Revalidation of *Myobradypterygius hauthali* Huene, 1927 and the phylogenetic signal within the ophthalmosaurid (Ichthyosauria) forefins

Lisandro Campos [a, b, *], Marta S. Fernández [a, b], Victor Bosio [a], Yanina Herrera [a, b], Agustina Manzo [a]

[a] *División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Av. 122 y 60, B1900 La Plata, Buenos Aires, Argentina*
[b] *Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina*

ABSTRACT

In the last decade, several new Cretaceous ichthyosaurs have been described and/or redescribed, challenging the traditional concept that, during the Cretaceous, ichthyosaurs were abundant but not diverse. Here, we redescribe the holotype and referred specimen of 'Platypterygius' hauthali Huene (1927) from the Barremian of Argentinean Patagonia and compare its appendicular anatomy with that of a referred specimen from the Valanginian - Hauterivian of Chile. These specimens consist almost entirely of anterior appendicular elements, so we explore quantitatively the phylogenetic signal contained in the forefin of the ophthalmosaurids and include them in a new phylogenetic analysis. Our results support the revalidation of the genus *Myobradypterygius* Huene, 1927, for the reception of the materials previously assigned to 'Pl.' hauthali. Moreover, we found that forefin characters present a strong phylogenetic signal, highlighting the utility of these characters as a source of systematic information.

© 2024 Elsevier Ltd. All rights reserved.

1. Introduction

The interpretation of ichthyosaur diversity during the Cretaceous and the final extinction of the lineage has significantly improved in recent years (e.g. Fischer et al., 2016; Motani, 2016). Traditionally, it has been assumed that, based on the poor and patchy Cretaceous records, the events around the Jurassic-Cretaceous boundary strongly affected them and that all surviving forms were, although abundant, not diverse (Tennant et al., 2016). The taxonomic consequence of this interpretation was that almost all Cretaceous ichthyosaurs were gathered within the catch−all genus 'Platypterygius' Huene, 1922 characterized by wide fins (with no fewer than seven digits) and tightly packed brick-like phalanges (McGowan 1972; McGowan and Motani 2003). However, during the last decade, many contributions (e.g. Fischer, 2012;

Fischer et al., 2012, 2014a, b, c, 2016; Maxwell et al., 2016, 2019; Páramo-Fonseca et al., 2021; Cortés et al., 2021) demonstrated that the taxonomic, phylogenetic and ecological diversity of Cretaceous ichthyosaurs were strongly underestimated.

Despite all the advances, the still persistent stratigraphic and geographic gaps in the Cretaceous records hinder the understanding of the global diversity of this successful group of marine tetrapods. Particularly, the western Gondwana records are patchy both geographically and stratigraphically. Thus, only four valid taxa (*Caypullisaurus bonapartei* Fernández 1997, 'Platypterygius' hauthali Huene 1927, *Kyhytysuka sachicarum* Páramo-Fonseca 1997, and *Muiscasaurus catheti* Maxwell et al., 2016) encompass the Early Cretaceous diversity described from South America (Table 1). These records are also uneven in terms of completeness and preservation. Rich Hauterivian−Aptian deposits of the Paja Formation yielded well-preserved and informative materials (including skull and postcranial remains) contrasting with the southern western Gondwana records that are still poorly known (e.g. Páramo-Fonseca, 1997; Maxwell et al., 2016, 2019; Cortés and Páramo-Fonseca, 2018; Cortés et al., 2021; Páramo-Fonseca et al., 2021). Thus, except for a specimen referred to as *Caypullisaurus bonapartei*

* Corresponding author. División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. Av. 122 y 60, B1900 La Plata, Buenos Aires, Argentina.
E-mail addresses: lcampos@fcnym.unlp.edu.ar (L. Campos), martafer@fcnym.unlp.edu.ar (M.S. Fernández), bosiovictor@gmail.com (V. Bosio), yaninah@fcnym.unlp.edu.ar (Y. Herrera), agustinamanz@gmail.com (A. Manzo).

Table 1
Ophthalmosaurids records from the Lower Cretaceous of South America.

Stage	Taxon	Localities	References
Berriasian	*Caypullisaurus bonapaertei*	Yesera del Tromen, Neuquén, Argentina	Fernández (2007)
Barremian	*Myobradypterygius hauthali*	Cerro Belgrano, Santa Cruz, Argentina	Huene (1925, 1927); Fernández and Aguirre-Urreta (2005)
Valanginian	Platypterygiinae indet.	Pichaihue, Neuquén, Argentina	Lazo et al. (2018)
Valanginian − Hauterivian	?*Platypterygius hauthali*, *Platypterygius* cf. *hauthali*, Ophthalmosauridae indet.	Tyndall Glacier, Torres del Paine National Park, Chile	Párdo-Pérez et al. (2012, 2015); Stinnisbeck et al. (2014)
Barremian−Aptian	*Kyhytysuka sachicarum*	Villa de Leyva, Boyacá, Colombia	Páramo-Fonseca (1997); Maxwell et al. (2019); Cortés et al., (2021)
Barremian	*Platypterygius* sp.	Loma La Cabrera, Boyacá, Colombia	Cortés and Páramo-Fonseca (2018)
Barremian-Aptian	*Muiscasaurus catheti*	Sáchica and Loma La Catalina, Boyacá, Colombia	Maxwell et al. (2016); Páramo-Fonseca et al. (2021)

and a few fragmentary Valanginian to Hauterivian specimens from Neuquén Province (Argentina) (Fernández, 2007; Lazo et al., 2018), the knowledge of Cretaceous ophthalmosaurids from Patagonia is restricted to the holotype and referred specimens of '*Platypterygius*' *hauthali*.

In recent years, the rich deposits of the Zapata Formation at Torres del Paine National Park (Southern Chile) have yielded more than 40 ichthyosaur specimens (Stinnesbeck et al., 2014). Most of the skeletons have suffered glacial erosion, although some of them preserved articulated forefins and have been tentatively identified as '*Pl.*' *hauthali* (Pardo-Pérez et al., 2012, 2015; Stinnesbeck et al., 2014). The characteristics observed in the anterior appendicular skeleton of the Patagonian specimens from Argentina and Chile indicate that these are referable to the same taxon and, on the other hand, that their position within '*Platypterygius*' is problematic. Moreover, a recent analysis of the morphological disparity of the ophthalmosaurid forefins depicted that the humerus morphology of '*Pl.*' *hauthali* is also peculiar, occupying a sector of morphospace that is clearly different from those of other species referred to '*Platypterygius*' (Campos et al., 2021). As '*Pl.*' *hauthali* is based on a fragmentary forefin, and some ophthalmosaurid taxa have been described based mainly on forefin morphology (e.g. Arkhangelsky and Zverkov, 2014; Tyborowski, 2016; Zverkov and Jacobs, 2021), we explore the quantitative assessment of the phylogenetic signal within the forefin. Here, and based on the strong phylogenetic signal and the unique forefin character combination, we reassign '*Pl.*' *hauthali* to *Myobradypterygius* Huene, 1927 and analyze its phylogenetic relationships with other ophthalmosaurids.

1.1. Taxonomical history

The first mention in the literature of the materials upon which *Myobradypterygius* was erected corresponds to Huene (1925). There, the author describes remains of the vertebral column and forelimbs (MLP 79-I-30-2) from an individual found at Cerro Belgrano, near Lake Belgrano (Santa Cruz Province, Argentina). Based on the shape and arrangement of the elements in the forelimbs, Huene reconstructed a significant portion of the forelimb (Huene, 1925: fig. 5) and identified two main characteristics: the presence of at least seven digits and an intermedium that distally had two subequal articular facets from which two digits developed. Based on this latter feature, Huene (1925) suggested that the Argentinean material was related to the 'Campylodon group', more specifically to the genus *Myopterygius* Huene, 1922, because the species *Ichthyosaurus kokeni* Broili, 1908 (= *Myopterygius kokeni* sensu Huene 1922: 98) from the Hauterivian of Germany had a similar intermedium element. However, Huene (1925) refrained from formally assigning these materials to any genus or species. Two years later, Huene (1927) described new appendicular remains, which included a humerus (MLP 79-I-30-1). Since the distal elements to

the humerus of this specimen were virtually identical to those of MLP 79-I-30-2, including an intermedium that had two articular facets distally, Huene (1927) concluded that they belonged to the same genus. However, the characteristics of the humerus, specifically the number of distal articular facets, were incompatible with those of the humerus of *Myopterygius*. For this reason, the author erected the name *Myobradypterygius hauthali* Huene, 1927 for the reception of these materials.

McGowan (1972) revised the Cretaceous ichthyosaurs and argued that due to the type material of *Myobradypterygius hauthali* was largely indeterminable and did not exhibit features contradicting its affinity with *Platypterygius*, *Myobradypterygius* should be considered as *nomen dubium*. In the case of the species, the author considered it should be retained as valid, transferred to *Platypterygius*, and that the 'Neocomian' specimens from South America should be assigned to this taxon. Similarly, McGowan and Motani (2003) proposed that *Platypterygius hauthali* was still valid and also serving for the reception of the Early Cretaceous 'new world material'. These authors also considered that in the future, it might be demonstrated that *Pl. hauthali* is synonymous with the European species *Platypterygius platydactylus*.

Fernández and Aguirre-Urreta (2005) redescribed the holotype and referred specimen of '*Platypterygius*' *hauthali* and provided a specific diagnosis for the taxon. These authors conclude that the forefin morphology of '*Pl.*' *hauthali* is quite different from those of the other species of '*Platypterygius*' and should be considered a valid taxon. It is also important to note that this contribution is the first to assign a Barremian age to these materials.

2. Material and methods

2.1. Material

We redescribed the holotype of *Myobradypterygius hauthali* (MLP 79-I-30-1) and the specimen referred to this taxon by Huene (1927) (MLP 79-I-30-2) and compared them with the specimen CPAP-2011-0019 from the Valanginian to Hauterivian deposits of the Zapata Formation, Chile (Pardo-Pérez et al., 2012). The CPAP-2011-0019 was originally referred to '*Platypterygius*' sp. by Pardo-Pérez et al. (2012) based on the presence of several appendicular features consistent with the diagnosis from McGowan and Motani (2003) for this genus. In the same contribution, the authors suggest that from all '*Platypterygius*' spp. the CPAP-2011-0019 was more similar to '*Pl.*' *hauthali* due to the presence of an hexagonal intermedium and several pre- and postaxial digits, among other characteristics. Several other specimens recovered from the Zapata Fm. Were tentatively referred to '*Pl.*' *hauthali* by Stinnesbeck et al. (2014) and Pardo-Pérez et al. (2015). However, only the CPAP-2011-0019 preserved the elements of the zeugopodium and

basipodium that would allow comparison with the specimens described by Huene (1925, 1927).

2.2. Methods

2.2.1. Phylogenetic analysis

To evaluate the phylogenetic position of *Myobradypterygius* within Ophthalmosauridae, we used the matrix from Campos (2022) generated with Mesquite v.3.31 (Maddison and Maddison, 2019). This matrix was built based on that of Campos et al. (2020) and expanded by adding various taxa recently described taxa, as well as characters gathered from multiple sources (Supplementary Information and references therein). We created two data sets: one considering the Argentinian (MLP 79-I-30-1 and MLP 79-I-30-2) and Chilean (CPAP-2011-0019) specimens as independent OTUs, and another coding *Myobradypterygius hauthali* based on the specimens mentioned above. The resulting datasets contain 52/53 OTUs and 130 characters, respectively (Supplementary Information). The phylogenetic analyses were run in TNT v.1.5 (Goloboff and Catalano, 2016), using a traditional search with 1000 replicates and tree bisection and reconnection with 100 trees retained per replication. All characters were treated as unordered and unweighted. Bremer support was calculated using the Bremer script ("*bremsup.run*"). The consensus tree, as well as all most parsimonious trees, were time-calibrated using the paleotree package (Bapst, 2012) in R Core Team (version 3.4.1, 2017). Occurrence data were collected from literature for each taxon (Supplementary Information).

2.2.2. Phylogenetic signal

The phylogenetic signal can be defined as the statistical non-independence among taxa trait values due to their phylogenetic relatedness (Münkemüller et al., 2012). We tested for the presence of a phylogenetic signal in characters of the forefin using Pagel's lambda (Pagel, 1999). Assuming a Brownian motion model of trait evolution, phylogenetic relationships among taxa solely determine the covariation of traits. Nevertheless, the presence of external factors unrelated to the phylogeny influencing trait evolution makes necessary to modify the significance of the phylogenetic influence. The lambda index determines this adjustment and is fitted to observed data in a way that it scales the Brownian phylogenetic covariances down to the actually observed ones (Freckleton et al., 2002). When using empirical data lambda retrieves values between 0 and 1, where 0 indicates that character states are distributed independent of phylogeny. Other indexes for estimating the phylogenetic signal, such as Fritz and Purvis's *D* (Fritz and Purvis, 2010) or Moran's *I* (Gittleman and Jot, 1990), were not implemented as these are better suitable for binary characters and would imply a large number of the characters to be discarded from our dataset which contains several multistate traits (Münkemüller et al., 2012; Molina-Venegas and Rodriguez, 2017). For each character, taxa scored as unknown were dropped from the trees. Pagel's lambda was calculated using the *fitdiscrete* function of the package geiger (Harmon et al., 2008) in R Core Team (version 3.4.1, 2017).

Institutional abbreviations. CPAP, Colecciones Paleontológicas de Antártica y Patagonia, Punta Arenas, Chile; MLP, Museo de La Plata, Buenos Aires, Argentina.

3. Results

3.1. Systematic paleontology

Ichthyosauria de Blainville, 1835.
Ophthalmosauridae Baur, 1887.

Myobradypterygius Huene, 1927.
Platypterygius McGowan 1972:17; Maisch and Matzke 2000:81; McGowan y Motani 2003: 118.
Type and only known species: *Myobradypterygius hauthali* Huene, 1927.
Diagnosis as for the type and only species.

Myobradypterygius hauthali Huene, 1927.
Figs.1-3
Platypterygius hauthali: McGowan, 1972.
Platypterygius hauthali: Gasparini and Goñi, 1990.
Platypterygius hauthali: Maisch and Matzke, 2000.
Platypterygius hauthali: McGowan and Motani, 2003.
Platypterygius hauthali: Fernández and Aguirre-Urreta, 2005.
Holotype. MLP 79-I-30-1, left humerus, and partially preserved zeugopodium and autopodium.
Type locality and horizon. Cerro Belgrano, Río Belgrano Formation (Barremian), Santa Cruz Province, Argentina (Aguirre-Urreta 2002).
Referred specimens. MLP 79-I-30-2, vertebral centra and a slab containing part of the zeugopodium and autopodium on each side recovered from the type locality; CPAP-2011-0019, articulated left forefin (Zapata Formation, Valanginian−Hauterivian, Torres del Paine National Park, Magallanes region, Chile) (Pardo-Pérez et al., 2012).
Revised diagnosis. Ophthalmosaurid ichthyosaur characterized by the following unique combination of characters: proximal and distal ends of the humerus with nearly equal anteroposterior development (shared with most ophthalmosaurids); humerus with three distal articular facets for an anterior accessory element, radius, and ulna (shared with most ophthalmosaurids except for *Brachypterygius*, *Aegirosaurus*, *Catutosaurus*, *Maiaspondylus*, *Kyhytysuka* and '*Platypteygius*' *americanus*); intermedium with hexagonal shape and distally bearing two sub-equal facets for articulation with the distal carpals of the primary digits III and IV (shared with *Catutosaurus*); at least three postaxial digits in the forelimb (shared with '*Pl.*' *australis*); tightly packed autopodial elements with rectangular shape (shared with Platypterygiinae and *Catutosaurus*).

3.2. Description

3.2.1. Preservation

The axial skeleton is preserved only in the referred specimen (MLP 79-I-30-2) and consists of a single presacral centrum and a small block containing three caudal centra (Fig. 1). The humerus of the holotype is well preserved and almost complete (Fig. 2). Only the dorsal process and deltopectoral crest are slightly eroded. In the holotype and the referred specimen (MLP 79-I-30-2) most of the zeugopodium and autopodium are preserved as impressions on the sedimentary matrix with a thin layer of bone included in it (Figs. 2E-J). Some isolated phalanges are also preserved in the referred specimen (MLP 79-I-30-2). For preservational aspects of the specimen CPAP-2011-0019 we refer to Pardo-Pérez et al. (2012).

3.2.2. Axial skeleton

A single posterior presacral centrum is preserved in a small block together with its corresponding neural arch and spine (Fig. 1A) (MLP 79-I-30-2). The exposed surface of the centrum is typically convex with a rounded pit on its centre. Dorsally, the neural canal surface is slightly raised and flanked by two thin, elevated processes. The dorsal portion of those processes is concave and forms the facets for the neural arches. The diapophysis is located halfway down on the lateral surface of the centrum, whereas the parapophysis is on the ventral half of the lateral surface.
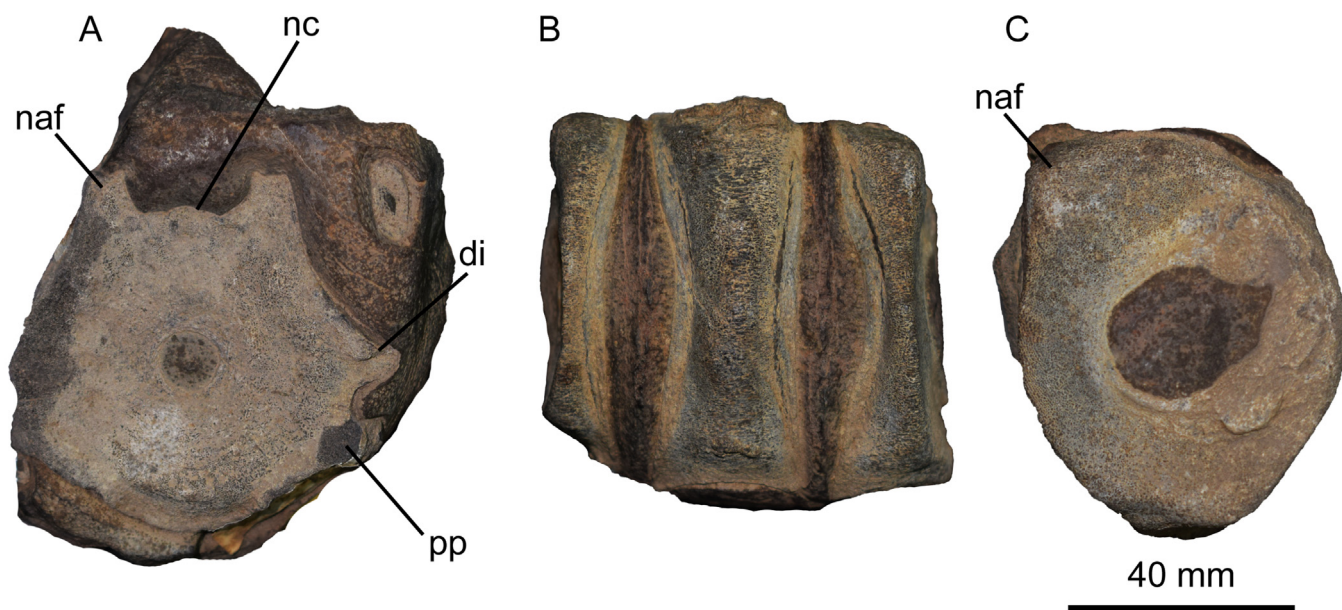
Fig. 1. Vertebral centra of *Myobradypterygius hauthali* (MLP 79-I-30-2). **A,** posterior presacral centrum in anterior/posterior view. **B,** caudal central in lateral. view. **C,** caudal centrum in anterior/posterior view. Abbreviations: di, diapophysis; naf, neural arch facet; nc, neural canal; pp, parapophysis.

A small series of three postflexural centra are preserved articulated (Fig. 1B-C). In anterior/posterior view, the ventral half is compressed, resulting in centra that are taller than wide. The processes for the reception of the neural arches take the form of small tubercles, and there are no indications of the presence of facets for the haemal arches.

3.2.3. Forefin

Humerus. In proximal view the proximal end of the humerus is rectangular and deeply pitted, indicating the presence of a thick cartilage cap over the epiphysis (Fig. 2A). The dorsal process is well developed and it is extended over more than half the length of the humerus shaft (Fig. 2C). Ventrally, the deltopectoral crest is less developed than the dorsal process and it is shifted towards the anterior edge (Fig. 2D). In dorsal and ventral views, the proximal end of the humerus is slightly anteroposteriorly more developed than the distal end in the holotype and in the CPAP-2011-0019. The maximum constriction of the midshaft is located near the distal end.

In the holotype, the distal end bears three articular facets (Figs. 2B). The anterior-most, for articulation with the anterior accessory element (AAE), is the shortest and 'D'-shaped with a convex anterior margin. In the referred specimen (CPAP-2011-0019), this facet is absent or lost (Fig. 3). In ventral and dorsal views, this facet is slightly anteriorly deflected. The radial facet is the most developed in both dorsoventral and anteroposterior direction and presents a squared outline. Posterior to this facet is the one for the articulation with the ulna, with a similar outline to that for the AAE but with a posterior convex margin. Also, the ulnar facet is less developed in dorsoventral direction. The articular surfaces of the radial and ulnar facets are facing distally.

Zeugopodium. In the holotype, the only zeugopodial element preserved is the incomplete ulna (Fig. 2 E-F), whereas in the referred specimen MLP 79-I-30-2, this element is almost complete, and it is articulated with a small fragment of the radius (Fig. 2H-I). The specimen CPAP-2011-0019 preserved the radius and the ulna and lacks the anterior accessory element (Fig. 3). The radius is roughly pentagonal and bears two equally developed distal facets for the articulation of the radial and intermedium. The ulna is also

pentagonal in shape and slightly larger than the radius. In ventral/dorsal view, the posterior margin is convex and rounded.

Proximal carpals. In the holotype and the specimen MLP 79-I-30-2, the only proximal carpals preserved are the intermedium and the ulnare, whereas in the referred specimen CPAP-2011-0019, the proximal carpal row also preserved the radiale (Fig. 3). The radiale is pentagonal with convex proximal and distal edges. Proximally, it articulates with the radial and the AAE. The anterior margin is straight and contacts the second element of the first preaxial accessory digit. Distally, the margin of the radiale contacts with distal carpals II and III. The intermedium is hexagonal and is more anteroposteriorly developed than proximodistal. The proximal edge bears two facets for articulation with the radius and ulna. The contact between the radius and ulna precludes the intermedium from reaching the distal surface of the humerus. Distally, the intermedium also bears two sub-equally articular facets for the contact with the distal carpals III and IV.

The ulnare has six articular facets for the pisiform, the element immediately distal to it, metacarpal 5, distal carpal IV, intermedium, and ulna.

Distal carpals. Both in the holotype and the MLP-79-I-30-2, distal carpals III and IV are almost completely preserved (Figs. 2E-F, H−I). These are pentagonal with two subequal articular facets on the proximal margin for reception of the intermedium. Distally, the margin of the carpals is flat and contacts the metacarpals corresponding to digits III and IV.

Digits. From the distal carpals row onwards, the elements of the forelimb are arranged as columns (Fig. 2E-J; 3). In the primary digits (II−V), the proximal phalanges are anteroposteriorly elongated and brick-like. The distal region of the forelimb of the holotype presents hexagonal phalanges with pointed anterior and posterior margins, which gives the contact among adjacent digits the appearance of a zipper.

There are at least two preaxial accessory digits as well as two or even three postaxial accessory digits. The proximal-most elements of the postaxial accessory digits, especially those in contact with the pisiform, differ from those of the primary in shape. In this case, the elements are markedly hexagonal and proximodistally elongated (Figs. 2E-F, H−I).
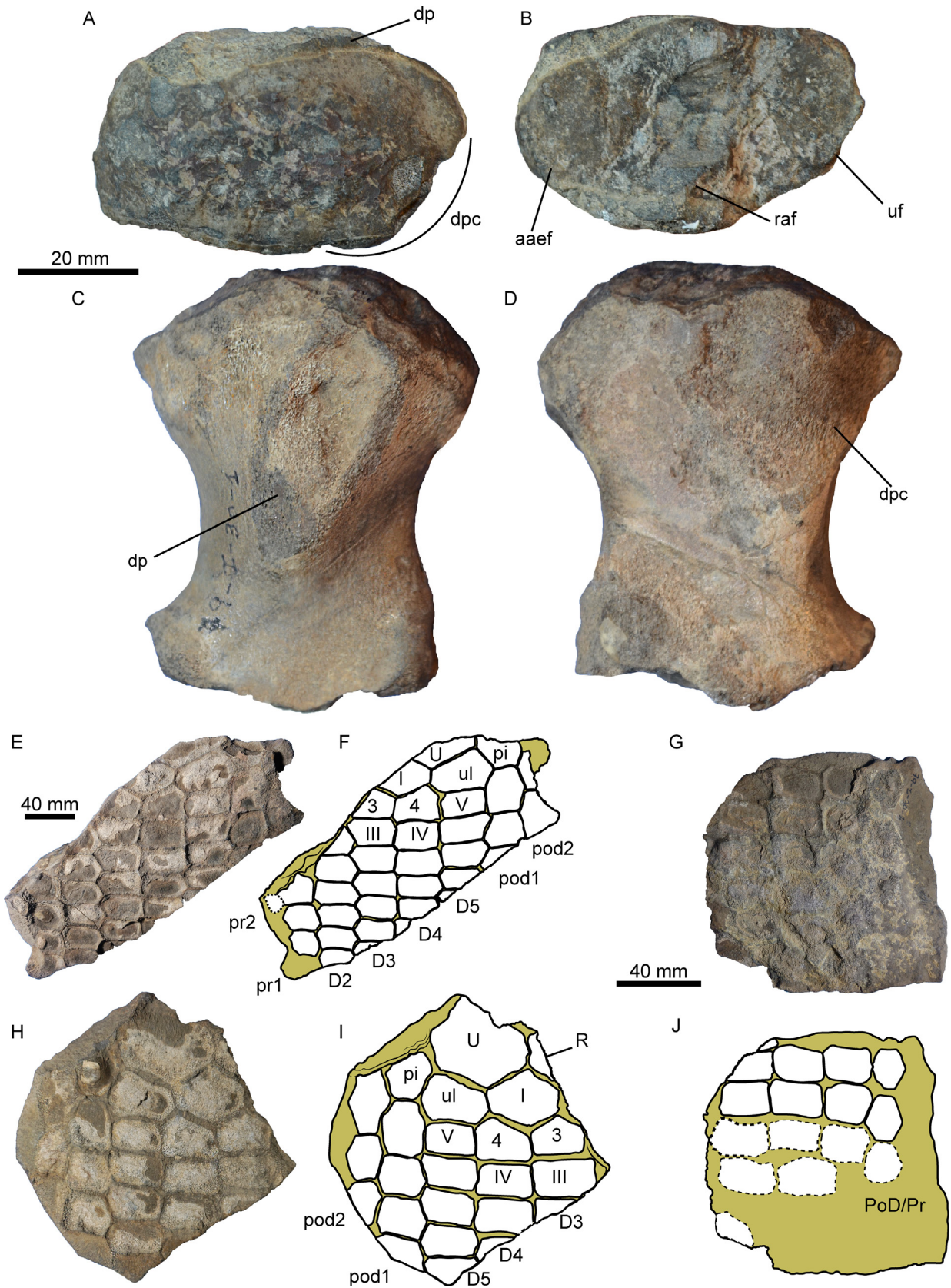
Fig. 2. Appendicular skeleton of *Myobradypterygius hauthali*. **A-D,** MLP. 79-I-30-1, left humerus in proximal (A), distal (B), dorsal (C), and ventral (D). views. **E-F,** MLP 79-I-30-1, zeugopodium and autopodium in dorsal/ventral view. **G-J,** MLP 79-I-30-2, zeugopodium and autopodium in dorsal/ventral view. Abbreviations: aef, anterior accessory element facet; D, primary digit; dp, dorsal process; dpc, deltopectoral crest; I, intermedium; pi, pisiform; pr, preaxial accessory digit; pod, postaxial accessory digit; R, radius; raf, radial facet; U, ulna; uf, ulnar facet; ul, ulnare; 3—4, distal carpals; III-V, metacarpals.
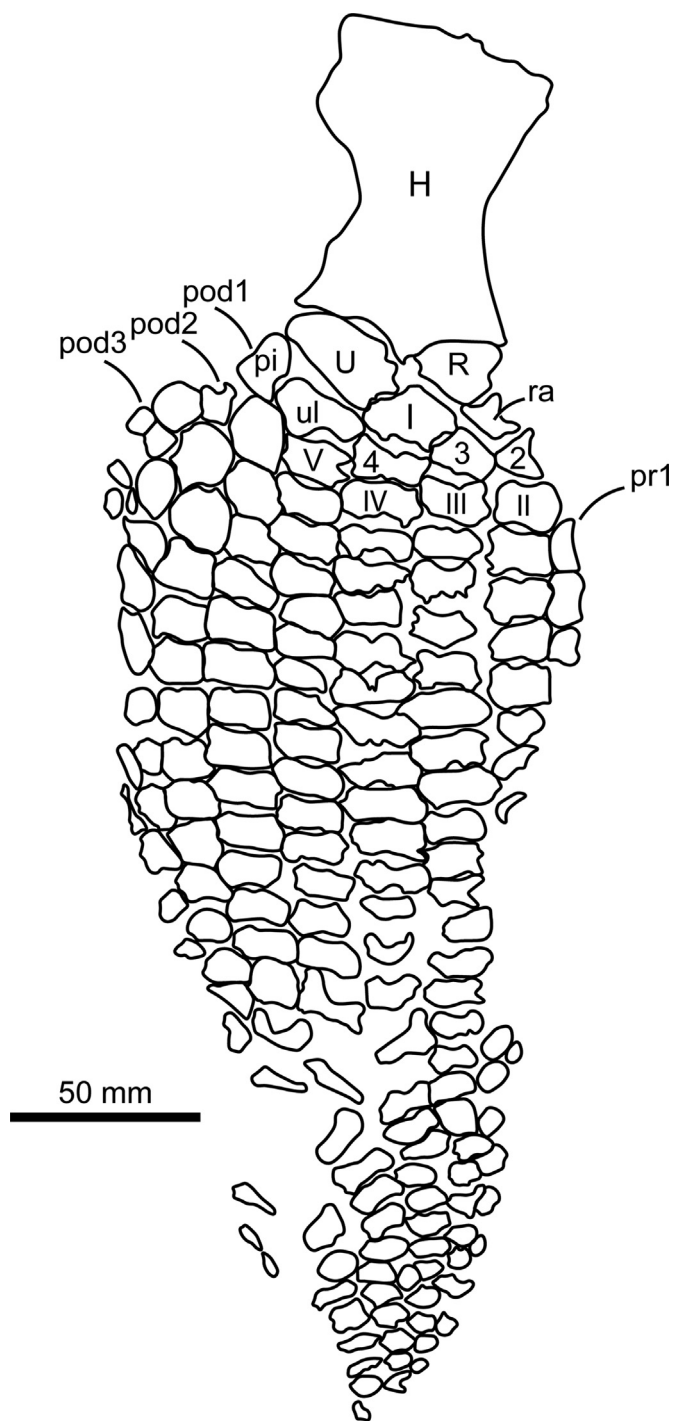
Fig. 3. Left forefin of *Myobradypterygius hauthali* (CPAP-2011-0019) in. ventral view. Abbreviations: H, humerus; I, intermedium; pi, pisiform; pr, preaxial. accessory digit; pod, postaxial accessory digit; R, radius; ra, radiale; U, ulna; ul; ulnare; 2–4, distal carpals; II-V, metacarpals. Redraw from Párdo-Pérez et al. (2012).

3.3. Phylogenetic results

The first analysis, considering the Argentinean (MLP 79-I-30-1 and MLP 79-I-30-2) and Chilean (CPAP-2011-0019) specimens as separate OTUs, resulted in six most parsimonious trees (MPTs) of 591 steps (consistency index, CI = 0.259; retention index, RI = 0.566). These trees yielded a strict consensus tree (CI = 0.255; RI = 0.556) with *Chacaicosaurus cayi* Fernández, 1994, as the sister taxon of Ophthalmosauridae. Ophthalmosauridae was recovered as

a well-supported clade internally branching into two main sub-clades. The second analysis was carried out by coding *Myo. Hauthali* I based on the Argentinean and Chilean specimens also resulted in six MPTs (591 steps; CI = 0.258; RI = 0.566), and the topology of the strict consensus is identical to that of the first analysis (Fig. 4).

Ophthalmosauridae is supported by an extensive lateral exposure of the angular (78:1), a plate-like dorsal process on the dorsal surface of the humerus (102:1), a well-developed humeral facet for an anterior accessory element and a triangular/squared surface (106:2), absence of notching on the leading edge elements of the forefin (113:1), the presence of a rounded/squared AAE (115:2), at least one preaxial accessory digit on the forefin (117:1) and prominent plate-like dorsal and ventral processes on the femur that extend distally and reach the midshaft (124:1).

The first analysis recovered the specimens referred to *Myobradypterygius hauthali* as a clade deeply nested within Platypterygiinae. When the scorings of the two OTUs are merged, the position of this taxon and the topology of the strict consensus tree do not change. In both analyses, *Myobradypterygius* is recovered as the sister taxon of a clade formed by *Caypullisaurus bonapartei* and *Maiaspondylus lindoei* (Fig. 4). In both analyses, Platypterygiinae is supported by the following character states: descending process of the nasal on the posterior dorsal border of the nares (13:1), a thin dorsal arch of the supraoccipital (70:1), a parallelogram-like articular (73:1), a complete fusion of the ischio-pubis (122:2) and a proximal femur more anteroposteriorly developed than the distal end (128:1).

3.4. Phylogenetic signal

From the 20 characters evaluated of the forefin, 10 presented lambda values of ≈ 1 (Supplementary Table 1). From these traits, four correspond to the humerus: presence of a plate-like dorsal ridge on the dorsal surface of the humerus, the presence and development of the facet for the anterior accessory element, the relative anteroposterior development of the midshaft and the compression of the posterior third of the humeral shaft. In the zeugopodial row onwards, strong phylogenetic signal was found in the shape of the posterior surface of the ulna, the shape of the AAE, the absence of notching on the anterior surface of the leading-edge elements of the forefin, the morphology of the distal margin of the intermedium, the presence of postaxial accessory digits and the shape of the phalanges. These results suggest that these characters are phylogenetically clustered within Ophthalmosauride. On the other hand, the presence of the pisiform, humerus-intermedium contact, the posterior deflection of the ulnar facet of the humerus, presence of an accessory epipodial element posterior to ulna and digital bifurcation retrieved lambda values near to zero, indicating independent distribution concerning the phylogenetic relationships of the ophthalmosaurids.

4. Discussion

4.1. Comparison of Myobradypterygius with 'Platypterygius'

Myobradypterygius was originally synonymized with '*Platypterygius*' by McGowan (1972), arguing the lack of inconsistency between these taxa and the incompleteness of the Argentinean specimens. He also considered that the species '*Pl.*' *hauthali* should be retained and serve for the reception of the 'Neocomian' material from South America.

'*Platypterygius*'' *platydactylus,* the type species of the genus, shares with *Myo. Hauthali,* the presence of several pre- and postaxial accessory digits, the rectangular shape of the autopodium elements (McGowan, 1972), and possibly the proximodistally elongated proximal elements of the accessory digits. On the other hand, the presence of a humeral facet for articulation with an anterior accessory element
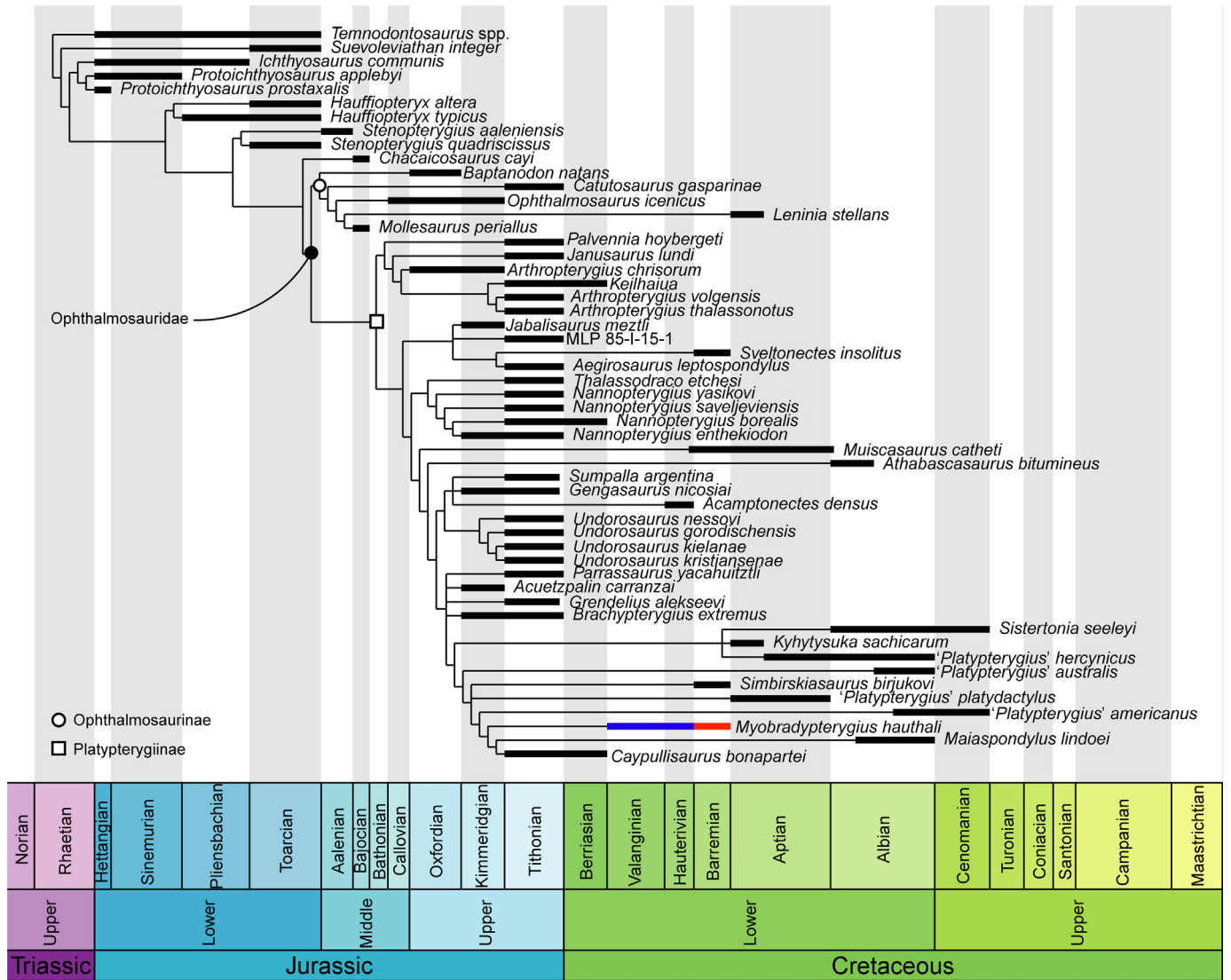
Fig. 4. Time-calibrated strict consensus tree considering the Argentinean and Chilean as the same OTU. The red bar represents the range extension of the Argentinean material, whereas the blue one corresponds to the Chilean.

and the hexagonal intermedium supporting distal carpals 3 and 4 in *Myo. Hauthali*, clearly differentiates it from '*Pl.*' *platydactylus*. Moreover, *Myobradypterygius* can be easily distinguished from other '*Platypterygius*' species based on the former trait: the intermedium of '*Pl.*' *hercynicus*, '*Pl.*' *australis* and '*Pl.*' *americanus* possesses a pentagonal shape, and its distal end is mainly defined by an anteroposteriorly oriented and almost straight facet for articulation with the distal carpal 3 (Kolb and Sander, 2009; Maxwell and Kear, 2010). The same distinction can rule out the specimens described and referred by Adams and Fiorillo (2011) and Cortés and Páramo-Fonseca (2018) to '*Platypterygius*'. The forefin of the specimen reported by Adams and Fiorillo (2011) has a pentagonal intermedium and most of its distal surface forms a straight horizontal facet for contact with the distal carpal 3 and possibly distal carpal 2. The forefin described by Cortés and Páramo-Fonseca (2018) also has a pentagonal intermedium, but in this case the distal facet only contacts distal carpal 3.

4.2. Comparison of Myobradypterygius with other ophthalmosaurids

Most Middle to Late Jurassic ophthalmosaurids can be easily distinguished from *Myobradypterygius hauthali* based on the

morphology of the forefin. The presence of rounded or oval phalanges, as opposed to the polygonal elements with clearly demarcated facets of *Myo. Hauthali*, is known in taxa like *Baptanodon*, *Arthropterygius*, *Palvennia*, *Janusaurus*, *Keilhauia* and *Thalassodraco* (Gilmore, 1905; Kirton, 1983; Maxwell 2010; Roberts et al., 2014; Delsett et al., 2017, 2018; Campos et al., 2020; Jacobs and Martill, 2020). Rounded phalanges are also found in the ophthalmosaurid specimen from the Upper Kimmeridgian of India (Prasad et al., 2017). *Aegirosaurus*, *Brachypterygius*, *Caypullisaurus,* and *Catutosaurus* are the only taxa with quadrangular/polygonal and tightly packed elements in the carpus and manus, similar to those of *Myobradypterygius hauthali* (Fernández, 1997, 2007; Bardet and Fernández, 2000; Fernández et al., 2021). In *Caypullisaurus*, the intermedium contacts distally with distal carpal III, forming a longitudinal column along digit III, thus differing from *Myo. Hauthali* in which the intermedium contacts distally distal carpals III and IV. The intermedium of *Catutosaurus* is very similar in shape and position to that of *Myo. Hauthali*, as in both cases, digits III and IV rise from the distal edge of the intermedium. However, the distal humerus of *Catutosaurus* bears four articular facets (Fernández et al., 2021), whereas in *Myo. Hauthali,* there are three, ruling out the possibility of synonymy. In *Brachypterygius*, and *Aegirosaurus*

the intermedium is in contact with the distal humerus (Huene, 1922; McGowan, 1997; Bardet and Fernández, 2000). Finally, it is important to note that while the distal section of the forefin in the Tithonian genus *Sumpalla* remains unknown, the intermedium is hexagonal and articulates distally with distal carpals 3 and 4, as in to *Myo. Hauthali*. However, the humeri of these taxa differ both in shape and relative anteroposterior development of the proximal and distal ends (Campos et al., 2021). In addition to the humeral differences, the position of the intermedium distinguishes these two taxa: distal to the radius and ulna in *Myo. Hauthali*, and situated between the radius and ulna in *Sumpalla*.

Besides '*Platypterygius*' spp., several Cretaceous ophthalmosaurid taxa have forefins comparable to those of *Myobradypterygius*. The humerus of *Acamptonectes densus* from the Hauterivian of England and Germany shares the presence of three distal articular facets for the AAE, radius, and ulna with that of *Myobradypterygius*. However, the ulnar facet is posteriorly deflected instead of distally facing, as in *Myobradypterygius*. The ulna, the only element known from the zeugopodial row in *Acamptonectes*, is posteriorly concave in dorsal view (Fischer et al., 2012), contrasting with the convex margin of the ulna in *Myobradypterygius*. Finally, *Acamptonectes* possesses rounded proximal phalanges, clearly different from those brick-like of *Myobradypterygius*. *Sveltonectes insolitus* and *Kyhytysuka sachicarum* are the only Barremian taxa preserving appendicular remains comparable to those of *Myo. Hauthali* (Fischer et al., 2011; Cortés et al., 2021). The humerus of *Sv. Insolitus* shares with *Myo. Hauthali* a rectangular cross-section of the proximal end, the presence of a well-developed dorsal process, and a distally facing ulnar facet on the distal end (Fischer et al., 2011). However, the humeri of both taxa are quite different, as the distal region of the humerus of *Sveltonectes* lacks a facet for the anterior accessory element (Fischer et al., 2011). The basipodial row also differs significantly as in *Sveltonectes* the radiale and the intermedium are pentagonal in shape with a straight proximal surface, whereas in *Myo. Hauthali* preserved basipodial elements are hexagonal and with a pointed proximal end. Finally, although most distal elements of the forefin are rectangular in dorsal or ventral view and are closely disposed, *Sveltonectes* only presents two accessory digits (one preaxial and the other postaxial), whereas in *Myobradypterygius* there are, at least, two pre- and three postaxial accessory digits (Figs. 2E–F, H–I; 3).

The appendicular skeleton of a recently described specimen of *Kyhytysuka sachicarum* (CIP-GA-01042014) from the late Barremian of La Paja Formation in Colombia, shows almost no resemblance with the forefin of *Myo. Hauthali* and the synonymy of these taxa has been previously discarded by Maxwell et al. (2019). Besides the clear difference between the intermedium and digits disposition among *Kyhytysuka* and *Myobradypterygius* it is also worth noting that the size of the distal end of the humerus in the first taxon is greater than that of the proximal end (Maxwell et al., 2019) whereas in *Myobradypterygius* such relation is inverted. Another difference is that in the case of *Kyhytysuka* the presence of postaxial digits is unlikely (Maxwell et al., 2019).

4.3. Phylogenetic position of Myobradypterygius *and* ophthalmosaurid phylogeny

Myobradypterygius hauthali was not incorporated in cladistic analyses until recently (Maxwell et al., 2019; Moon, 2019). A comparison with the results of Moon (2019) is difficult as the phylogenetic hypothesis presented by this author recovers Ophthalmosauridae as a clade, but its internal relationships are unresolved. For this reason, our comparison is mostly restricted to the results from Maxwell et al. (2019). As mentioned above, '*Platypterygius*' is recovered herein as a non-monophyletic assemblage

differing from the results of Maxwell et al. (2019). There, *Myobradypterygius hauthali* is recovered forming a clade together with '*Pl.*' *platydactylus*, '*Pl.*' *americanus,* and *Kyhytysuka sachicarum*. As previously discussed, most of the resemblances in the forefin of *Myobradypterygius hauthali* with species within '*Platypterygius*' are also shared with other platypterygiines and *Catutosaurus*.

Most differences with other phylogenetic proposals rely on the internal composition of the two main clades of ophthalmosaurids. The genus *Arthropterygius* and closely related taxa have been recovered in previous studies as members of Ophthalmosaurinae (e.g. Barrientos-Lara and Alvarado-Ortega, 2021; Zverkov and Grigoriev, 2021), Platypterygiinae (e.g. Cortés et al., 2021; Fernández et al., 2021) or even as sister clade of Ophthalmosaurinae or Platypterygiinae (Zverkov and Prilepskaya, 2019). Here, *Arthropterygius* spp. and closely related forms are recovered as an early-branching member of Platypterygiinae. This lack of congruence among results may reflect the extreme incompleteness of some regions of the skeleton among the taxa belonging to this clade. For instance, most species recovered in this clade preserve much of their occipital region in the cranium, as well as the humeri and zeugopodial row (Maxwell, 2010; Roberts et al., 2014; Delsett et al., 2017, 2019; Campos et al., 2020). Nevertheless, many of them such as *Ar. chrisorum*, *Ar. thalassonotus*, *Ar. volgensis* and *Palvennia hoybergeti* lack a great part of the regions that are considered diagnostics for the two main clades (e.g. distal portion of the forefin, pelvic girdle elements).

4.4. Phylogenetic signal of the forefin

Our exploration of the phylogenetic signal among the ophthalmosaurid forefins showed that at least half of the characters evaluated are strongly associated with the phylogenetic relationships of the clade. Some of these characters are widely considered synapomorphies of Ophthalmosauridae, such as the presence of a plate-like dorsal process on the humerus (e.g. Fischer et al., 2011, 2012; Moon, 2019; Campos et al., 2020; Barrientos-Lara and Alvarado-Ortega, 2021) or the facet for the AAE anteriorly located to the radial facet (e.g. Fischer et al., 2012; Fernández et al., 2021). Other characters, such as those describing the morphology of the ulna and phalanges, are interpreted as diagnostic for the two main ophthalmosaurid subclades (Ophthalmosaurinae and Platypterygiinae) (e.g. Fischer et al., 2012; Zverkov and Grigoriev, 2021). Traits describing anteroposterior development and compression of the humeral shaft are considered to be diagnostic of *Arthropterygius* spp. and closely related taxa (Campos et al., 2020, 2021). These results indicate that the set of traits here analyzed carry a strong phylogenetic signal expressed at different hierarchical levels.

The weak phylogenetic signal in some of the characters, such as the posteriorly deflected ulnar facet, the contact humerus/intermedium, and the presence of epipodial elements posterior to the ulna, is probably due to the independent evolution of these traits among distantly related ophthalmosaurids. A posteriorly deflected ulnar facet, as well as, epipodial elements posteriorly located to the ulna are present in the forefins of both, Ophthalmosaurinae (e.g. *Ophthalmosaurus*, *Catutosaurus gaspariniae*) and Platypterygiinae (e.g. *Maiaspondylus lindoei*, '*Pl.*' *americanus*) (Kirton, 1983; Maxwell and Caldwell 2010; Maxwell and Kear 2010; Fernández et al., 2021). The contact between the distal surface of the humerus and the intermedium seems to be restricted to some Kimmeridgian–Tithonian platypterygiines, namely, *Brachypterygius extremus*, *Aegirosaurus leptospondylus*, *Parrasaurus yacahuitztli* and several individuals assigned to the problematic genus *Grendelius* (McGowan 1997; Bardet and Fernández, 2000; Zverkov et al., 2015; Barrientos-Lara and Alvarado-Ortega, 2021). Most recent phylogenetic analysis have failed in recovering a clade containing

exclusively all aforementioned taxa (e.g. Delsett et al., 2017, 2019; Maxwell et al., 2019; Campos et al., 2020, 2021; Cortés et al., 2021; Jacobs and Martill, 2020; Zverkov and Grigoriev 2021), although some proposals have identified *Br. extremus* and *Ae. Leptospondylus* (e.g. Jacobs and Martill, 2020; Zverkov and Grigoriev 2021) or *Br. extremus* and *Parrasaurus yacahuitztli* (Barrientos-Lara and Alvarado-Ortega 2021) as sister taxa and distantly related to *Grendelius*. This suggests an independent acquisition of a humerus/intermedium contact. On the other hand, we hypothesize that the presence and location of the pisiform as well as the digital bifurcation, retain plesiomorphic states within Ophthalmosauridae as the presence of both is known in many Early Jurassic non-ophthalmosaurids (e.g. Motani, 1999; Lomax et al., 2017; Massare and Lomax, 2018).

5. Conclusions

The re-evaluation and comparison of the holotype and referred specimens of *Myobradypterygius hauthali* brings new information for a deeper comprehension of ophthalmosaurid interrelationships and the evolution of the appendicular skeleton. The morphological evidence, which consists of a unique combination of appendicular characters, along with the results of our cladistic analysis that position *Myo. Hauthali* as phylogenetically distant from any '*Platypterygius*' species, provides strong support for the revalidation of this taxon.

The results obtained herein depict the ichthyosaurian forefin as a valuable source of characters in which all different kinds of elements (e.g. humerus, zeugopodium, and autopodium) carry a strong phylogenetic signal. Yet, new and more complete specimens are needed to evaluate intrageneric/specific variation of the forefin within Ophthalmosauridae.

Authors statement

The authors L. Campos, M. Fernández, V. Bosio, Y. Herrera and A. Manzo, certify that all of us have seen and approved the final version of the manuscript, which is being submitted.

We warrant that the article is the authors' original work, has not received prior publication and is not under consideration for publication elsewhere.

CRediT authorship contribution statement

Lisandro Campos: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing — original draft, Writing — review & editing. **Marta S. Fernández:** Funding acquisition, Investigation, Project administration, Resources, Writing — original draft, Writing — review & editing. **Victor Bosio:** Data curation, Formal analysis, Methodology, Writing — original draft, Writing — review & editing. **Yanina Herrera:** Investigation, Project administration, Resources, Writing — original draft, Writing — review & editing. **Agustina Manzo:** Data curation, Investigation, Visualization, Writing — review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data used in this contribution is available as Supplementary Information.

References

Adams, T.L., Fiorillo, A., 2011. *Platypterygius* Huene, 1922 (Ichthyosauria, Ophthalmosauridae) from the Late Cretaceous of Texas, USA. Palaeontologia Electronica 14 (3), 19a, 12pp.

Aguirre-Urreta, M.B., 2002. Invertebrados del cretácico inferior. In: Haller, M.J. (Ed.), Geología y Recursos Naturales de Santa Cruz: XV Congreso Geológico Argentino. Asociación Geológica Argentina, Buenos Aires, pp. 439–459.

Arkhangelsky, M.S., Zverkov, N.G., 2014. On a new ichthyosaur of the genus *Undorosaurus*. Труды Зоологического института РАН 318, 187–196.

Bapst, D.W., 2012. paleotree: an R package for paleontological and phylogenetic analyses of evolution. Methods in Ecology and Evolution 3 (5), 803–807.

Bardet, N., Fernández, M., 2000. A new ichthyosaur from the Upper Jurassic lithographic limestones of Bavaria. Journal of Paleontology 74 (3), 503–511.

Barrientos-Lara, J.I., Alvarado-Ortega, J., 2021. A new Tithonian ophthalmosaurid ichthyosaur from Coahuila in northeastern Mexico. Alcheringa: An Australasian Journal of Palaeontology 45, 203–216.

Baur, G., 1887. Ueber den ursprung der extremitäten der ichthyopterygia. Oberrheinischer Geologischer Verein.

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 (Vol. 4). Impr. Et fonderie de Fain, Paris, France.

Broili, F., 1908. Ichthyosaurierreste aus der Kriede. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. Beilage 25, 422–442.

Campos, L., 2022. Oftalmosáuridos (Ichthyosauriomorpha: Ichthyosauria) del Jurásico Tardío-Cretácico Temprano de Patagonia Argentina: diversidad, disparidad y evolución. Unpubl. PhD esis. Universidad Nacional de La Plata, Buenos Aires, p. 420.

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. Zoological Journal of the Linnean Society 188, 180–201.

Campos, L., Fernández, M.S., Herrera, Y., Garrido, A., 2021. Morphological disparity in the evolution of the ophthalmosaurid forefin: new clues from the Upper Jurassic of Argentina. Papers in Palaeontology 7, 1995–2020.

Cortés, D., Maxwell, E.E., Larsson, H.C., 2021. Re-appearance of hypercarnivore ichthyosaurs in the Cretaceous with differentiated dentition: revision of '*Platypterygius*' *sachicarum* (Reptilia: Ichthyosauria, Ophthalmosauridae) from Colombia. Journal of Systematic Palaeontology 19, 969–1002.

Cortés, D., Páramo-Fonseca, M.E., 2018. Restos apendiculares de un ictiosaurio oftalmosáurido del Barremiano inferior de Villa de Leiva, Colombia. Boletin de Geologia 40, 15–30.

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

Delsett, L.L., Roberts, A.J., Druckenmiller, P.S., y Hurum, J.H., 2019. Osteology and phylogeny of Late Jurassic ichthyosaurs from the Slottsmoya Member Lagerstätte (Spitsbergen, Svalbard). Acta Palaeontologica Polonica 64, 717–743.

Fernández, M.S., 1994. A new long-snouted ichthyosaur from the Early Bajocian of Neuquén Basin (Argentina). Ameghiniana 31, 283–290.

Fernández, M.S., 1997. A new ichthyosaur from the Tithonian (Late Jurassic) of the Neuquén Basin, northwestern Patagonia, Argentina. Journal of Paleontology 71, 479–484.

Fernández, M.S., 2007. Redescription and phylogenetic position of *Caypullisaurus* (Ichthyosauria: Ophthalmosauridae). Journal of Paleontology 81, 368–375.

Fernández, M.S., Aguirre-Urreta, M.B., 2005. Revision of *Platypterygius hauthali* von Huene, 1927 (Ichthyosauria: Ophthalmosauridae) from the Early Cretaceous of Patagonia, Argentina. Journal of Vertebrate Paleontology 25, 583–587.

Fernández, M.S., Campos, L., Maxwell, E.E., Garrido, A.C., 2021. *Catutosaurus gaspariniae*, gen. et sp. nov. (Ichthyosauria, Thunnosauria) of the Upper Jurassic of

Patagonia and the Evolution of the Ophthalmosaurids. Journal of Vertebrate Paleontology 41, e1922427.

Fischer, V., Masure, E., Arkhangelsky, M.S., Godefroit, P., 2011. A new Barremian (Early Cretaceous) ichthyosaur from western Russia. Journal of Vertebrate Paleontology 31, 1010–1025.

Fischer, V., 2012. New data on the ichthyosaur Platypterygius hercynicus and its implications for the validity of the genus. Acta Palaeontologica Polonica 57, 123–134.

Fischer, V., Maisch, M.W., Naish, D., Kosma, R., Liston, J.J., Joger, U., Kruger, F.J., Pérez, J.P., 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., Arkhangelsky, M.S., Naish, D., Stenshin, I.M., Uspensky, G.N., Godefroit, P., 2014a. *Simbirskiasaurus* and *Pervushovisaurus* reassessed: implications for the taxonomy and cranial osteology of Cretaceous platypterygiine ichthyosaurs. Zoological Journal of the Linnean Society 171, 822–841.

Fischer, V., Arkhangelsky, M.S., Uspensky, G.N., Stenshin, I.M., Godefroit, P., 2014b. A new Lower Cretaceous ichthyosaur from Russia reveals skull shape conservatism within Ophthalmosaurinae. Geological Magazine 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. Nature Communications 7, e10825.

Fischer, V., Bardet, N., Guiomar, M., Godefroit, P., 2014c. High diversity in Cretaceous ichthyosaurs from Europe prior to their extinction. PLos One 9, e84709.

Freckleton, R.P., Harvey, P.H., Pagel, M., 2002. Phylogenetic analysis and comparative data: a test and review of evidence. The American Naturalist 160 (6), 712–726.

Fritz, S.A., Purvis, A., 2010. Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. Conservation Biology 24, 1042–1051.

Gasparini, Z., Goñi, R., 1990. Los ictiosaurios jurásico-cretácicos de la Argentina. Comité Sudamericano del Jurásico y Cretácico 299–311.

Gilmore, C.W., 1905. Osteology of *Baptanodon* (Marsh). Memoirs of the Carnegie Museum 2, 77–129.

Gittleman, J.L., Kot, M., 1990. Adaptation: Statistics and a null model for estimating phylogenetic effects. Systematic Biology 39, 227–241.

Goloboff, P., Catalano, S., 2016. TNT, version 1.5, with a full implementation of phylogenetic morphometrics. Cladistics 32, 221–238.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E., Challenger, W., 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24, 129–131.

Huene, v.F.R.F., 1922. Die ichthyosaurier des Lias und ihre zusammenhänge. Verlag von gebrüder Borntraeger, Berlin, p. 114.

Huene, v.F.R.F., 1925. Ichthyosaurier aus der kreide argentiniens. Revista del Museo de La Plata 28, 234–242.

Huene, v.F.R.F., 1927. Beitrag zur Kenntnis mariner Mesozoischer Wirbeltiere in Argentinien. Centralblatt für Mineralogie. Geologie und Paläontologie 1, 22–29.

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 (12), e0241700.

Kirton, A.M., 1983. A review of British Upper Jurassic ichthyosaurs. Unpublished Ph.D. Thesis. University of Newcastle, Newcastle upon Tyne, p. 239.

Kolb, C., Sander, P.M., 2009. Redescription of the ichthyosaur *Platypterygius hercynicus* (Kuhn 1946) from the Lower Cretaceous of Salzgitter (Lower Saxony, Germany). Palaeontographica Abteilung A 288, 151–192.

Lazo, D.G., Talevi, M., Cataldo, C.S., Aguirre-Urreta, B., Fernández, M.S., 2018. Description of ichthyosaur remains from the Lower Cretaceous Agrio Formation (Neuquén Basin, west-central Argentina) and their paleobiological implications. Cretaceous Research 89, 8–21.

Lomax, D.R., Massare, J.A., Mistry, R.T., 2017. The taxonomic utility of forefin morphology in Lower Jurassic ichthyosaurs: *Protoichthyosaurus* and *Ichthyosaurus*. Journal of Vertebrate Paleontology 37, e1361433.

Maddison, W.P., Maddison, D.R., 2019. Mesquite: a modular system for evolutionary analysis (data analysis software system). Available at: http://www.mesquiteproject.org/.

Maisch, M.W., Matzke, A.T., 2000. The Ichthyosauria. Stuttgarter Beiträge zur Naturkunde: Serie B (Geologie und Paläontologie) 298, 1–59.

Massare, J.A., Lomax, D.R., 2018. A taxonomic reassessment of Ichthyosaurus communis and I. intermedius and a revised diagnosis for the genus. Journal of Systematic Palaeontology 16, 263–277.

Maxwell, E.E., 2010. Generic reassignment of an ichthyosaur from the Queen Elizabeth Islands, northwest territories, Canada. Journal of Vertebrate Paleontology 30, 403–415.

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. Journal of Vertebrate Paleontology 39, e1577875.

Maxwell, E.E., Dick, D., Padilla, S., Parra, M.L., 2016. A new ophthalmosaurid ichthyosaur from the E arly Cretaceous of Colombia. Papers in Palaeontology 2, 59–70.

Maxwell, E.E., Kear, B.P., 2010. Postcranial anatomy of *Platypterygius americanus* (Reptilia: Ichthyosauria) from the Cretaceous of Wyoming. Journal of Vertebrate Paleontology 30, 1059–1068.

McGowan, C., 1972. The systematics of Cretaceous ichthyosaurs with particular reference to the material from North America. Rocky Mountain Geology 11, 9–29.

McGowan, C., 1997. The taxonomic status of the Late Jurassic ichthyosaur Grendelius mordax: a preliminary report. Journal of Vertebrate Paleontology 17, 428–430.

McGowan, C., Motani, R., 2003. Handbook of paleoherpetology, Part 8, Ichthyopterygia. Verlag Dr. Friedrich Pfeil, München, p. 175.

Molina-Venegas, R., Rodríguez, M.Á., 2017. Revisiting phylogenetic signal; strong or negligible impacts of polytomies and branch length information? BMC Evolutionary Biology 17, 1–10.

Moon, B.C., 2019. A new phylogeny of ichthyosaurs (Reptilia: Diapsida). Journal of Systematic Palaeontology 17, 129–155.

Motani, R., 2016. Palaeobiology: born and gone in global warming. Current Biology 26, R466–R468.

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., Thuiller, W., 2012. How to measure and test phylogenetic signal. Methods in Ecology and Evolution 3, 743–756.

Páramo-Fonseca, M.E., García-Guerrero, J., Benavides-Cabra, C.D., Padilla-Bernal, S., Castañeda-Gómez, A.J., 2021. A benchmark specimen of *Muiscasaurus catheti* from the upper Aptian of Villa de Leiva, Colombia: New anatomical features and phylogenetic implications. Cretaceous Research 119, 104685.

Páramo-Fonseca, M.E., 1997. *Platypterygius sachicarum* (Reptilia, Ichthyosauria) nueva especie del Cretácico de Colombia. Revista Ingeominas 6, 1–12.

Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401, 877–884.

Pardo-Pérez, J., Frey, E., Stinnesbeck, W., Fernández, M.S., Rivas, L., Salazar, C., Leppe, M., 2012. An ichthyosaurian forefin from the Lower Cretaceous Zapata Formation of southern Chile: implications for morphological variability within *Platypterygius*. Palaeobiodiversity and Palaeoenvironments 92, 287–294.

Pardo-Pérez, J., Otero, R.A., Suárez, M.E., 2015. Síntesis del registro fósil de ictiosaurios (Reptilia: Ichthyosauria) en Chile, vol. 63. Publicación Ocasional del Museo Nacional de Historia Natural (Chile), pp. 113–150.

Roberts, A.J., Druckenmiller, P.S., Sætre, G.P., y Hurum, J.H., 2014. A new Upper Jurassic ophthalmosaurid ichthyosaur from the Slottsmøya Member, Agardhfjellet Formation of central Spitsbergen. PLoS One 9, e103152.

Stinnesbeck, W., Frey, E., Rivas, L., Pérez, J.P., Cartes, M.L., Soto, C.S., Lobos, P.Z., 2014. A Lower Cretaceous ichthyosaur graveyard in deep marine slope channel deposits at Torres del Paine National Park, southern Chile. Geological Society of America Bulletin 126, 1317–1339.

Tennant, J.P., Mannion, P.D., Upchurch, P., 2016. Sea level regulated tetrapod diversity dynamics through the Jurassic/Cretaceous interval. Nature Communications 7 (1), 12737.

Tyborowski, D., 2016. A new ophthalmosaurid ichthyosaur from the Late Jurassic of Owadów-Brzezinki Quarry, Poland. Acta Palaeontologica Polonica 61, 791–803.

Zverkov, N.G., Arkhangelsky, M.S., Stenshin, I.M., 2015. A review of Russian Upper Jurassic ichthyosaurs with an intermedium/humeral contact. Reassessing *Grendelius* McGowan, 1976. Proceedings of the Zoological Institute RAS 319, 558–588.

Zverkov, N.G., Grigoriev, D.V., 2021. An unrevealed lineage of platypterygiines (Ichthyosauria) with peculiar forefin structure and semiglobal distribution in the mid-Cretaceous (Albian–Cenomanian). Cretaceous Research 115, 104550.

Zverkov, N.G., Jacobs, M.L., 2021. Revision of *Nannopterygius* (Ichthyosauria: Ophthalmosauridae): reappraisal of the 'inaccessible' holotype resolves a taxonomic tangle and reveals an obscure ophthalmosaurid lineage with a wide distribution. Zoological Journal of the Linnean Society 191, 228–275.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2023.105818.