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Original article

## The genus *Arthropterygius* Maxwell (Ichthyosauria: Ophthalmosauridae) in the Late Jurassic of the Neuquén Basin, Argentina<sup>☆</sup>

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### ARTICLE INFO

#### Article history:

Received 15 July 2011

Accepted 9 February 2012

Available online 26 September 2012

#### Keywords:

Ichthyosauria  
 Ophthalmosauridae  
*Arthropterygius*  
 Neuquén Basin  
 Argentina

### ABSTRACT

Recent discovery of a skull and forefin of an ophthalmosaurid ichthyosaur from the Tithonian (Late Jurassic) of the Neuquén Basin, Argentina, shows a peculiar morphology of the braincase and forefin, including the opening for internal carotids situated on the posterior surface of the parabasisphenoid and dorsoventral compression of the posterior part of the humerus. These characteristics appear unique within ophthalmosaurids, and probably within Ichthyosauria, and are diagnostic of the genus *Arthropterygius*, a taxon to date only known from the Oxfordian–Kimmeridgian of Northwest Territories, Canada. The new finding increases the knowledge of this peculiar ophthalmosaurid and represents, up to the present, the first evidence for a potentially widespread and climatically diverse distribution of this rare genus.

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### 1. Introduction

Ichthyopterygia was a successful group of Mesozoic marine reptiles. Its fossil record spans the Early Triassic (Olenekian) to the Late Cretaceous (Cenomanian–Turonian boundary) (Bardet, 1992; Sander, 2000; McGowan and Motani, 2003). During most of the Mesozoic, fish-shaped ichthyosaurs (i.e., Parvipelvia) were one of the main predatory clades in the oceans (Massare, 1988; Motani, 2005). There is a general consensus that all Callovian and post Callovian ichthyosaurs form a clade, the Ophthalmosauridae, nested within Parvipelvia (Motani, 1999a; Maisch and Matzke, 2000; Fernández, 2007a; Druckenmiller and Maxwell, 2010; Maisch, 2010; Sander, 2000).

Historically, most research on ophthalmosaurids has focused on northern hemisphere records. Particularly, in the case of Middle–Upper Jurassic, most of the studies have been based on fossil records from two Lagerstätten: the Oxford Clay (Callovian) of England, and the Sundance Formation (Oxfordian) of the Western Interior, United States. This situation generated certain bias in the interpretation of the evolutionary history of ophthalmosaurids. As most of the specimens recovered from these two Lagerstätten are referred to two species of a single genus: *Ophthalmosaurus icenicus* Seeley, 1874, and *O. natans* (Marsh, 1879), respectively, there was

an implicit assumption that Callovian and Late Jurassic ichthyosaurs were widespread and formed a significant fraction of the marine reptile fauna, but were not taxonomically diverse (McGowan, 1991).

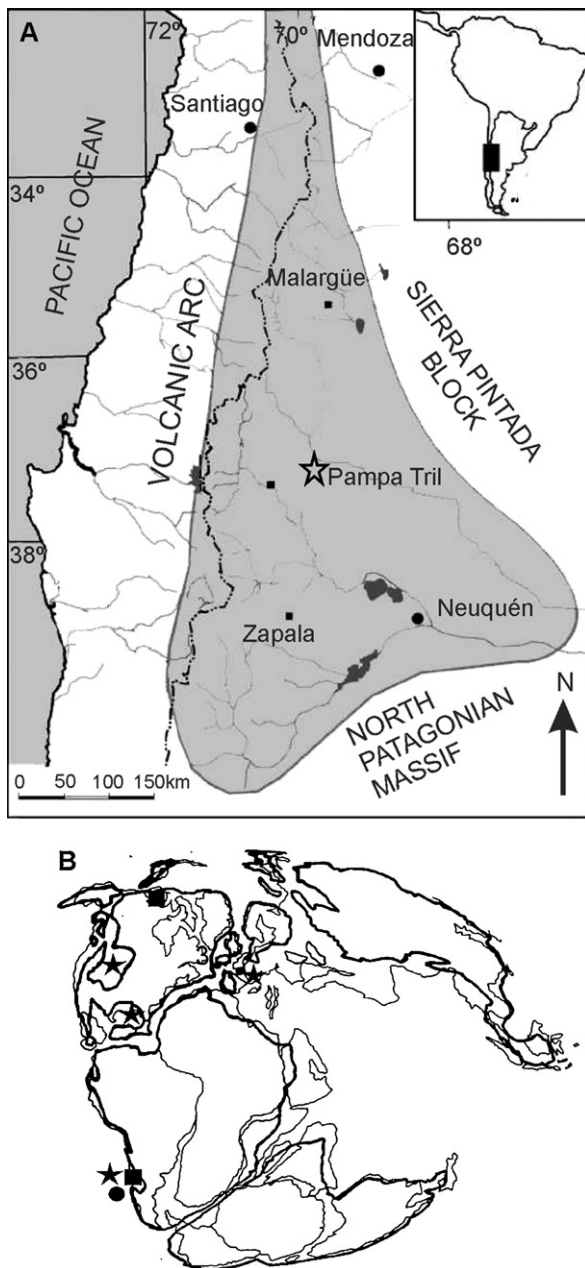
However, in the last 15 years significant Late Jurassic ophthalmosaurid material has been recovered and/or re-described from Germany, Mexico, Canada, and Russia (Arkhangelsky, 1997, 1998; Bardet and Fernández, 2000; Buchy and López Oliva, 2009; Buchy, 2010; Maxwell, 2010), and also from the southern Oriental Pacific, in the Neuquén Basin (northwest Patagonia, Argentina). These findings showed that the diversity of Jurassic ophthalmosaurids has apparently been underestimated. Within the Neuquén Basin, ophthalmosaurid material is most abundant in Tithonian–Berriasian deposits of the Vaca Muerta Formation, and the majority of specimens can be referred to *Caypullisaurus bonapartei* Fernández, 1997. Not abundant, but very significant, are Aalenian–Bajocian ophthalmosaurids. A fragment of a forefin recovered from the Aalenian–Bajocian boundary of Quebrada Remoredo (Mendoza province, Argentina) represents the oldest definitive record of an ophthalmosaurid (Fernández, 2003), and the holotypes of *Mollesaurus periallus* Fernández, 1999, and *Stenopterygius cayi* (= *Chacaicosaurus cayi* Fernández, 1994), document the co-occurrence of ophthalmosaurian and non-ophthalmosaurid parvipelvians in the early Bajocian of the Neuquén Basin (Fernández, 2007b).

During the last years, field trips to the Pampa Tril area (Neuquén province, Argentina) resulted in the discovery of new ichthyosaur

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**Fig. 1.** A. Map of the Neuquén Basin, Argentina, showing the location of Pampa Tril (star). B. Occurrence of Late Jurassic ichthyosaurs *Arthropterygius* (■), *Caypullisaurus* (●), and *Ophthalmosaurus* (★).

specimens from Tithonian strata of the Vaca Muerta Formation (Fig. 1(A)). Among these, skull fragments and a forefin of one specimen (MOZ 6145) were briefly mentioned and identified as *Ophthalmosaurus* sp. (Fernández, 2007b). Recently, Maxwell (2010) examined an Oxfordian–Kimmeridgian ichthyosaur from Melville Island (Northwest Territories, Canada) that was originally described as *Ophthalmosaurus chrisorum* Russell, 1993. She provided a detailed description of this material and concluded that it cannot be assigned to *Ophthalmosaurus*, and erected upon it the new genus *Arthropterygius*. Further preparation of the specimen MOZ 6145, recovered from the Neuquén Basin, indicates that it can also be assigned to *Arthropterygius* Maxwell, a taxon up to the present only known from the Oxfordian–Kimmeridgian of Canada (Maxwell, 2010; Fig. 1(B)).

## 2. Material and methods

The specimen MOZ 6145 was found in two main blocks, one bearing the posterior part of the skull and snout exposed in lateral view, and the other containing a right forefin with its elements partially articulated. The skull was damaged during initial excavation, however general proportions of the skull can still be observed. In addition, because the diagnostic features of *Arthropterygius* mainly relate to the pattern of the braincase and articular surfaces of the forefin, the basioccipital and humerus of MOZ 6145 were completely removed from the matrix for a closer examination. Other elements of the braincase, such as the basisphenoid, could not be removed from the surrounding sediments without risk of damage. However, in the case of the basisphenoid, the ventral, most of the posterior, and the right lateral surfaces have been exposed. The epipodial elements, while also present, were not removed from the matrix, but were prepared in ventral view.

**Institutional abbreviations:** CMN, Canadian Museum of Nature (Ottawa, Canada); MOZ, Museo Prof. Pedro Olsacher de Zapala (Argentina).

## 3. Systematic paleontology

Order ICHTHYOSAURIA Blainville, 1835

Family OPHTHALMOSAURIDAE Baur, 1887

Genus *Arthropterygius* Maxwell, 2010

**Type species:** *Arthropterygius chrisorum* (Russell, 1993).

**Holotype:** CMN 40608.

**Occurrence:** Melville Island, Northwest Territories, Canada (type locality); Pampa Tril, Neuquén province, Argentina.

**Stratigraphic range:** Upper Jurassic. Ringnes Formation (Oxfordian to Kimmeridgian); Vaca Muerta Formation (Tithonian).

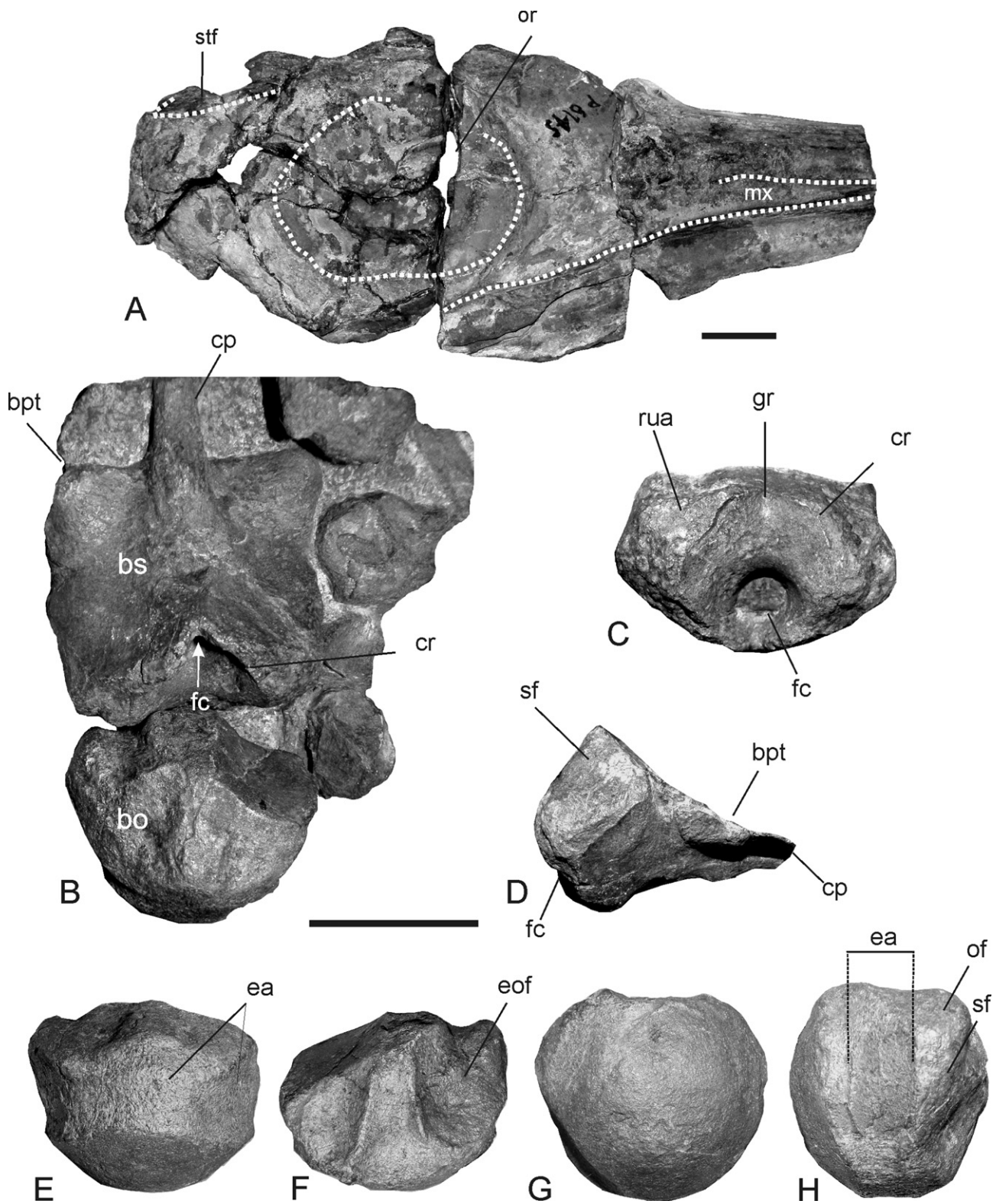
*Arthropterygius* sp.

**Referred specimen:** MOZ 6145, consisting of the posterior part of the skull and forefin, including humerus, zeugopodium and autopodium of one individual collected from the Vaca Muerta Formation cropping out at Pampa Tril, in the North of Neuquén province, Argentina.

**Description:** Although the skull is poorly preserved in lateral aspect, it is significant as the general aspect of the skull of *Arthropterygius* was completely unknown. The postorbital region is not reduced and the maxilla has a relatively large exposure on the lateral surface of the skull (Fig. 2(A)).

The anterior surface of the basioccipital is not well preserved so it cannot be confirmed if the notochordal tip is dorsally covered by bone, or if it is dorsally exposed (Fig. 2(B)). The extracondylar area is extremely reduced and not clearly offset, being almost completely hidden in posterior view (Fig. 2(G)). In dorsal view, the extracondylar area is slightly wider than the condyle, and the widest point of the bone is located at the level of the opisthotic facets. On the dorsal surface of the bone, the exoccipital facets are well developed, forming two concave areas (Fig. 2(F)). The best preserved is the facet for the right exoccipital. Medial to this facet there is an anteromedially-directed crest that separates the exoccipital facet from the floor of the braincase, which is smooth and concave. The opisthotic and stapedial facets are not well preserved. The condyle is slightly wider than high and its ventral margin is not notched. All around it, except for its dorsal margins, the condyle is surrounded by a blunt crest.

The basisphenoid–parasphenoid sutures are not visible due to the complete fusion of these elements. The parabasisphenoid is mainly exposed on its ventral aspect (Fig. 2(C, D)). The most conspicuous features of the parabasisphenoid are the configuration of its ventral surface, and the location of the posterior opening for the internal carotid arteries. The ventral surface of the



**Fig. 2.** MOZ 6145, *Arthropterygius* sp. **A.** Skull in lateral view; dashed lines indicate the structures or bones that can be confidently traced. **B.** General view of the floor of the braincase in ventral view. **C.** Parabasisphenoid posterior view. **D.** Parabasisphenoid lateral view. **E–H.** Basioccipital in (E) ventral, (F) dorsal, (G) posterior, and (H) lateral views. Abbreviations: bo, basioccipital; bpt, basiptyergoid process; bs, basisphenoid; cp, cultriform process; cr, crest; ea, extracondylar area; eof, exoccipital facet; fc, posterior foramen for the internal carotid artery; gr, groove; mx, maxilla; of, opisthotic facet; or, orbit; rua, rugose area; sf, stapedial facet; stf, supra-temporal fenestra. Scale bars: 5 cm.

parabasisphenoid is roughly rectangular in outlines. The basiptyergoid processes are directed anterolaterally, and their anteroven-tral margins are almost straight and perpendicular to the long axis of the cultriform process. On the posteroventral margins of the basiptyergoid processes there are two depressed areas (as seen in

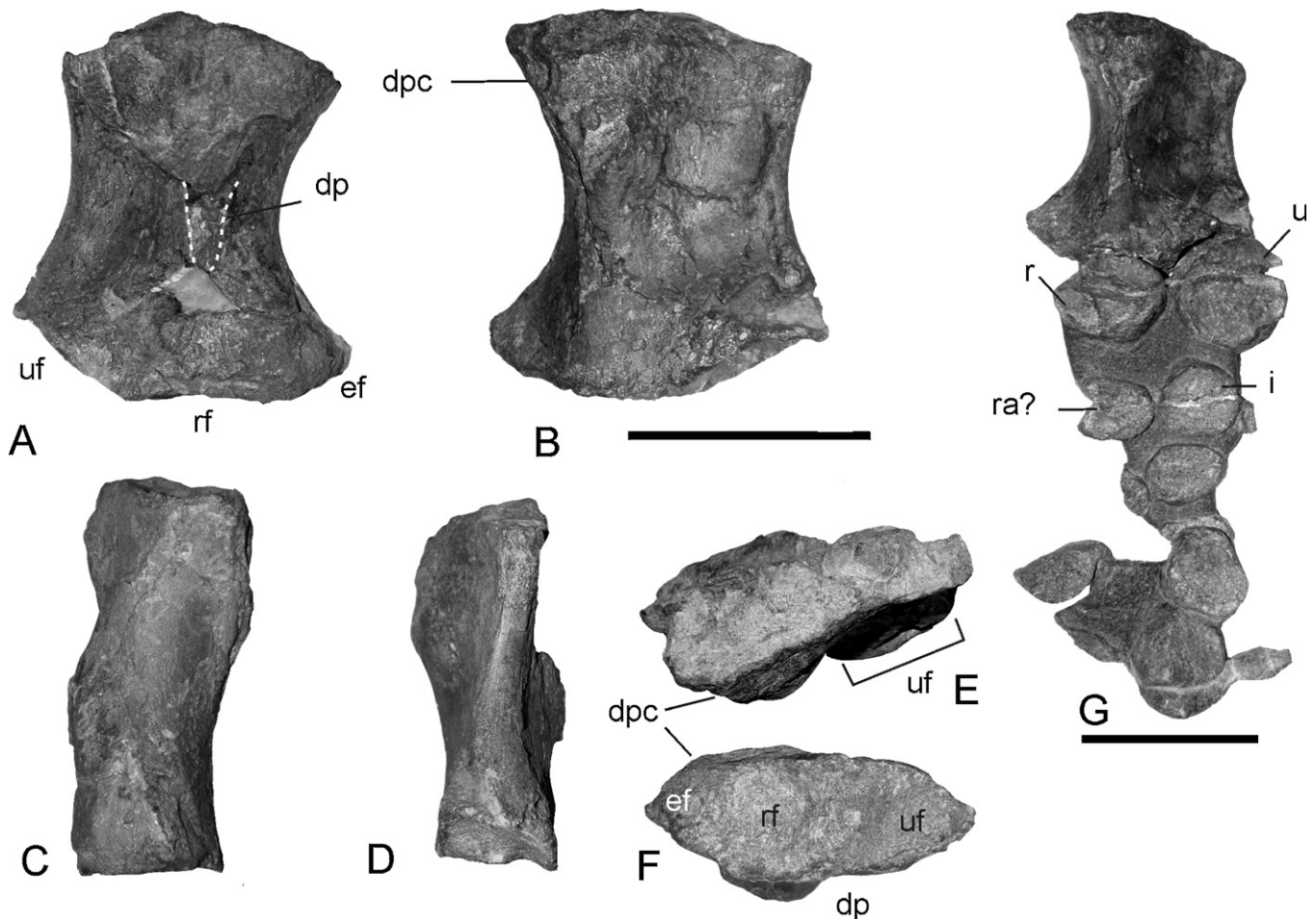
ventral view). Posterior to the basiptyergoid processes, the ventral surface of the parabasisphenoid slopes ventromedially. In posteri-or view, the parabasisphenoid can be divided into a dorsoventrally oriented plane formed by the ventral portion of the element and containing the foramen for the internal carotid arteries, and a

second plane dorsal to this that is strongly sloping anteriorly. On the former there is a large and deep recessed area bearing a smooth bone texture. The posterior opening for the internal carotid arteries is located deep in this area, and on its ventral half (Fig. 2(C)). The recessed area of the MOZ 6145 basisphenoid is demarcated by a delicate crest that separates it from the surrounding irregular pitted surfaces (Fig. 2(B)).

Only a partial right forefin was recovered from the postcranial region (Fig. 3). The humerus is a stout element. The bone of the dorsal surface at its proximal end, in the area in which the plate-like dorsal process is developed in all ophthalmosaurids, has been eroded forming a triangular depressed area. However the distal-most part of the dorsal process can be roughly outlined, depicting that it extends distally more than half the length of the humeral shaft (Fig. 3(A)). On its ventral surface, the deltopectoral crest is also broken; however, as in the case of the dorsal process, the distal extent of this crest can also be outlined (Fig. 3(B)). The deltopectoral crest is shifted anteriorly, and does not extend more than half the length of the shaft. In dorsal and ventral views, the anterior margin of the shaft is more markedly concave than the posterior margin. The most conspicuous features of the humerus are that the posterior half of the bone is dorsoventrally compressed, and that the angle formed by the long axes of the proximal and distal ends of the humerus (i.e., humerus torsion; Maxwell, 2010) is reduced. From preaxial to postaxial, there are three distal articular surfaces for the preaxial element, the radius and the ulna. The articular surfaces for the radius and ulna are

subequal in length and separated, in distal view, by a crest. Both are concave but the concavity of the ulnar facet is more pronounced. This latter facet is offset proximally and rotated slightly ventrally. The elements of the forefin distal to the humerus are dorsoventrally thick and their outlines are, in general, gently curved (Fig. 3(G)). The preaxial elements have not been recovered. The radius and ulna have been preserved in articulation with the humerus. The radius is smaller than the ulna. The facets of the radius and ulna for articulation with the humerus are rounded while their distal articular facets are relatively more straight in ventral view. The proximal articular surfaces for articulation with the humerus are rugose and convex and fit into the concave radial and ulnar facets of the humerus. The ulna is better preserved than the radius. The anterior edge is notably thicker than the posterior edge (dorsoventral height of the anterior ulnar edge/dorsoventral height of the posterior ulnar edge = 3), and its contact with the radius restricted to the most proximal edges. The intermedium has been displaced distally from its natural position and has a narrow contact with an anterior element interpreted as the radial. Its proximal edges define two facets, the anterior for the radius and the other for the ulna, and the remaining edges are gently rounded.

**Remarks:** As in most ophthalmosaurids, but in contrast to *Ophthalmosaurus* and *Aegirosaurus*, the postorbital region of the skull of MOZ 6145 is not reduced and the maxilla has a relatively large exposure on the skull lateral surface. The basioccipital is similar in morphology to that of the *Arthropterygius chrisorum* holotype, with an extremely reduced extracondylar area (sensu



**Fig. 3.** MOZ 6145, *Arthropterygius* sp. right forelimb elements. **A–F.** Humerus in (A) dorsal, (B) ventral, (C) anterior, (D) posterior, (E) proximal, and (F) distal views. **G.** Forefin in ventral view. Abbreviations: dp, dorsal process; dpc, deltopectoral crest; ef, facet for articulation with the preaxial element; i, intermedium; r, radius; ra, radial; rf, facet for articulation with the radius; u, ulna; uf, facet for articulation with the ulna. Scale bars: 10 cm.

Fernandez, 2007a) and the widest point of the element found at the level of the opisthotic facets. The re-orientation of the posterior opening for internal carotids posteriorly on the basisphenoid is shared with *A. chrisorum*, and differs from the ventral opening of all other ophthalmosaurids (Maxwell, 2010). However, the basi-sphenoid of *A. chrisorum* differs from that of MOZ 6145 in that there is no conspicuous recessed smooth area surrounding the carotid foramen, and the basiptyergoid processes are directed less anteriorly. The depressed areas on the posteroventral margins of the basiptyergoid processes are in a similar position to the grooves hypothesized to be the osteological correlates of the palatine ramus of facial nerve VII described in *Ophthalmosaurus icenicus*, *Brachypterygius extremus* (Boulenger, 1904), *Platypterygius australis* (M'Coy, 1867), and *A. chrisorum* (Kirton, 1983; Kear, 2005; Maxwell, 2010).

The humerus of MOZ 6145 shares many similarities with the holotype of *A. chrisorum*, including an anteriorly shifted deltopectoral crest, the decreased dorsoventral width of the posterior humerus, and the orientation and position of the ulnar facet. The posterior ulna also exhibits decreased dorsoventral width in both specimens. This configuration of the humerus, specifically the relatively small and anteriorly shifted deltopectoral crest, remains unique among ophthalmosaurids (Fischer et al., 2011: character 31). The thickened forefin elements distal to the humerus are found in all ophthalmosaurids; their loosely packed arrangement and rounded shape are shared with *Ophthalmosaurus*, while many other ophthalmosaurids, such as *Platypterygius* and *Caypullisaurus*, have tightly packed rectangular distal limb elements (Fischer et al., 2011: character 42).

#### 4. Discussion and conclusions

##### 4.1. Taxonomic referral

MOZ 6145 can be assigned to the Ophthalmosauridae Baur, 1887 *sensu* McGowan and Motani (2003) based on braincase and forefin features. It shares with all other members of the family the reduction of the extracondylar area of the basioccipital and the presence of an extra-zeugopodial element (preaxial element) anterior to the radius. Also, although broken, the presence of a stout dorsal process on the humerus can be inferred. In most phylogenetic analyses, these features have been consistently found as synapomorphies of the clade Ophthalmosauridae (Motani, 1999b; Fernández, 2007a; Druckenmiller and Maxwell, 2010; Maxwell, 2010; Fischer et al., 2011). While most contributions considered Ophthalmosauridae as a well-supported clade, internal relationships, as well as the alpha taxonomy of Ophthalmosauridae, are still controversial. In all cladistic analyses carried out in the last years, internal branches have low branch supports. Within Ophthalmosauridae, McGowan and Motani (2003) consider as valid generic names *Aegirosaurus*, *Brachypterygius*, *Caypullisaurus*, *Mollesaurus*, *Nannopterygius*, *Ophthalmosaurus*, *Platypterygius*, and *Undorosaurus*. To this list, new monotypic genera have been added: *Maiaspondylus*, *Arthropterygius*, *Athabascasaurus*, and *Sveltonectes* (Maxwell and Caldwell, 2006; Druckenmiller and Maxwell, 2010; Fischer et al., 2011). However, Maisch and Matzke (2000) and Maisch (2010) considered *Mollesaurus* to be a junior synonym of *Ophthalmosaurus*, and Druckenmiller and Maxwell (2010), based on a species-level phylogenetic analysis of Ophthalmosauridae, found the only two non-monotypic genera (*Ophthalmosaurus* and *Platypterygius*) to be paraphyletic; the paraphyly of *Platypterygius* was also recovered by Fischer et al. (2011).

To clarify the alpha taxonomy of ophthalmosaurids, as well as the internal relationships of its members, it is crucial to re-evaluate character definitions before performing a comprehensive phylogenetic analysis including all taxa. However, despite the lack of

consensus about the alpha taxonomy of the ophthalmosaurids, the affinities of MOZ 6145 can be explored as it preserves unusual morphologies of diagnostic parts of the skeleton. The braincase of MOZ 6145 strongly resembles that of *A. chrisorum*. In particular, the parabasisphenoid is characterized by the re-orientation of the foramen for internal carotid arteries which pierces the posterior surface of the bone. This change, as has been argued by Maxwell (2010), most likely involves the posterior extension of the parasphenoid and is unusual not only for ophthalmosaurids but also for most ichthyosaurs. The forefin of MOZ 6145 also resembles that of *A. chrisorum*, in that the humerus shares a peculiar dorsoventral compression of the posterior part of the bone and an anteriorly shifted deltopectoral crest. This morphology has not been reported in any other ophthalmosaurid. They also share a markedly concave facet on the distal end of the humerus for the articulation of the ulna. At present, the character combination of a basioccipital with an extremely reduced extracondylar area, humerus with a facet for the preaxial element, and forefin with thick and gently rounded outlined forefin elements (“*Ophthalmosaurus*-type” forefin) is also only seen in *Arthropterygius*. Thus, the character states and character combinations exhibited by MOZ 6145 guarantee its referral to the genus *Arthropterygius* (for a complete comparison of *A. chrisorum* with all other ophthalmosaurids, see Maxwell, 2010). However, in spite of the high degree of confidence in the generic assignment, minor differences exist between *A. chrisorum* and MOZ 6145, such as the enlarged posterior excavation and the ventral flexure of the posteroventral surface of the parabasisphenoid, and the angle of the basiptyergoid processes. Also, the holotype of *A. chrisorum* and MOZ 6145 differ in size: the humerus length equals 220 mm in *A. chrisorum* and 148 mm in MOZ 6145, while the width of the basioccipital condyle is 74 and 68 mm respectively. Taken together, these differences could indicate that the two specimens represent different species within the same genus. New, still unprepared material may clarify this taxonomic issue.

##### 4.2. Palaeobiogeographic implications

The presence of *Arthropterygius* in the Tithonian of the Neuquén basin is very interesting from a paleobiogeographic point of view. Tithonian strata of the Vaca Muerta Formation have yielded a rich marine herpetofauna including ichthyosaurs, plesiosaurs, marine turtles and metriorhynchids (Gasparini et al., 1999; Gasparini, 2007). Among ichthyosaurs, most of the discoveries can be referred to *Caypullisaurus*, a taxon known only from the Neuquén basin. However, this pattern of distribution may not represent endemism but rather a preservational bias attributable to uneven collecting efforts. The holotype of “*Ancanamunia mendozana*” (Rusconi, 1940), a humerus, radius and ulna, is consistent with *Ophthalmosaurus*, and represents the only record of this widespread genus in the Tithonian of the Neuquén Basin (Rusconi, 1948: figs. 65, 66).

Gasparini (1992) highlighted the affinities between the Neuquén Basin marine herpetofauna with that of the Western Tethys, and proposed a Caribbean seaway (i.e., Hispanic Corridor) as one of the most important dispersal routes for marine reptiles acting, although intermittently, since the beginning of the Jurassic. A shallow marine connection between the Western Tethys and Eastern Pacific through central Pangea has also been proposed by numerous authors based on the presence of the same genera and even species of marine invertebrates (Damborenea and Manceñido, 1979; Hallam, 1983; Riccardi, 1991; Aberhan, 2001; Damborenea, 2002). In the last decade the discovery of well preserved Oxfordian marine reptiles collected from the Jagua Formation (Cuba) provided direct evidences of the Hispanic Corridor acting as a seaway for pelagic marine reptiles. Although the general pattern of marine reptiles distribution for the Late

Jurassic indicates affinities of Neuquén basin assemblages with those of the Western Tethys (Gasparini and Iturralde-Vinent, 2006), the occurrences of *Arthropterygius* complicates this pattern, suggesting similarities with the high-latitude fauna of North America.

Damborenea (2002), in a comprehensive analysis of Jurassic bivalve distributions, recognized and quantitatively characterized palaeobiogeographic units (biochoremas), and classified bivalve genera according to their palaeobiogeographic affinities in pandemic, endemic, low-latitude (= Tethyan), high-latitude (Austral, Boreal and didemic) and trans-temperate. She recognized a South Andean unit, which includes the Neuquén Basin, through most of the Jurassic, and included it in a major South Pacific unit (Realm/subrealm) due to the common presence of didemic genera. In the particular case of bivalves, the phenomenon of bipolarity, although it can be traced back to the Early Jurassic, is more clearly seen in the Late Jurassic, especially in the Tithonian stage (Crame, 1993). The distributional pattern outlined for the bivalves and other mollusks is also consistent with that of decapod distribution, and it had been interpreted to have been possible by means of passage through the tropical regions along deeper, cooler water pathways (Feldmann and Schweitzer, 2006).

Whether *Arthropterygius* had a distribution restricted to high latitudes in both hemispheres, as did many Tithonian invertebrates, or if it was cosmopolitan needs further scrutiny. However, the idea that all ichthyosaurs were spatially widespread or truly cosmopolitan in distribution (i.e., pandemic; McGowan, 1978) also needs to be tested.

## Acknowledgments

We thank Alberto Garrido (Museo Pedro Olsacher de Zapala, Neuquén, Argentina) for providing access to the MOZ 6145, and B. Kear and P. Druckenmiller for reviewing the manuscript. This research has been supported by the following grants: Agencia Nacional de Promociones Científicas y Tecnológicas de Argentina (PICT 0261), Consejo Nacional de Investigaciones Científicas y Tecnológicas (PIP 0426), and Programa de Incentivos UNLP N607 (Argentina), Alexander von Humboldt Foundation and NSERC postdoctoral research grants to EM.

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