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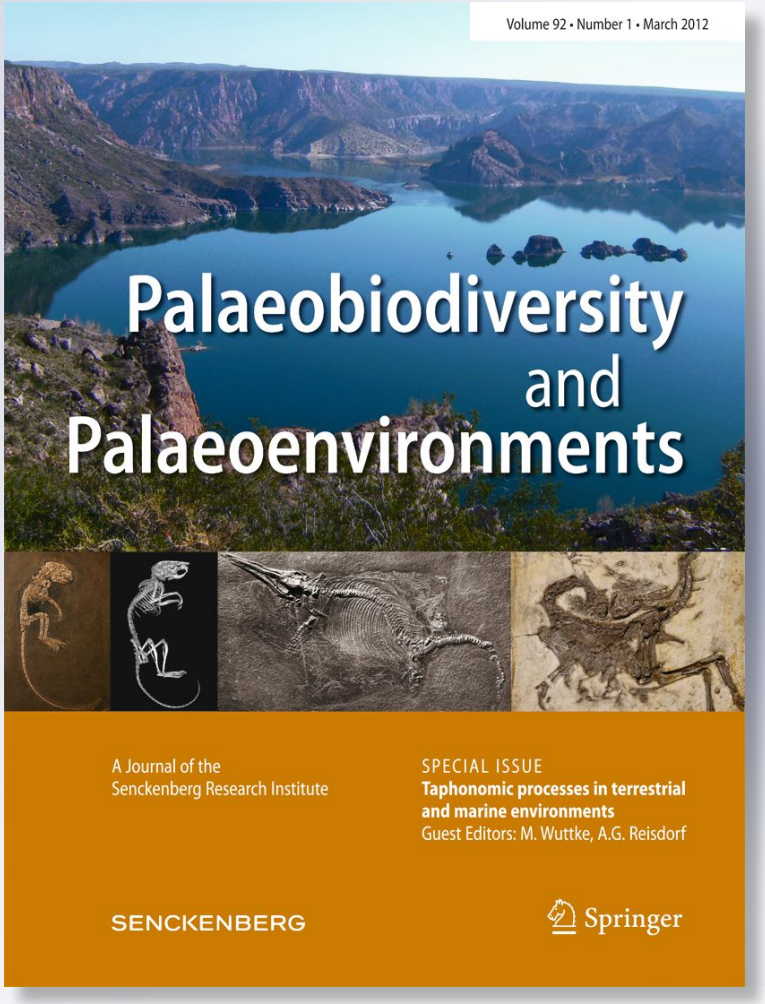

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ORIGINAL PAPER

An ichthyosaurian forefin from the Lower Cretaceous Zapata Formation of southern Chile: implications for morphological variability within *Platypterygius*

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Abstract Expeditions to the Tyndall Glacier (Torres del Paine National Park, South Chile) in 2009 and 2010 recovered an articulated ichthyosaurian forefin that displayed traits consistent with *Platypterygius*. The combination of features observed in this forefin has not been observed in other *Platypterygius* species, i.e.: (1) one preaxial row and three or even four postaxial rows; (2) the distal articulation of ulna with metacarpal five; (3) the shape and the articulation context of distal carpal three, metacarpal three and four; (4) the hexagonal shape of the intermedium; and (5) the presence of only two distal articular facets on the humerus. Nevertheless, the forefin is not referred to a new species, because it was found isolated and no other diagnostic skeletal elements are present. The forefin presented here is the first complete and articulated forefin of a *Platypterygius* from the South Pacific margin, and together with other ichthyosaurs from the Tyndall area, represents the southernmost occurrence of Early Cretaceous ichthyosaurs in the Americas.

Keywords Ichthyosaurs · *Platypterygius* · Torres del Paine · Tyndall Glacier · Chile

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Introduction

The fossil record of Cretaceous ichthyosaurs has been traditionally assigned to the genus *Platypterygius,* the remnants of which have been found all over the world (Arkhangelsky et al. 2008; Efimov 1997; Fernández and Aguirre-Urreta 2005; Kear 2003; Kiprijanoff 1881; Kuhn 1946; M'Coy 1867 in McGowan and Motani 2003; Nace 1939; Páramo 1997; Wade 1984; Zammit 2010). McGowan and Motani (2003) considered *Platypterygius* as the most representative genus of the Early Cretaceous. However, during the past five years, new discoveries drastically increased our knowledge on Cretaceous ichthyosaurs, and four new monotypic genera have been erected: *Maiaspondylus* Maxwell and Caldwell (2006b) from the Albian of the Northwest Territories of Canada; *Athabascasaurus* Druckenmiller and Maxwell (2010) from the Early Albian of Alberta, Canada; *Sveltonectes* Fischer et al. (2011) from the Late Barremian of Western Russia; and *Acamptonectes* Fischer et al. (2012) from the Hauterivian of North Yorkshire, UK and Cremlingen area,

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Lower Saxony, Germany. The last one demonstrated that the Jurassic–Cretaceous extinction did not affect at all ichthyosaurs and that these marine reptiles were more diverse during the Early Cretaceous than previously thought.

Some articulated forefins of Early Cretaceous ichthyosaurs have been preserved. These include: a partially complete right forefin of *Platypterygius ochevi* (Albian-Cenomanian) from the Voronezh Region, Russia (Arkhangelsky et al. 2008); both forefins of *Sveltonectes insolitus* (Fischer et al. 2011); both forefins of *Platypterygius hercynicus* from the Albian of Lower Saxony, Germany (Kolb and Sander 2009); forefins of *Playtpterygius australis* from the ?Albian of north-central Queensland, Australia (McGowan 1972; Wade 1984, 1990; Zammit et al. 2010); a forefin of *Platypterygius* sp. from the Albian of Loon River Formation, Canada (Maxwell and Caldwell 2006a); a forefin of *Platypterygius platydactylus* from the Aptian of Lower Saxony, Germany (Broili 1907), destroyed during WWII; two incomplete forefins of *Platypterygius hauthali* from the Barremian of Santa Cruz Province, Argentina (Fernández and Aguirre-Urreta 2005); the left humerus of an undeterminated Ophthalmosauridae from the Albian of the Clearwater Formation, Canada (Maxwell and Druckenmiller 2011); a left incomplete forefin of *Maiaspondylus lindoei* (Maxwell and Caldwell 2006b); a semi complete forefin of *P. americanus* (Maxwell and Kear 2010; Nace 1939); the articulated left and right forefins of the nomen dubium *P. bedengensis* (Efimov 1997); a humerus and ulna of *Acamptonectes densus* from the Hauterivian of Speeton Clay, Glasglow, UK (Fischer et al. 2012); as well as numerous isolated humeri of *P.* cf. *campylodon* (e.g. Kiprijanoff 1881; Kuhn 1946; Sauvage 1882). A right humerus and the articulated left forefin referred to *Platypterygius* sp. (Adams and Fiorillo 2010) was preserved from the Early Cenomanian of Tarrant County in Texas. Despite this material comes from the Late Cretaceous, the forefin share characteristics with CPAP-2011-0019, and for this reason it is considered here.

In the year 2009, an articulated ichthyosaurian forefin was discovered adjacent to the Tyndall Glacier in the Torres del Paine National Park in South Chile. The forefin was found during a paleontological expedition conducted by researchers of the Institute of Earth Sciences of Heidelberg University, the Staatliches Museum für Naturkunde Karlsruhe, and the Instituto Antártico Chileno. Together with this forefin, more ichthyosaur material was found, which is preserved articulated or near articulated (Pardo et al., in review). The forefin described here shows a unique combination of morphological characters that differ from those of other Cretaceous ichthyosaurian forefins. Due to the scarcity of Cretaceous ichthyosaurs from South America, particularly from the southernmost parts of the continent, this material yields significant information on the diversity of ichthyosaurs that lived along the southeastern coasts of the Paleopacific during the Early Cretaceous, and on the morphological diversity of ophthalmosaurid forefins.

Geological setting

The ichthyosaur-bearing sequence at the Tyndall Glacier, Torres del Paine National Park, Magallanes Province, southern Chile, belongs to the Zapata Formation, which is of ? Tithonian, Berriasian to Aptian-Albian age (Cañón 2000; Cecioni 1951 in Prieto 1994; Fildani and Hessler 2005; Fildani et al. 2008; Katz 1963; Romans et al. 2011). Abundant belemnites (e.g. *Belemnopsis* sp.), ammonites (e.g. ?*Substeueroceras* sp.; ?*Cuyaniceras* sp.; ?*Thurmanniceras* sp. and *Favrella* sp.), inoceramid bivalves, fishes, and plant remains are associated with the ichthyosaur remains. The ammonite assemblage indicates that the ichthyosaur-bearing sediment unit is ?latest Tithonian, Berriasian to Hauterivian in age. The articulated forefin (Fig. 2a) was found isolated on a polished turbidite bed at the edge of a cliff near the Tyndall Glacier (51°06′46.2″S, 073°17′47.7″W), Torres del Paine National Park, Magellanes Region, Southern Chile (Fig. 1).

Institutional abreviations

GEOW, (Geowissenschaften) Institute of Earth Sciences of Heidelberg University, Germany; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; INACH, Instituto Antártico Chileno; CPAP, Colecciones Paleontológicas de Antártica y Patagonia. The forefin remains in dependences of the INACH with the collection number CPAP-2011-0019, until the material is temporarily sent to Germany. Once the material is in Germany, it will be prepared in the SMNK. Subsequent to the preparation, the specimen will be sent back to Chile where it will be housed at the Antarctic Museum of the INACH, which is currently under construction.

Systematic palaeontology

Order Ichthyosauria de Blainville, 1835
Family Ophthalmosauridae Baur, 1887
Subfamily Platypterygiinae Arkhangelsky, 2001
Genus *Platypterygius* von Huene, 1922

Platypterygius sp.
(Fig. 2).

Referred material: CPAP-2011-0019). One complete and almost fully articulated isolated left forefin (Fig. 2a).
Description: The specimen CPAP-2011-0019 consists of a complete articulated and isolated forefin. Based on the convexity of the caput humeri (Johnson 1977), CPAP-2011-

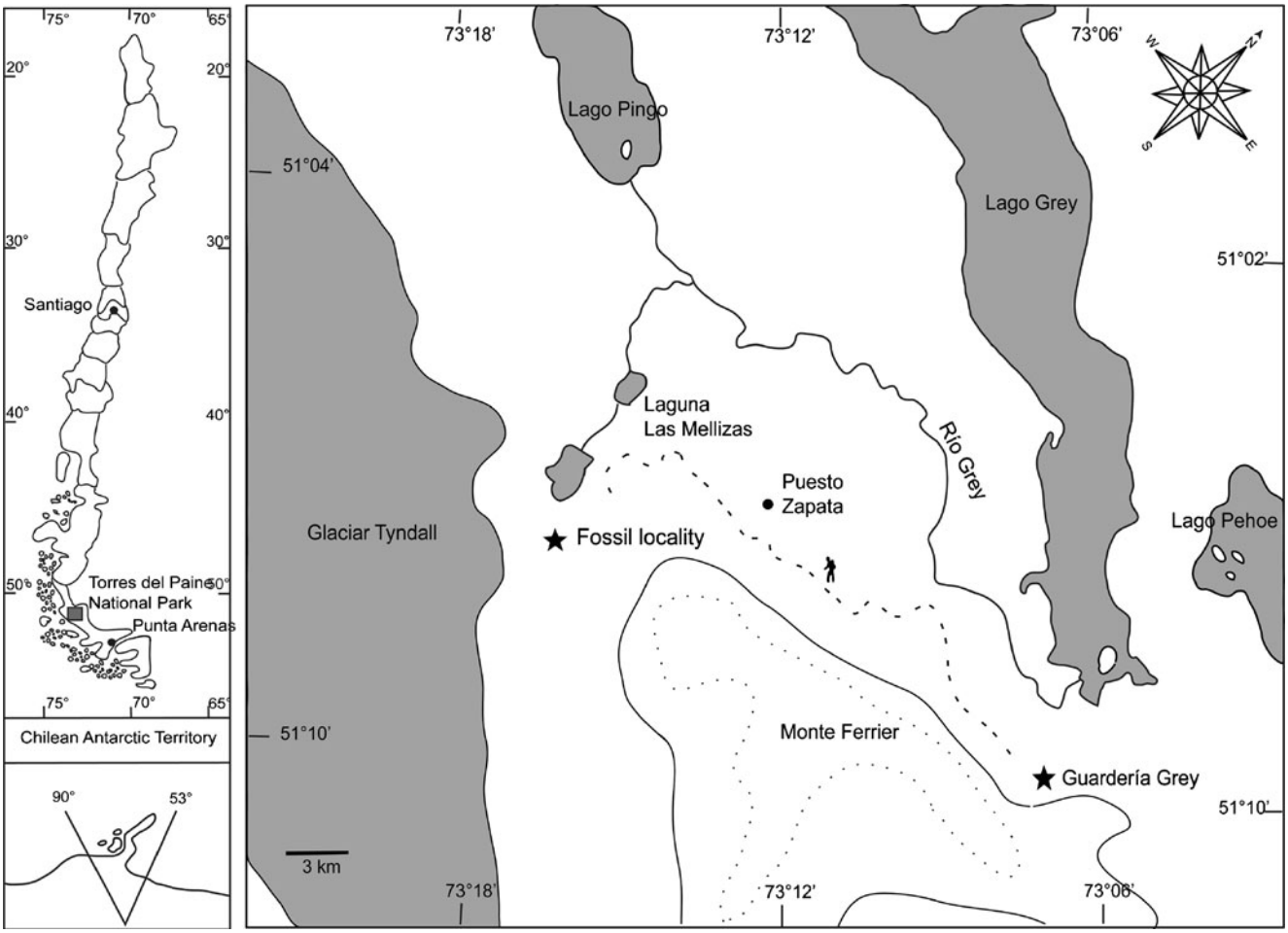

Fig. 1 The fossil area in the Torres del Paine National Park, South Chile

0019 comes from an adult ichthyosaur. CPAP-2011-0019 is preserved on a single slab of turbiditic sandstone that was cut out of an undisturbed, glacier-polished bed of about 15 m^2. All bones of the forefin were subject to the same polishing and are abraded to the level of the matrix. A few of them are partially covered in the matrix, e.g. radius, radiale, distal carpal two, two phalanges of the postaxial row, and the small phalanges of the distal end of the forefin.

The forefin is identified as the left one based on: (1) convexity of the preaxial and postaxial rows; (2) dimensions of the ulna, which is one-third larger than the radius; and (3) the crescentic shape of the pisiform. However, the distal phalanges of the anterior and posterior edge have suffered disarticulation. In addition, there are some ophtalmosaurids in which the radius is higher and wider than the ulna, among them *Caypullisaurus* (Fernández 1997), or in which the two bones reach the same size, e.g. *P. autralis* (Zammit et al. 2010). The complete forefin measures 410 mm.

The long and slender humerus has a length of 94 mm, and it is 61 mm wide at its proximal margin and 56 mm wide at its distal extremity (Table 1). The humerus has two concave distal articular facets, the larger of which articulates with the ulna. The smaller one, which has about one third the length of the ulnar facet, articulates with the radius (Fig. 2a).

The radius has a polished pentagonal shape. A small part of its anterior margin is covered by sediment. Proximally, the radius articulates with the anterior facet of the humerus. Anterodistally, a small facet articulates with the radiale. On the posterior margin of the radius, there is a small articular facet with the ulna. Finally, the radius articulates posterodistally with the intermedium in a straight facet.

The ulna is one-third larger than the radius and has an asymmetrical shape. It has five articular facets: Its proximal margin is convex and articulates with the posterior distal articular facet of the humerus. A small facet in the anterior margin of the ulna articulates with the radius. Distally, another facet, twice as large as the facet for the radius, articulates with the intermedium. A larger and straight facet articulates with the ulnare. These two last articular facets of the ulna form an angle of 105° with each other. A small articular facet in the posterior margin articulates with the pisiform.

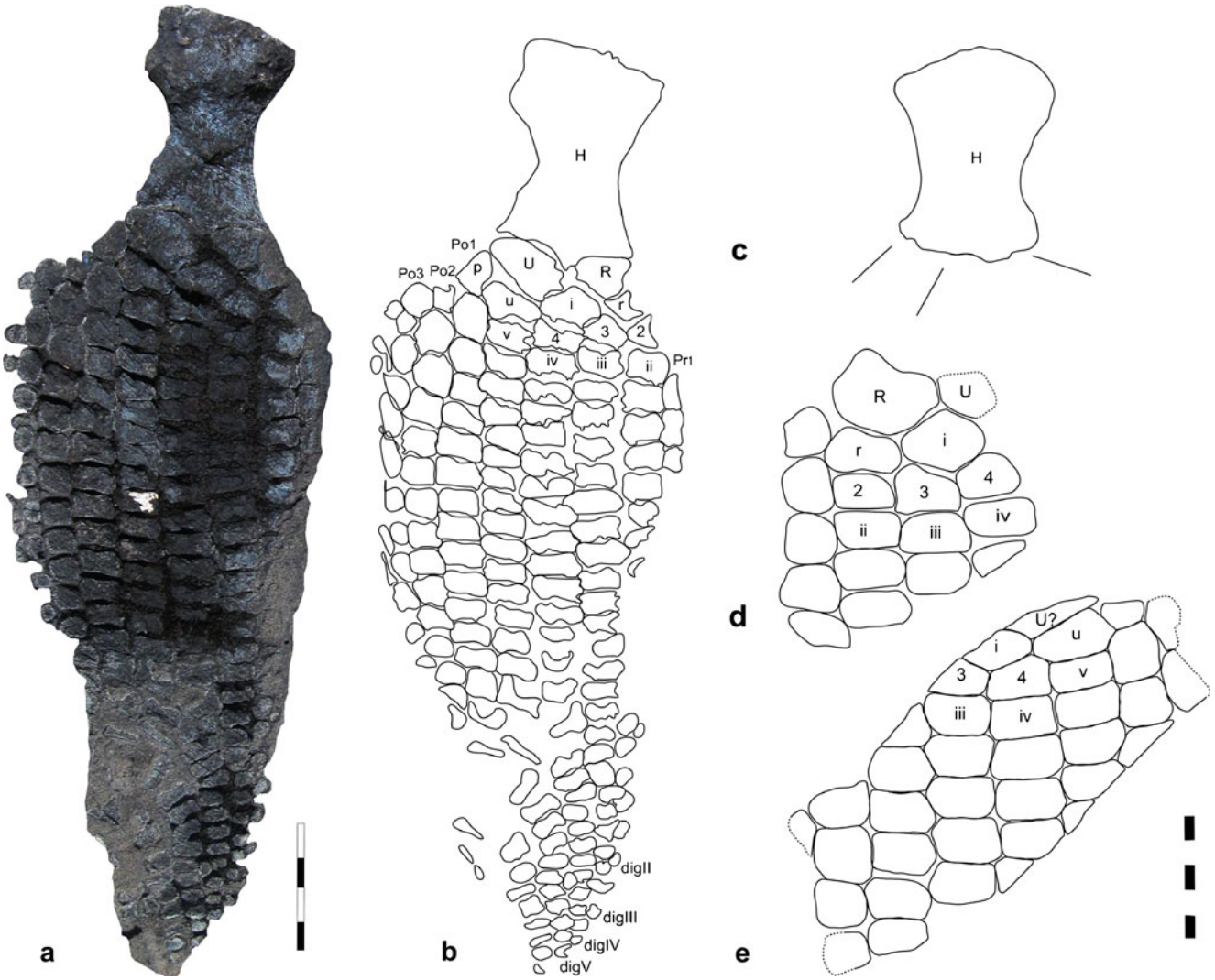

Fig. 2 **a** CPAP-2011-0019, general view. **b** Interpretative drawing of CPAP-2011-0019. *Scale bars* 5 cm. **c**–**e** *P. hauthali*. **c** Humerus of MLP 79-1-30.1. The *lines* indicate the three facets of the humerus. **d** Fragment of a forefin of MLP 79-1-30.1. **e** Fragment of forefin of MLP 79-1-30.2. *Scale bars* 3 cm. *dp* distal process; *H* humerus; *i* intermedium; *R* radius; *r* radiale; *U* ulna; *u* ulnare; *p* pisiform; *2* distal carpal two; *3* distal carpal three; *4* distal carpal four; *ii* metacarpal two; *iii* metacarpal three; *iv* metacarpal four; *V* metacarpal five; *Pr1* digit preaxial one; *Po1* digit postaxial one; *Po2* digit postaxial two; *Po3* digit postaxial three; *digII* digit two; *digIII* digit three; *digIV* digit four; *digV* digit five

The pisiform is crescentic in outline and lacks distinct articular facets. There is a narrow contact with the ulna proximally. Distally, the pisiform articulates with the first element of the first postaxial row and the ulnare.

The intermedium is hexagonal in outline. The proximal articular facets of the intermedium, which articulates with the ulna and radius, are nearly equal in length, with the ulnar facet being 16 mm long and the radial 15 mm long. These two articular facets form an angle of 115° with each other.

Anteriorly, the intermedium articulates with the radiale and distal carpal three, respectively. A posterodistal facet, which is twice as large as the carpal three facet, articulates with the distal carpal four. A small contact with the ulnare is present on the posterior margin of the intermedium.

The anterior half of the radiale is covered by sediment, but four articulation facets are recognised. Proximally, the radiale bears a concave facet that articulates with the radius. Distally, it articulates with distal carpal two and with distal carpal three. On its posterior margin, the smallest articular facet of the radiale articulates with the intermedium.

The ulnare is 16 mm wider than the radiale and is pentagonal in outline. Two small facets on the anterior margin of the ulnare articulate with the intermedium and distal carpal four, respectively. The ulnare articulates with metacarpal five via a facet that is twice as large as the facet of distal carpal four. The posterior margin of the ulnare articulates with the first element of the first postaxial digit and the pisiform.

Table 1 Measurements of elements of the forefin CPAP-2011-0019

Element	Width (mm)	Length (mm)
Humerus	61 (proximal) 56 (distal)	94
Radius	23	17
Ulna	35	22 (anterior margin) 16 (posterior margin)
Radiale	10	13
Ulnare	26	16
Intermedium	26	17
Pisiform	9 (proximal) 11 (distal)	17
Carpal two	10	11
Carpal three	19	12
Carpal four	21	13
Metacarpal two	17	13
Metacarpal three	21	12
Metacarpal four	21	11
Metacarpal five	18	11

The distal carpal two is covered by sediment with the exception of a small portion on its posterior margin. The exposed portion of distal carpal two articulates proximally with the radial. Distally it articulates with metacarpal two. On the posterior margin, a small articulation facet contacts distal carpal three.

Remarks: CPAP-2011-0019 was diagnosed as *Platypterygius* because the majority of characters observed in this specimen are associated with this genus (compare McGowan and Motani 2003). These characters include (1) a humerus with two distal articular facets (as in *P. campylodon* and *P. platydactylus*), (2) an intermedium without contact with the humerus (as in *P. australis*; *P. platydactylus*; *P. hercynicus*; *P. hauthali*; *P. ochevi*; *P. americanus*; *P. bedengensis*; *P. campylodon; Platypterygius* sp., Maxwell and Caldwell 2006a; *Platypterygius* sp., Adams and Fiorillo 2010), (3) the presence of pre- and postaxial digits (as in *P. australis*; *P. platydactylus*; *P. hercynicus*; *P. hauthali*; *Platypterygius* sp., Maxwell and Caldwell 2006a, and at least three postaxial digits in *P. ochevi*), (4) pre- and postaxial phalanges which are not in contact with the humerus (as in *P. platydactylus*), (5) a forefin with more than seven digits (as in *P. platydactylus*; *P. hercynicus*; *P. australis*; *P. hauthali*; *P. bedengensis; Platypterygius* sp., Maxwell and Caldwell 2006a), and (6) phalanges with rectangular outline, except towards the distal tip (as in *P. hauthali*).

Moreover, CPAP-2011-0019 shows a unique combination of characters: (1) one preaxial row (as in *Platypterygius* sp.; Maxwell and Caldwell 2006a) and three or even four postaxial rows (as in *P. australis* and *Platypterygius* sp.; Maxwell and Caldwell 2006a); (2) the distal facet of the ulna articulates with the metacarpal five and not with the metacarpal four, or metacarpal four and five as in the other *Platypterygius* spp.; (3) distal carpal three of CPAP-2011-0019 has six articular facets (as *P. ochevi* and *P. platydactylus*), whereas *P. hauthali* has seven, while the distal carpal three in *P. australis*, *P. hercynicus and P. americanus* has five articular facets; (4) the metacarpal three bears six articular facets as in *P. hauthali* and *Platypterygius* sp. (Adams and Fiorillo 2010), while in *P. platydactylus*, *P. ochevi*, *P. australis* and *P. hercynicus* the metacarpal three has five articular facets; and (5) the metacarpal four of CPAP-2011-0019 has six facets of articulation as in *Platypterygius* sp. (Adams and Fiorillo 2010), while in *P. platydactylus*, *P. australis*, *P. hercynicus* and *P. hauthali* it articulates with five. This element is not preserved in *P. ochevi* and *P. americanus*.

Nevertheless, some features are also present in another ophthalmosaurids: (1) the humerus of *Sveltonectes insolitus* Fischer et al. (2011) also has two distal articular facets; (2) the intermedium is not in contact with the humerus; this characteristic is shared with *Caypullisaurus bonapartei* Fernández (1997); *Sveltonectes* and *Plutoniosaurus bedengensis* Efimov (1997) (nomen dubium by McGowan and Motani 2003); and (3) the presence of pre- and postaxial digits is shared with *Sveltonectes* (one preaxial and one postaxial digit), *Maiaspondylus lindoei* Maxwell and Caldwell (2006b) (one postaxial digit), and *Plutoniosaurus* (one preaxial and one postaxial), which exemplifies the high variation in the limbs of ichthyosaurs.

Of all species of *Platypterygius*, CPAP-2011-0019 shows most morphological similarities with *Platypterygius hauthali* Fernández and Aguirre-Urreta 2005, from the Barremian of the Cerro Belgrano Formation, Argentina, especially in the hexagonal diamond shape of the intermedium, which supports two digits instead of a single one. This leads to a "latipinnate" condition, which is exclusive for *P. hauthali* and differs from *Caypullisaurus*, *P. platydactylus*, *P. ochevi*, *P. hercynicus*, *Maiaspondylus*, *P. australis*, *P. campylodon*, and *P. bedengensi*. In these taxa, the intermedium has a single distal articular facet ("longipinnate" condition) (Appleby 1979; McGowan 1972). However, there are some differences that do not allow an unequivocal referral of CPAP-2011-0019 to *P. hauthali*: (1) the humerus of *P. hauthali* has a third distal facet for the anterior extrazeugopodial element, which is absent in CPAP-2011-0019; (2) the proximal margin of the humerus is straight in CPAP-2011-0019, but deeply convex in *P. hauthali*; according to Johnson (1977), this feature of the humerus in *P. hauthali* could be a sign of the mature state of the animal (Fernández and Aguirre-Urreta 2005); (3) CPAP-2011-0019 has one preaxial row and three or even four postaxial rows, while *P. hauthali* has at least three preaxial rows (specimen MLP 70-I-30-1); (4) the intermedium of CPAP-2011-0019 has a distal facet for the articulation with distal carpal four, which is twice as long as the distal articular facet for distal carpal three; in the intermedium of *P. hauthali*, these facets are of the

same length. (5) distal carpal three of CPAP-2011-0019 has six articular facets (as *P. ochevi* and *P. americanus*), while the holotype of *P. hauthali* (specimen MLP 70-I-30-1) has seven; the additional facet articulates with metacarpal four; (6) metacarpal three in both CPAP-2011-0019 and *P. hauthali* (specimen MLP 70-I-30-1) bears six articulations with phalanges; however, the posterior facets of the metacarpal three in CPAP-2011-0019 articulate posteroproximally with distal carpal four and posterodistally with metacarpal four, which is not the case in *P. hauthali*; and (7) metacarpal four of CPAP-2011-0019 articulates with six phalanges of the digits three, four and five; while in *P. hauthali* (specimen MLP 70-I-30-1) this bone articulates with digit five (Fig. 2d).

Discussion

The description of McGowan and Motani (2003) for *Platypterygius* shows autapomorphies that were recently also identified in other ophthalmosaurids (Fischer et al. 2011; Maxwell and Caldwell 2006b). Indeed, intra- and interspecific variation is also found in forefins of *Platypterygius* spp; for instance, the humerus of CPAP-2011-0019 has two distal articular facets. In *Platypterygius ochevi* Arkhangelsky et al. 2008, *Platypterygius hauthali* Fernández and Aguirre-Urreta 2005, *Platypterygius australis* (M'Coy 1867) and *Platypterygius americanus* (Nace 1939), the humerus possesses three distal facets. The third distal facet of the humerus of *P. ochevi* articulates with an anterior extrazeugopodial element. This facet is the largest of the three with a length of 28 mm compared with the articular facets for radius (25 mm) and ulna (24 mm; Arkhangelsky et al. 2008). In *P. hauthali* and *P. australis,* the third distal facet of the humerus that articulates with an anterior extrazeugopodial element is half the size compared with the facets for radius and ulna. The proximal facet of the extrazeugopodial element is almost straight in *P. hauthali* but markedly convex in *P. australis* (Fernández and Aguirre-Urreta 2005; Zammit et al. 2010). In addition to these interspecific variations, there are also intraspecific ones: *P. australis* (specimen QMF2573) has a fourth posterodistal facet on the humerus that articulates with the pisiform (Zammit et al. 2010). The third posterodistally-situated facet of the humerus in *P. americanus* also articulates with the pisiform (Maxwell and Kear 2010). The humerus of *Platypterygius* sp. (Maxwell and Caldwell 2006a) has four distal articular facets for an extrazeugopodial element, radius, ulna and a pisiform. The intermedium of this forefin articulates with the ulna and radius in the proximal facets and with the radiale and ulnare in the anterior and posterior margins respectively, as in CPAP-2011-0019. However, the intermedium of *Platypterygius* sp. is pentagonal in shape and hexagonal in CPAP-2011-0019.

P. hercynicus (Kuhn 1946) has a humerus with four distal articular facets (Kolb and Sander 2009). In contrast, *P. platydactylus* (Broili 1907) has a humerus with only two distal articular facets, coincident with CPAP-2011-0019. Nevertheless, the intermedium of *P. platydactylus* bears seven articular facets, whereas CPAP-2011-0019 has only six. The intermedium of the left forefin of *Sveltonectes insolitus* has six articular facets, while the same element in the right forefin has five (Fischer et al. 2011).

The ulna of *Platypterygius* sp. (Adams and Fiorillo 2010) is larger and wider than the radius. Its distal facet is slightly concave and the anterodistal facet is rounded (as in CPAP-2011-0019). The radius is roughly pentagonal in shape, and proximally articulates with the humerus in a convex facet, as in CPAP-2011-0019. The anterior margin is concave and articulates with the extrazeugopodial element. This feature is not completely visible in CPAP-2011-0019, because the anterior margin of the radius is covered by matrix, but in the posteroproximal margin of this element, a small part of the bone is uncovered and has a rounded shape, as in the *Platypterygius* specimen. Nevertheless, there are also differences between CPAP-2011-0019 and *Platypterygius* sp. (Adams and Fiorillo 2010): The humerus of *Platypterygius* sp. (Adams and Fiorillo 2010) has four distal articular facets, while CPAP-2011-0019 has two. The intermedium in this specimen of *Platypterygius* has six articular facets as CPAP-2011-0019, but they differ in the distal articulations of this element. The distal facet of the intermedium in CPAP-2011-0019 is larger and articulates with the distal carpal four; the anterodistal facet is shorter than the previous one and articulates with the distal carpal three. In *Platypterygius* sp. (Adams and Fiorillo 2010), the distal facet of the intermedium is also larger and articulates with the distal carpal four, whereas the posterodistal facet articulates with the distal carpal three.

CPAP-2011-0019 shares more morphological similarities with *P. hauthali* than with other species of *Platypterygius,* regarding the hexagonal intermedium, the "latipinnate" condition and the geo-stratigraphic position. Even though there are differences in humerus, ulna, intermedium and metacarpals of CPAP-2011-0019, these differences could represent a case of intraspecific variation in *P. hauthali* that should not be excluded.

The isolated forefin CPAP-2011-0019 from the Torres del Paine National Park is of special importance, because it represents the first complete and articulated forefin of a *Platypterygius* ichthyosaur from the Early Cretaceous of South America. Even though the specimen clearly differs from *P. hauthali* and other related taxa in the shape of its phalanges and humerus, CPAP-2011-0019 cannot be identified beyond *Platypterygius* sp. for two reasons: (1) it is not associated with further diagnostic skeletal elements, and (2) the intra- and interspecific variation in forefins is not

sufficiently known. Paddles may therefore not be reliable elements for species identification. Thus, CPAP-2011-0019 either proves evidence for a high anatomical variability in the forefin of *Platypterygius,* or it indeed represents a new species, which then needs to be proven by further and more complete specimens from the Torres del Paine National Park localities.

Platypterygius has been found on every continent (Arkhangelsky et al. 2008; Broili 1907; Fernández and Aguirre-Urreta 2005; Kear 2003; Kolb and Sander 2009; Maxwell and Kear 2010; Zammit et al. 2010), which demonstrates the cosmopolitan distribution of this genus during the Early Cretaceous. The presence of this genus in Australia, Argentina and now the Chilean Patagonia supports the hypothesis that a seaway existed, which formed a passage that ichthyosaurs could use after the break-up of Gondwana and the separation of Africa from Antarctica, Australia and South America, possibly since the lower Tithonian (Gasparini 1992; Gasparini and Fernández 1997).

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