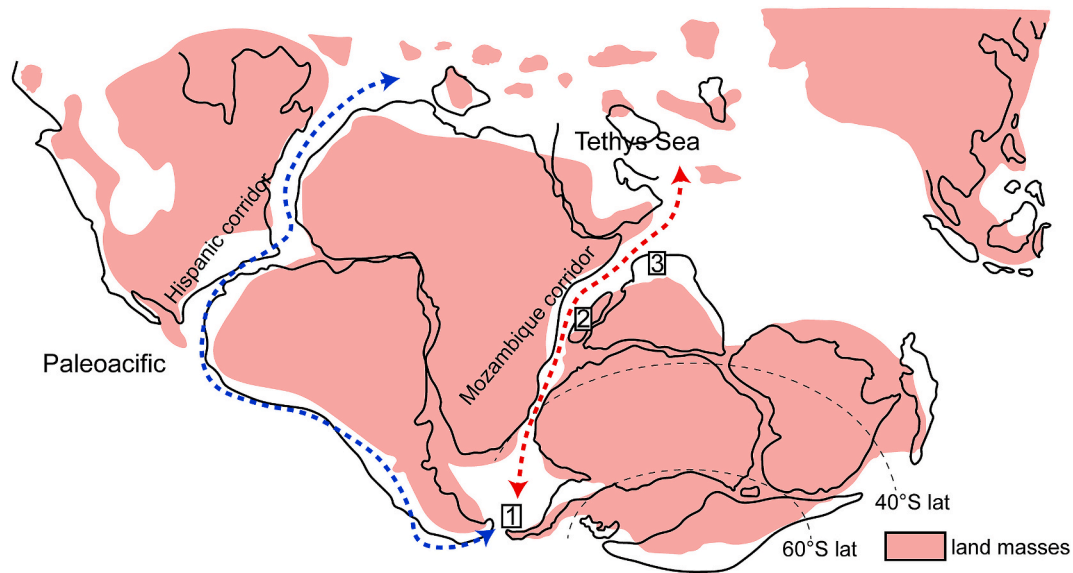A similar palaeobiogeographic scenario is also reported for other

Fig. 8. Late Jurassic palaeobiogeographic map after Challinor and Hikuroa (2007), showing the marine corridors between the Western Tethys and the Paleopacific and regions where ophthalmosaurids are reported along the Mozambique Corridor. **1**, Antarctica; **2**, Madagascar; **3**, India.

marine reptile clades like plesiosaurs and metriorhynchids, which exhibited a widespread distribution (Bardet et al., 2014). Up to date, several dispersion/migration routes have been proposed to explain these distribution patterns. Until the break-up of Pangea, a phenomenon that began by the Triassic, the principal routes of dispersion for Mesozoic marine reptiles were peri-Pangean, Tethyan, and trans-Panthalassan (Bardet et al., 2014). The aperture and functioning of the Hispanic Corridor during the Pliensbachian–Toarcian had several climatic consequences related to changes in water circulation and reduction of the seasonality in the Tethys Sea (Arias 2008; Damborenea 2017). Such route has been invoked as one of the main seaways that allowed the faunal interchange between the Tethys and Paleopacific Seas, for both benthonic and nektonic invertebrates (*e.g.* Damborenea and Manceñido 1979; Riccardi 1991) as well as for marine vertebrates (*e.g.* Fernández and Iturralde-Vinent 2000; Arratia et al., 2004; Gouiric-Cavalli 2015, 2016, 2017; Herrera et al., 2021). As an alternative to this, the opening of the Mozambique Corridor (=Trans-Erythraean Seaway = Trans--Gonwana = South African Seaway) during Late Jurassic–Early Cretaceous separating Madagascar-India-Antarctica from southeastern Africa has been pointed out as a route of dispersion connecting the Tethys and Palaeopacific seas, again for both vertebrate (*e.g.* Prasad et al., 2017; Gouiric-Cavalli 2017; O`Gorman et al., 2018; Gouiric-Cavalli et al., 2019) and invertebrate faunas (*e.g.* Damborenea 2017) (Fig. 8). Recent contributions regarding palaeoclimatic and palaeogeographical reconstructions of the Mozambique Corridor seem to support this idea. During the Early to Middle Jurassic, marine conditions were established in East Africa and western Madagascar, and India (Ali Kassim et al., 2002; Geiger et al., 2004; Alberti et al. 2012, 2019), although it is not until the Late Jurassic when such conditions are registered in Mozambique (Salman and Abdula 1995). During the interval comprising late Callovian to Kimmeridgian, water temperatures estimated from stable isotope analyses on both benthonic and nektopelagic invertebrates from the Kachchh Basin, ranged between ~11.2° and 18 °C (Alberti et al., 2012). The same kind of analyses carried out on invertebrates from the Morondava Basin show a similar trend in water temperatures for the same time (~12.3°-19.3 °C) (Alberti et al., 2019).

On the other hand, water temperatures estimated for the sea surface at Falkland Plateau during the Callovian–lower Tithonian interval ranged between ~25° and 30 °C (Jenkyns et al., 2012). All the palaeotemperature evidence from the Callovian–Late Jurassic interval coupled with major events of global sea-level rise during the Callovian

and late Oxfordian–Kimmeridgian times (Hallam 2001), points the Mozambique Corridor as a plausible candidate for an ichthyosaur dispersion route. In this context, the new ophthalmosaurid records, especially those from the Antarctic Peninsula, add new support to a palaeobiogeographical scenario in which ichthyosaurs would have dispersed, together with other large marine reptiles like plesiosaurs, through the Mozambique Corridor among the Antarctic bay and the Tethys Sea.

6. Conclusions

The new findings from the Upper Jurassic levels of the Ameghino Formation provide the first unambiguous evidence of ichthyosaurs from Antarctica. The materials correspond to postcranial remains of three specimens, showing traits that indicate these were juvenile individuals at the moment of death. One of them (IAA- Pv 712) can be identified as a platypterygiine ophthalmosaurid, and the other two as Ichthyosauria indet. Comparison with Late Jurassic ichthyosaurs from Madagascar (two of them identified as ophthalmosaurids) brings additional support to the hypothesis of the Mozambique Corridor as an active southern dispersion route for ophthalmosaurids at least since the Late Jurassic.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https ://doi.org/10.1016/j.jsames.2021.103259.

Credit author statement

References

Alberti, M., Fürsich, F.T., Pandey, D.K., 2012. The Oxfordian stable isotope record (δ18O, δ13C) of belemnites, brachiopods, and oysters from the Kachchh Basin (western India) and its potential for palaeoecologic, palaeoclimatic, and palaeogeographic reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 344, 49–68.

Alberti, M., Arabas, A., Fürsich, F.T., Andersen, N., Ziółkowski, P., 2019. The Middle to Upper Jurassic stable isotope record of Madagascar: linking temperature changes with plate tectonics during the break-up of Gondwana. Gondwana Res. 73, 1–15.

Ali Kassim, M., Carmignani, L., Conti, P., Fantozzi, P.L., 2002. Geology of the Mesozoic-Tertiary sedimentary basins in south-western Somalia. J. Afr. Earth Sci. 34, 3–20.

Arias, C., 2008. Palaeoceanography and biogeography in the early jurassic panthalassa and Tethys oceans. Gondwana Res. 14, 306–315.

Arkhangelsky, M.S., 2001. The historical sequence of Jurassic and Cretaceous ichthyosaurs. Paleontol. J. 35, 521–524.

Arratia, G., Scasso, R.A., Kiessling, W., 2004. Late jurassic fishes from longing gap, antarctic Peninsula. J. Vertebr. Paleontol. 24, 41–55.

Bardet, N., Falconnet, J., Fischer, V., Houssaye, A., Jouve, S., Pereda Suberbiola, X., Pérez-García, A., Rage, J.-C., Vincent, P., 2014. Mesozoic marine reptile palaeobiogeography in response to drifting plates. Gondwana Res. 26, 869–887.

Baur, G., 1887. On the morphology and origin of the Ichthyopterygia. Am. Nat. 21, 837–840.

Besairie, H., 1972. — Géologie de Madagascar. I. – les terrains sédimentaires. Ann. Geol. Madag. 35, 1–463.

Blainville, H.M.D., 1835. Description de quelques espèces de reptiles de la Californie: précédée de l'analyse d'un système général d'erpétologie et d'amphibiologie. Nouvelles Annales du Muséum d'Histoire Naturelle 4, 233–296.

Caldwell, M.W., 1997a. Modified perichondral ossification and the evolution of paddle-like limbs in ichthyosaurs and plesiosaurs. J. Vertebr. Paleontol. 17, 534–547.

Caldwell, M.W., 1997b. Limb ossification patterns of the ichthyosaur *Stenopterygius*, and a discussion of the proximal tarsal row of ichthyosaurs and other neodiapsid reptiles. Zool. J. Linn. Soc. 120, 1–25.

Campos, L., Fernández, M.S., Herrera, Y., 2020. A new ichthyosaur from the Late Jurassic of north-west Patagonia (Argentina) and its significance for the evolution of the narial complex of the ophthalmosaurids. Zool. J. Linn. Soc. 188, 180–201.

Challinor, A.B., Hikuroa, D.C., 2007. New middle and upper Jurassic belemnite assemblages from West Antarctica (Latady Group, Ellsworth Land): taxonomy and paleobiogeography. Palaeontol. Electron. 10, 1–29.

Charbonnier, S., Garassino, A., Pasini, G., 2012. Revision of Mesozoic decapod crustaceans from Madagascar. Geodiversitas 34, 313–357.

Chinsamy, A., Raath, M.A., 1992. Preparation of fossil bone for histological examination. Palaeontographia Africana 29, 39–44.

Concheyro, A., Scasso, R.A., 1999. Nanofósiles calcáreos de la Formación Ameghino (jurásico tardío), península antártica. XIV congreso geológico Argentino. Salta, Argentina. Acta I, 47.

Crame, J.A., 1982. Late mesozoic bivalve biostratigraphy of the antarctic Peninsula region. J. Geol. Soc. 139, 771–778.

Damborenea, S.E., 2017. Revisión de los biocoremas marinos globales del jurásico según la distribución de los moluscos bivalvos. PE-APA 17, 31–49.

Damborenea, S.E., Manceñido, M.O., 1979. On the palaeogeographical distribution of the pectinid genus *Weyla* (Bivalvia, Lower Jurassic). Palaeogeogr. Palaeoclimatol. Palaeoecol. 27, 85–102.

Delsett, L.L., Novis, L.K., Roberts, A.J., Koevoets, M.J., Hammer, Ø., Druckenmiller, P.S., Hurum, J.H., 2016. The Slottsmøya marine reptile Lagerstätte: depositional environments, taphonomy and diagenesis. Geol. Soc. Lond. Spec. Publ. 434, 165–188.

Delsett, L.L., Roberts, A.J., Druckenmiller, P.S., Hurum, J.H., 2017. A new ophthalmosaurid (Ichthyosauria) from Svalbard, Norway, and evolution of the ichthyopterygian pelvic girdle. PloS One 12, e0169971.

del Valle, Núñez, 1988. Estratigrafía de la regiión comprendida entre el Cerro Torre y el Cabo Longing, en el borde NE de la Península Antártica. Contribución Científica Del Instituto Antártico Argentino 332, 1–83.

Delsett, L.L., Druckenmiller, P.S., Roberts, A.J., Hurum, J.H., 2018. A new specimen of *Palvennia hoybergeti*: implications for cranial and pectoral girdle anatomy in ophthalmosaurid ichthyosaurs. PeerJ 6, e5776.

Delsett, L.L., Roberts, A.J., Druckenmiller, P.S., Hurum, J.H., 2019. Osteology and phylogeny of late jurassic ichthyosaurs from the Slottsmøya member lagerstätte (spitsbergen, svalbard). Acta Palaeontol. Pol. 64, 717–743.

Doyle, P., Whitham, A.G., 1991. Palaeoenvironments of the nordenskjöld formation: an antarctic late jurassic—early cretaceous black shale-tuff sequence. Geol. Soc. Lond. Spec. Publ. 58, 397–414.

Druckenmiller, P.S., Maxwell, E.E., 2010. A new lower Cretaceous (lower Albian) ichthyosaur genus from the Clearwater Formation, Alberta, Canada. Can. J. Earth Sci. 47, 1037–1053.

Druckenmiller, P.S., Maxwell, E.E., 2014. A Middle jurassic (bajocian) ophthalmosaurid (reptilia, ichthyosauria) from the tuxedni formation, Alaska and the early diversification of the clade. Geol. Mag. 151, 41–48.

Druckenmiller, P.S., Hurum, J.H., Knutsen, E.M., Nakrem, H.A., 2012. Two new ophthalmosaurids (reptilia: ichthyosauria) from the Agardhfjellet Formation (upper jurassic: volgian/tithonian), svalbard, Norway. Norw. J. Geol. 92, 311–339.

Farquharson, G.W., 1982. Late mesozoic sedimentation in the northern antarctic Peninsula and its relationship to the southern andes. J. Geol. Soc. London 139, 721–727.

Fernández, M.S., 1994. A new long-snouted ichthyosaur from the early bajocian of neuquén basin (Argentina). Ameghiniana 31, 283–290.

Fernández, M.S., 1997a. On the paleogeographic distribution of Callovian and Late Jurassic ichthyosaurs. J. Vertebr. Paleontol. 17, 752–754.

Fernández, M.S., 1997b. A new ichthyosaur from the tithonian (late jurassic) of the neuquén basin, northwestern patagonia, Argentina. J. Paleontol. 71, 479–484.

Fernández, M.S., 1999. A new ichthyosaur from the Los Molles formation (early Bajocian), Neuquén basin, Argentina. J. Paleontol. 73, 677–681.

Fernández, M.S., 2003. Ophthalmosauria (ichthyosauria) forefin from the aalenian-bajocian boundary of Mendoza province, Argentina. J. Vertebr. Paleontol. 23, 691–694.

Fernández, M.S., Aguirre-Urreta, M.B., 2005. Revision of *Platypterygius hauthali* von Huene, 1927 (ichthyosauria: Ophthalmosauridae) from the early cretaceous of patagonia, Argentina. J. Vertebr. Paleontol. 25, 583–587.

Fernández, M.S., Iturralde-Vinent, M., 2000. An Oxfordian ichthyosauria (Reptilia) from Viñales, western Cuba: paleobiogeographic significance. J. Vertebr. Paleontol. 20, 191–193.

Fernández, M.S., Talevi, M., 2013. Ophthalmosaurian (ichthyosauria) records from the aalenian–bajocian of patagonia (Argentina): an overview. Geol. Mag. 151, 49–59.

Fernández, M.S., Herrera, Y., Vennari, V.V., Campos, L., de la Fuente, M., Talevi, M., Aguirre-Urreta, B., 2019. Marine reptiles from the jurassic/cretaceous transition at the high andes, Mendoza, Argentina. J. South Am. Earth Sci. 92, 658–673.

Fischer, V., Masure, E., Arkhangelsky, M.S., Godefroit, P., 2011. A new barremian (early cretaceous) ichthyosaur from western Russia. J. Vertebr. Paleontol. 31, 1010–1025.

Fischer, V., Maisch, M.W., Naish, D., Kosma, R., Liston, J., Joger, U., Krüger, F.J., Pardo-Pérez, J.M., Tainsh, J., Appleby, R.M., 2012. New ophthalmosaurid ichthyosaurs from the European Lower Cretaceous demonstrate extensive ichthyosaur survival across the Jurassic–Cretaceous boundary. PloS One 7, e29234.

Fischer, V., Appleby, R.M., Naish, D., Liston, J., Riding, J.B., Brindley, S., Godefroit, P., 2013a. A basal thunnosaurian from Iraq reveals disparate phylogenetic origins for Cretaceous ichthyosaurs. Biol. Lett. 9, 1–6.

Fischer, V., Arkhangelsky, M.S., Uspensky, G.N., Stenshin, I.M., Godefroit, P., 2013b. A new Lower Cretaceous ichthyosaur from Russia reveals skull shape conservatism within Ophthalmosaurinae. Geol. Mag. 151, 60–70.

Fischer, V., Bardet, N., Benson, R.B.J., Arkhangelsky, M.S., Friedman, M., 2016. Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. Nat. Commun. 7, 10825.

Foffa, D., Young, M.T., Stubbs, T.L., Dexter, K.G., Brusatte, S.L., 2018. The long-term ecology and evolution of marine reptiles in a Jurassic seaway. Nat. Ecol. Evol. 2, 1548–1555.

Gasparini, Z., Iturralde-Vinent, M., 2006. The Cuban Oxfordian herpetofauna in the Caribbean seaway. Neues Jahrbuch Geol. Palaontol. Abhand. 240, 343–371.

Geiger, M., Schweigert, G., 2006. Toarcian–Kimmeridgian depositional cycles of the south-western Morondava Basin along the rifted continental margin of Madagascar. Facies 52, 85–112.

Geiger, M., Clark, D.N., Mette, W., 2004. Reappraisal of the timing of the breakup of Gondwana based on sedimentological and seismic evidence from the Morondava Basin, Madagascar. J. Afr. Earth Sci. 38, 363–381.

Gouiric-Cavalli, S., 2015. *Jonoichthys challwa* gen. et sp. nov., a new Aspidorhynchiformes (Osteichthyes, Neopterygii, Teleosteomorpha) from the marine Upper Jurassic sediments of Argentina, with comments about paleobiogeography of Jurassic aspidorhynchids. C.R. Palevol 14, 291–304.

Gouiric-Cavalli, S., 2016. A new late jurassic halecomorph fish from the marine vaca muerta formation, Argentina, south-western Gondwana. Fossil Rec 19, 119–129.

Gouiric-Cavalli, S., 2017. Large and mainly unnoticed: the first lower Tithonian record of a suspension-feeding pachycormid from Southern Gondwana. Ameghiniana 54, 283–289.

Gouiric-Cavalli, S., Rasia, L.L., Márquez, G.J., Rosato, V., Scasso, R.A., Reguero, M., 2019. First pachycormiform (actinopterygii, pachycormiformes) remains from the late jurassic of the antarctic Peninsula and remarks on bone alteration by recent bioeroders. J. Vertebr. Paleontol. 38, e1524384.

Hallam, A., 2001. A review of the broad pattern of Jurassic sea-level changes and their possible causes in the light of current knowledge. Palaeogeogr. Palaeoclimatol. Palaeoecol. 167, 23–37.

Herrera, Y., Fernández, M.S., Vennari, V.V., 2021. *Cricosaurus* (thalattosuchia, metriorhynchidae) survival across the J/K boundary in the high andes (Mendoza province, Argentina). Cretac. Res. 118, 104673.

Hikuroa, D.C., 2009. Short note: second Jurassic marine reptile from the Antarctic Peninsula. Antarct. Sci. 21, 169–170.

Houssaye, A., Nakajima, Y., Sander, P.M., 2018. Structural, functional, and physiological signals in ichthyosaur vertebral centrum microanatomy and histology. Geodiversitas 40, 161–170.

Jacobs, M.L., Martill, D.M., 2020. A new ophthalmosaurid ichthyosaur from the upper jurassic (early tithonian) kimmeridge clay of dorset, UK, with implications for late jurassic ichthyosaur diversity. PloS One 15, e0241700.

Jenkyns, H.C., Schouten-Huibers, L., Schouten, S., Sinninghe Damsté, J.S., 2012. Warm Middle jurassic–early cretaceous high-latitude sea-surface temperatures from the southern ocean. Clim. Past 8, 215–226.

Johnson, R., 1977. Size independent criteria for estimating age and the relationships among growth parameters in a group of fossil reptiles (Reptilia: ichthyosauria). Can. J. Earth Sci. 14, 1916–1924.

Kear, B.P., Zammit, M., 2014. In utero foetal remains of the Cretaceous ichthyosaurian *Platypterygius*: ontogenetic implications for character state efficacy. Geol. Mag. 151, 71–86.

Kiessling, W., Scasso, R., Zeiss, A., Riccardi, A., Medina, F., 1999. Combined radiolarian-ammonite stratigraphy for the Late Jurassic of the Antarctic Peninsula: implications for radiolarian stratigraphy. Geodiversitas 21, 687–713.

Kolb, C., Sander, P.M., 2009. Redescription of the ichthyosaur *Platypterygius hercynicus* (kuhn 1946) from the lower cretaceous of salzgitter (lower saxony, Germany). Palaeontograph. Abteilung 288, 151–192.

Leanza, H.A., Vennari, V.V., Aguirre-Urreta, M.B., Concheyro, A., Lescano, M., Ivanova, D., Kietzmann, D.A., López-Martínez, R., Martz, P.A., Paolillo, M.A., Guler, M.V., Pujana, I., Paz, M., 2020. Relevant marine paleobiological markers of the vaca muerta formation. In: Minisini, D., Fantín, M., Lanusse Noguera, I., Leanza, H. (Eds.), Integrated Geology of Unconventionals: the Case of the Vaca Muerta Play, Argentina, vol. 121. AAPG Memoir, pp. 61–98.

Massare, J.A., 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. J. Vertebr. Paleontol. 7, 121–137.

Maxwell, E.E., 2010. Generic reassignment of an ichthyosaur from the queen elizabeth islands, northwest territories, Canada. J. Vertebr. Paleontol. 30, 403–415.

Maxwell, E.E., Cortés, D., 2020. A revision of the Early Jurassic ichthyosaur Hauffiopteryx (Reptilia: ichthyosauria), and description of a new species from south-western Germany. Palaeontol. Electron. 23, 1–43.

Maxwell, E.E., Kear, B.P., 2010. Postcranial anatomy of *Platypterygius americanus* (reptilia: ichthyosauria) from the cretaceous of Wyoming. J. Vertebr. Paleontol. 30, 1059–1068.

Maxwell, E.E., Fernández, M.S., Schoch, R.R., 2012. First diagnostic marine reptile remains from the Aalenian (Middle Jurassic): a new ichthyosaur from southwestern Germany. PloS One 7, e41692.

Maxwell, E.E., Scheyer, T.M., Fowler, D.A., 2014. An evolutionary and developmental perspective on the loss of regionalization in the limbs of derived ichthyosaurs. Geol. Mag. 151, 29–40.

Maxwell, E.E., Cortés, D., Patarroyo, P., Ruge, M.L.P., 2019. A new specimen of *Platypterygius sachicarum* (Reptilia, Ichthyosauria) from the Early Cretaceous of Colombia and its phylogenetic implications. J. Vertebr. Paleontol. 39, e1577875.

McGowan, C., 1973. The cranial morphology of the Lower Liassic latipinnate ichthyosaurs of England. Bull. br. Mus. nat. Hist. Geol. 24, 1–109.

Medina, F.A., Ramos, A.M., 1983. Geología de las Inmediaciones del Refugio Ameghino (64°26'S, 58°59'W) Tierra de San Martin, Península Antártica, 229. Contribución del Instituto Antártico Argentino, p. 14.

Miedema, F., Maxwell, E.E., 2019. Ontogeny of the braincase in *Stenopterygius* (reptilia, ichthyosauria) from the lower jurassic of Germany. J. Vertebr. Paleontol. 39, e1675164.

Moon, B.C., Kirton, A.M., 2016. Ichthyosaurs of the British Middle and upper jurassic. Part 1 *Ophthalmosaurus*. Monogr. Palaeontogr. Soc. 170, 1–84.

Moon, B.C., Kirton, A.M., 2018. Ichthyosaurs of the British Middle and upper jurassic. Part 2 *Brachypterygius, Nannopterygius, macropterygius* and taxa invalida. Monogr. Palaeontogr. Soc. 172, 85–177.

Motani, R., 2005. Evolution of fish-shaped reptiles (Reptilia: ichthyopterygia) in their physical environments and constraints. Annu. Rev. Earth Planet Sci. 33, 395–420.

Motani, R., Jiang, D.-Y., Chen, G.-B., Tintori, A., Rieppel, O., Ji, C., Huang, J.D., 2015. A basal ichthyosauriform with a short snout from the Lower Triassic of China. Nature 517, 485–488.

O'Gorman, J.P., Gouiric-Cavalli, S., Scasso, R.A., Reguero, M., Moly, J.J., Acosta-Burlaille, L., 2018. A late jurassic plesiosaur in Antarctica: evidence of the dispersion of marine fauna through the trans-erythraean seaway? C.R. Palevol 17, 158–165.

Paparella, I., Maxwell, E.E., Cipriani, A., Roncacè, S., Caldwell, M., et al., 2016. The first ophthalmosaurid ichthyosaur from the Upper Jurassic of the Umbrian–Marchean Apennines (Marche, Central Italy). Geol. Mag. 154, 837–858.

Prasad, G.V.R., Pandey, D.K., Alberti, M., Fürsich, F.T., Thakkar, M.G., Chauhan, G.D., 2017. Discovery of the first ichthyosaur from the Jurassic of India: implications for Gondwanan palaeobiogeography. PloS One 12, e0185851.

Riccardi, A.C., 1991. Jurassic and cretaceous marine connections between the southeast pacific and Tethys. Palaeogeogr. Palaeoclimatol. Palaeoecol. 87, 155–189.

Roberts, A.J., Druckenmiller, P.S., Sætre, G.-P., Hurum, J.H., 2014. A new upper jurassic ophthalmosaurid ichthyosaur from the Slottsmøya member, Agardhfjellet Formation of central spitsbergen. PloS One 9, e103152.

Salman, G., Abdula, I., 1995. Development of the Mozambique and Ruvuma sedimentary basins, offshore Mozambique. Sediment. Geol. 96, 7–41.

Sander, P.M., 2000. Ichthyosauria: their diversity, distribution, and phylogeny. Paläontol. Z. 74, 1–35.

Swaby, E.J., Lomax, D.R., 2020. A revision of temnodontosaurus crassimanus (reptilia: ichthyosauria) from the lower jurassic (toarcian) of whitby, yorkshire, UK. Hist. Biol. 1–17.

Talevi, M., Campos, L., Fernández, M.S., 2021. Microanatomy and histology of the distal limb elements of Ophthalmosaurids from the Middle Jurassic to the Lower Cretaceous from Neuquén Basin, Patagonia, Argentina. Cretac. Res, 104737.

Talevi, M., Fernández, M.S., Salgado, L., 2012. Variación en la histología ósea de *Caypullisaurus bonapartei* Fernández, 1997 (Ichthyosauria: Ophthalmosauridae). Ameghiniana 49, 38–46.

Torsvik, T.H., Van der Voo, R., Preeden, U., Mac Niocaill, C., Steinberger, B., Doubrovine, P.V., van Hinsbergen, D.J.J., Domeier, M., Gaina, C., Tohver, E., Meert, J.G., McCausland, P.J.A., Cocks, L.R.M., 2012. Phanerozoic polar wander, palaeogeography and dynamics. Earth Sci. Rev. 114, 325–368.

Tyborowski, D., 2016. A new ophthalmosaurid ichthyosaur from the late jurassic of owadów-brzezinki quarry, Poland.). Acta Palaeontol. Pol. 61, 791–803.

van Hinsbergen, D.J.J., de Groot, V.L., van Schaik, S.J., Spakman, W., Bijl, P.K., Sluijs, A., Langereis, C.G., Brinkhuis, H., 2015. A paleolatitude calculator for paleoclimate studies. PloS One 10, e0126946.

Whitham, A.G., 1993. Facies and depositional processes in an Upper Jurassic to Lower Cretaceous pelagic sedimentary sequence, Antarctica. Sedimentology 40, 331–349.

Whitham, A.G., Doyle, P., 1989. Stratigraphy of the upper jurassic-lower cretaceous nordenskjöld Formation of eastern graham land, Antarctica. J. South Am. Earth Sci. 2, 371–384.

Whitham, A.G., Storey, B.C., 1989. Late jurassic-early cretaceous strike-slip deformation in the nordenskjöld Formation of graham land. Antarct. Sci. 1, 269–278.

Zammit, M., Norris, R.M., Kear, B.P., 2010. The Australian Cretaceous ichthyosaur *Platypterygius australis*: a description and review of postcranial remains. J. Vertebr. Paleontol. 30, 1726–1735.

Zverkov, N.G., Efimov, V.M., 2019. Revision of Undorosaurus, a Mysterious Late jurassic ichthyosaur of the boreal realm. J. Syst. Paleontol. 17, 1183–1213.

Zverkov, N.G., Grigoriev, D.V., 2020. An unrevealed lineage of platypterygiines (Ichthyosauria) with peculiar forefin structure and semiglobal distribution in the mid-Cretaceous (Albian–Cenomanian). Cretac. Res. 115, 104550.

Zverkov, N.G., Prilepskaya, N.E., 2019. A prevalence of *Arthropterygius* (ichthyosauria: Ophthalmosauridae) in the late jurassic–earliest cretaceous of the boreal realm. PeerJ 7, e6799.

Zverkov, N.G., Arkhangelsky, M.S., Pardo, P.J., Beznosov, P.A., 2015. On the upper jurassic ichthyosaur remains from the Russian north. Proceedings of the Zoological Institute RAS 319, 81–97.

Further reading

Challinor, Hikuroa, 2007. New Middle and Upper Jurassic belem-nite assemblages from West Antarctica (Latady Group, EllsworthLand): taxonomy and paleobiogeography. Palaeontol. Electron. 10, 1.

Challinor, Hikuroa, 2007. New Middle and Upper Jurassic belem-nite assemblages from West Antarctica (Latady Group, EllsworthLand): taxonomy and paleobiogeography. Palaeontol. Electron. 10, 1.

Fernández, 1999. A new ichthyosaur from the Los Molles formation (early Bajocian), Neuquén basin, Argentina. Journal of Paleontology 677–681.

Fernández, 1999. A new ichthyosaur from the Los Molles formation (early Bajocian), Neuquén basin, Argentina. Journal of Paleontology 677–681.

Talevi, Campos, Fernández, et al., 2021. Microanatomy and histology of the distal limb elements of Ophthalmosaurids from the Middle Jurassic to the Lower Cretaceous from Neuquén Basin, Patagonia, Argentina. Cretac. Res.

Talevi, Campos, Fernández, et al., 2021. Microanatomy and histology of the distal limb elements of Ophthalmosaurids from the Middle Jurassic to the Lower Cretaceous from Neuquén Basin, Patagonia, Argentina. Cretac. Res.