Evidence for a second species of the ichthyosaur *Platypterygius* in North America: a new record from the Loon River Formation (Lower Cretaceous) of northwestern Canada

E.E. Maxwell and M.W. Caldwell

Abstract: To date, all Cretaceous ichthyosaur material from North America has been referred to the species *Platypterygius americanus*. This species is generally identified based on skull and paddle morphology, but all non-diagnostic material from North America has been assigned to this species. A new Lower Cretaceous ichthyosaur from the Loon River Formation at Hay River, Northwest Territories, Canada, is described here. The specimen in question consists of the anterior portion of a large ichthyosaur, of which only the pectoral girdle is well preserved. It is assignable to *Platypterygius*, but is inconsistent with *P. americanus* based on paddle morphology. It shares most similarities with European and Australian species; unfortunately, it cannot be definitively assigned to any one taxon because of poor preservation of the skull. This specimen increases our knowledge of the diversity of North American Cretaceous ichthyosaurs, and suggests that the Cretaceous Western Interior Seaway was capable of sustaining a large taxonomic diversity of these marine reptiles, similar to the high numbers of *Platypterygius* species known from Europe.

Résumé : À ce jour, tout le matériel ichtyosaure crétacé de l'Amérique du Nord a été affecté à l'espèce *Platypterygius americanus*. Si l'identification de cette dernière repose généralement sur la morphologie du crâne et des nageoires, tout le matériel non diagnostique nord-américain lui a également été attribué. Un nouvel ichtyosaure du Crétacé inférieur de la Formation de Loon River, à Hay River, dans les Territoires du Nord-Ouest (Canada) est décrit. Le spécimen en question consiste en la portion antérieure d'un grand ichtyosaure dont seule la ceinture scapulaire est bien préservée. Ce spécimen est attribuable au genre *Platypterygius*, mais la morphologie de ses nageoires ne concorde pas avec *P. americanus*. Si c'est avec des espèces européennes et australiennes qu'il partage le plus de caractères semblables, il ne peut malheureusement être affecté de façon définitive à un taxon précis en raison de la piètre conservation du crâne. Ce spécimen vient parfaire les connaissances concernant les ichtyosaures crétacés de l'Amérique du Nord et laisse penser que, à l'instar du grand nombre d'espèces de *Platypterygius* connues en l'Europe, la mer intérieure de l'Ouest au Crétacé pouvait soutenir une grande diversité taxonomique de ces reptiles marins.

[Traduit par la Rédaction]

Introduction

Ichthyosaurs were a highly successful group of diapsid reptiles that became modified for an aquatic mode of life. They are found in rocks dating from the Lower Triassic (Spathian) to the Upper Cretaceous (Cenomanian) (Sander 2000; Arkhangelsky 2001; McGowan and Motani 2003; Motani 2005). All parvipelvian ichthyosaurs are presumed to be monophyletic as they share certain key features, such as the pattern of rib articulations, a tailbend, aulacodont tooth implantation, and the absence of the antebrachial space between the radius and the ulna. This clade originated in the Upper Triassic and was the only group of ichthyosaurs to survive into the Jurassic and Cretaceous (Sander 2000; Motani 2005).

There is a single genus, *Platypterygius* Huene (1922), to which almost all species of Cretaceous ichthyosaurs have traditionally been referred; the concept of the genus *Platyterygius*, and thus of Cretaceous ichthyosaurs, is also tightly linked to the idea that this single Cretaceous taxon represents the final decline of the once far more diverse ichthyosaurs. The geologic range of the genus extends from the Valanginian to the upper Cenomanian — a span of 50 million years (Arkhangelsky 2001).

Platypterygius is diagnosed by the presence of four bones in the epipodial row of the forefin: the lageniform, radius, ulna, and pisiform (Wade 1984). The intermedium never contacts the humerus and this helps to distinguish *Platypterygius* from other ophthalmosaurs, such as *Brachypterygius* Huene (1922) and *Aegirosaurus* Bardet and Fernández (2000) (Motani 1999*a*; Fernández 2001). The forefin is made up of seven primary digits and at least one accessory digit, and the humerus is not expanded distally. There are a large number of presacral vertebrae, the eyes are reduced, and the maxilla

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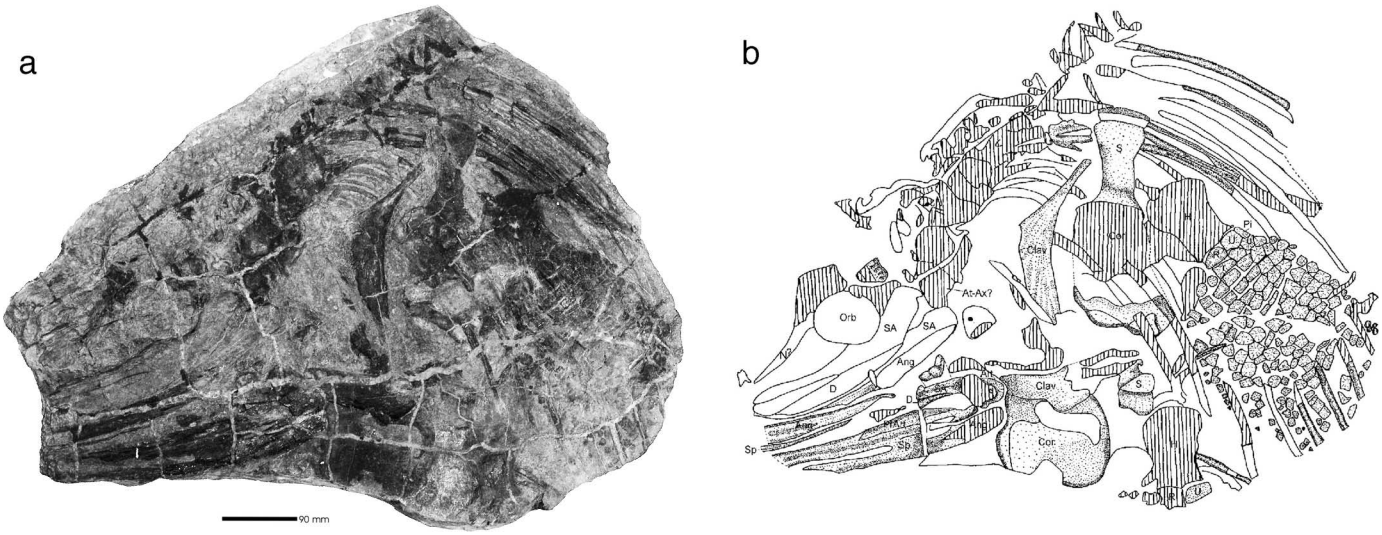
Fig. 1. UALVP 45636 (*a*) photograph (*b*) line drawing. Stippling represents undamaged bone, striping indicates bones whose external features are obliterated, and outlines demarcate impressions on the rock. Ang, angular; Art, articular; At-Ax, atlas–axis; Clav, clavicle; Cor, coracoid; H, humerus; i, intermedium; N, nasal; Orb, orbit; Pi, pisiform; PrArt, prearticular; R, radius; r, radiale; S, scapula; SA, surangular; Sp, splenial; U, ulna; u, ulnare. Scale bar = 90 mm.



is elongate compared to Jurassic genera (McGowan 1972*a*; Sander 2000).

All Cretaceous North American material referred to this genus has been assigned to the species *Platypterygius americanus* (Nace, 1939) (McGowan 1972*b*). Up to this point, material diagnosed as *P. americanus* included the type material described by Nace (1939), a complete skull described by Romer (1968), and the forefins associated with this skull, described by McGowan (1972*b*). All of these specimens came from the Graneros Formation of Wyoming, which is Albian in age (McGowan 1972*b*). Vertebral centra and other non-diagnostic material have been found at numerous sites in western North America (Merriam and Gilmore 1928; Shimada 1996; Main and Fiorillo 2002).

Platypterygius had a cosmopolitan distribution, with specimens having been recovered from Europe, Russia, Australia, North and South America (Arkhangelsky 2001). Species, however, tend to be much more localized in distribution. For instance, material referred to *P. americanus* has not been recovered from outside of the Western Interior Seaway of North America (McGowan 1972*b*), and, similarly, material diagnosable as *P. australis* (formerly known by the junior synonym *P. longmani* and synonymized by McGowan and Motani (2003)) has only been found on the Australian continent (Kear 2003).

An ichthyosaur specimen consistent with the genus *Platypterygius* was recovered from the bed of Hay River, Northwest Territories, Canada (60°01′N, 116°57′W) in 1971. The rocks in which it was found belong to the Loon River Formation, which is Middle Albian in age (Singh 1971). This formation is exclusively marine and comprises black marine shales and limestones at the locality in question (Forey 1975). Other vertebrates found in association with *Platypterygius* include holostean, aspidorhynchiform, bananogmiid, and clupeomorph fishes, as well as several ophthalmosaurs distinct from *Platypterygius,* (Forey 1975; Maxwell and Caldwell 2006); the new ichthyosaur described by Maxwell and Caldwell (2006) hints at unsuspected diversity among lowermost Upper Cretaceous ichthyosaurs.

Materials

UALVP 45636 is a large ichthyosaur preserved as a compression fossil on a large and heavily cemented block of siltstone; the fossilized remains include both bone and natural molds of bones, where the latter weathered away after exposure of the slab. The specimen is composed of portions of the lower jaw and cranium, cervical and anterior thoracic vertebrae, ribs, both forefins, and the pectoral girdle (Fig. 1). It was collected from an outcrop of the Loon River Formation, Lower Cretaceous (Albian; 110 million years ago, Singh 1971), along the Hay River (60°01′N, 116°57′W), Northwest Territories, Canada.

Institutional abbreviations

University of Alberta, Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada (UALVP) and University of Wyoming, Laramie, Wyoming (UW).

Systematic palaeontology

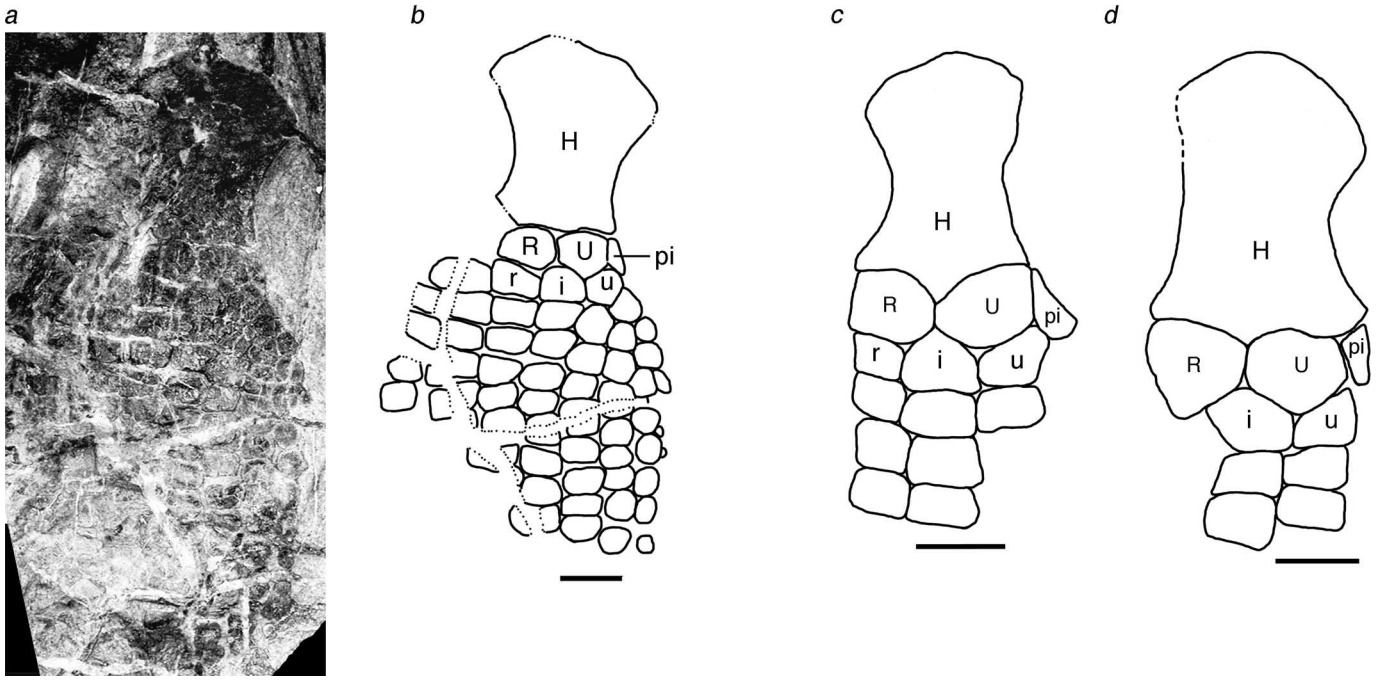
Ichthyosauria (De Blainville, 1835)
Ophthalmosauria (Motani, 1999*b*)
Genus *Platypterygius* (Huene, 1922)
Type species *Platypterygius platydactylus* (Broili, 1907), from the Aptian of Germany.

DIAGNOSIS: Epipodium four bones wide, with the radius and ulna located medially and accessory digits on either side; extreme hyperphalangy, forefin eight or more digits wide (Wade 1984; Bardet 1989).

REFERRED SPECIMEN: *Platypterygius* sp. UALVP 45636 (Fig. 1).

DESCRIPTION: This partial specimen is a large ichthyosaur, lying

Fig. 2. Comparative illustration of the paddles of some common *Platypterygius* species, right forefin, ventral view. (*a*) Photo of UALVP 45636. (*b*) Line drawing of UALVP 45636. Dotted lines represent mineral-filled cracks in the rock. (*c*) *P. americanus* (modified from McGowan 1972*b*). (*d*) *P. australis* (modified from Wade 1984). H, humerus; i, intermedium; pi, pisiform; R, radius; r, radiale; U, ulna; u, ulnare. Scale bar = 30 mm.



on its right side. The mandibular and cranial fragments, cervical and anterior thoracic vertebrae, ribs, and left forefin are poorly preserved. Some portions of the cranial region are also preserved as natural molds although the resolution is too poor to distinguish specific bones. The pectoral girdle and the right forefin are well enough preserved to merit a description and to be of use in the classification of the specimen.

Pectoral girdle: The interclavicle is absent. The clavicles are prominent relative to the rest of the pectoral girdle. Although the left clavicle is incomplete, the right one is almost entirely preserved. It forms a broad wing-like structure ventrally, thinning into a splint-like element as it curves dorsally. The coracoids are not in articulation and are damaged to the point where their shape is not discernible. The scapula is elongate, as is typical of post-Triassic ichthyosaurs (Sander 2000), and is slightly expanded proximally. Although it widens distally, the distal end is obscured by the fragmentary state of the coracoid.

Humerus: The humerus is shorter than the scapula. It is slightly more expanded proximally than distally, and there is little difference in the degree of curvature between the radial and the ulnar edge. Topographical features of the bone (trochanters, etc.) are not preserved. There are four distinct articular facets for the epipodials, the third from the preaxial margin being the largest and presumably articulating with the ulna, with the second from the preaxial margin being the second largest and articulating with the radius (Fig 2*a*). The anterior articular facet is steeply angled and is larger than the posterior one.

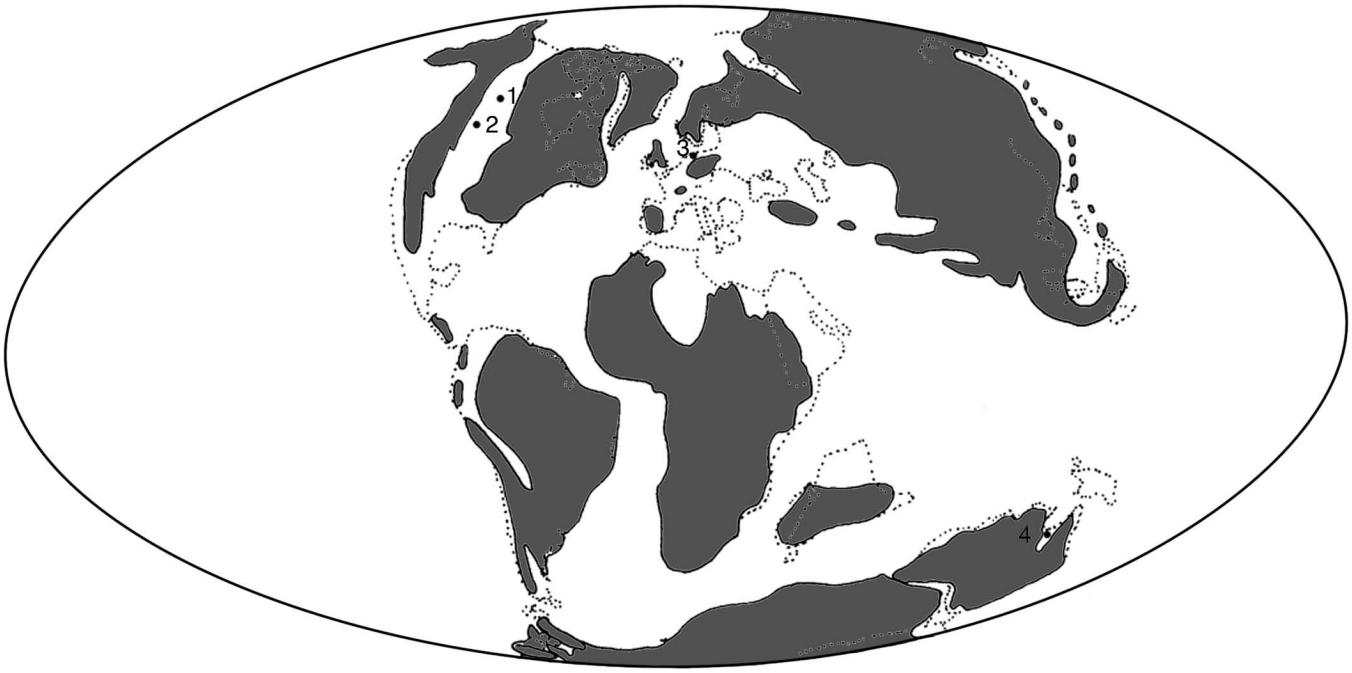
Epipodium: The epipodium consists of four elements. The pisiform (the posterior element) is a mid-sized bone, which is rounded anteriorly but has a flat posterior edge. It articulates with the humerus, ulna, and ulnare. The ulna is equal in length to the radius, but is much wider. Its posterior edge is concave to articulate with the pisiform. It is round in shape, except for a distinct corner postero-distally. The radius is thick and rounded posteriorly, but tapers anteriorly and becomes more rectangular. The most anterior element is not preserved.

Mesopodium and phalanges: The mesopodium, including the radiale, intermedium, and ulnare, is at least five elements wide. The radiale is a rectangular element that tapers posteriorly and is the largest element in the mesopodium. The intermedium is roughly pentagonal, with an elongate posterior margin. The ulnare is the smallest element in the mesopodium and is isodiametric. At its widest point, the paddle is more than seven digits wide, but the exact width is difficult to determine because of disassociation of the phalanges along the anterior edge. The phalangeal elements in the first few rows are narrow and rectangular, but become rounded to polygonal distally. The distal end of the paddle is disarticulated.

Discussion

UALVP 45636 is consistent with *Platypterygius* in having a very long, broad paddle produced by the cumulative effects of both extreme hyperdactyly and hyperphalangy. Wade (1984) had originally proposed that the presence of four bones in the epipodium be used to diagnose the genus. We consider

Fig. 3. Location of several *Platypterygius* finds mentioned in the text, imposed on a Cretaceous palaeogeographical map (modified from Scotese 2001). 1, Hay River locality (UALVP 45636); 2, *P. americanus*; 3, *P. hercynicus*; 4, *P. australis*.



this character valid providing that the two largest elements, presumed to be the radius and ulna, are medial and are not the smaller intermedium, as in *Brachypterygius*. The ulnar facet is the most pronounced, rather than the radial facet as in *Caypullisaurus* Fernández, 1997 (Fernández 1997; Motani 1999*a*). *Platypterygius* has also been described by various authors as having a stout humerus that is not expanded distally (Bardet 1989; Maisch and Matzke 2000).

The number of epipodial elements that contact the humerus, as well as certain features of the skull, are used to define species (Wade 1990). In *P. australis*, the pisiform and the lageniform, as well as the radius and the ulna, may articulate with the humerus compared to *P. americanus*, in which only the radius, ulna, and pisiform make contact (Fig. 2) (McGowan 1972*b*; Wade 1984). The cranial region of UALVP 45636 is too poorly preserved to allow a positive specific diagnosis; however, the presence of four articular facets on the humerus is consistent with both *P. hercynicus* Kuhn (1946) from the Aptian of Germany and *P. australis* (McCoy 1867) from the Albian of Australia, but not with *P. americanus* (Wade 1990).

Platypterygius was a large, free-swimming animal that probably fed on pelagic prey (Kear et al. 2003), and as such would be expected to have a cosmopolitan distribution similar to other ichthyosaurian genera (Sander and Mazin 1993). At the genus level, this prediction is indeed borne out (Fig. 3), however, species have historically appeared to be much more localized in their distribution patterns. This new find does not support the pattern of species-level provinciality, as it is possible that the Hay River ichthyosaur represents a European taxon.

UALVP 45636 is clearly distinct from *Platypterygius americanus*, and thus, this find demonstrates that there were at least two members of the genus living in the Western Interior Seaway during the Cretaceous. The interspecifc relationships within *Platypterygius* have never been examined, and the genus is in need of revision, so it is currently unknown how important paddle morphology is in indicating broad-scale evolutionary trends within the genus.

Conclusion

Prior to this discovery, all *Platypterygius* material from North America was referred to the species *P. americanus*. UALVP 45636 is more similar to European and Australian species based on forefin construction; although poor preservation of the skull material prevents a definitive referral to a species. This find is important in that it increases the number of ichthyosaurian taxa known from North American Cretaceous deposits to three, suggesting that the Western Interior Seaway supported a larger ichthyosaur fauna than was previously acknowledged. This find also overturns the notion of provinciality in Cretaceous ichthyosaur species distribution and suggests that existing observations of non-overlapping species distribution might be a taxonomic artifact exacerbated by the limited number of complete specimens.

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