

Review

Cretaceous Ichthyosaurs: Dwindling Diversity, or the Empire Strikes Back?

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Abstract: Recent descriptions of new taxa and recognition of survivorship of Jurassic genera across the Jurassic–Cretaceous boundary bring the total number of Cretaceous ichthyosaur genera to eight. Taxa currently known from the Cretaceous include *Ophthalmosaurus*, *Caypullisaurus*, *Aegirosaurus*, *Platypterygius*, *Maiaspondylus*, *Athabascasaurus*, *Sveltonectes*, and *Acamptonectes*. This review summarizes the occurrence of all Cretaceous genera. A discussion of morphological diversity demonstrates the different, though overlapping, ecological niches occupied by the different taxa, while the comparison of phylogenetic hypotheses shows the problems inherent in understanding the evolutionary relationships between Cretaceous genera. The Late Jurassic radiation indicated in the competing phylogenetic hypotheses may correlate with the opening of the Atlantic Ocean or additional dispersal routes established by the breakup of Gondwana. Inclusion of the stratigraphically oldest *Platypterygius* species may aid in resolving these evolutionary relationships.

Keywords: Jurassic; Cretaceous; Ichthyosauria; ecological niche; phylogeny

1. Introduction

Ichthyosaur fossils have been found on all continents [1], and range in age from Late Triassic–early Late Cretaceous [2]. During this time, ichthyosaur diversity was thought to be greatest in the Middle Triassic, lower in the Jurassic with a peak in the Liassic, but dwindled to a single genus, *Platypterygius*, in the Cretaceous [3]. Low diversity in the Cretaceous was also noted by Mazin *et al.* [4], though Bardet [5,6] thought that additional genera were present.

Recent finds have shown that *Platypterygius* was not the only Cretaceous genus. Five genera are now known to occur only in the Cretaceous—*Platypterygius* [2,7], *Maiaespondylus* [8], *Athabascasaurus* [9], *Sveltonectes* [10], and *Acamptonectes* [11]. In addition, several Jurassic genera have been shown to extend into the Cretaceous, contradicting the end-Jurassic extinction hypothesis for ichthyosaurs and further increasing ichthyosaur diversity [12]. Previous reviews on Cretaceous ichthyosaur occurrences (e.g., [6,13]) predate the recent interest generated by these new discoveries. As a result, a review of Cretaceous ichthyosaur occurrences is timely. Here, this review is combined with a discussion of ecological niches as determined by tooth morphology, and the current phylogenetic theories (and thus, evolutionary hypotheses) for the last known members of the Ichthyosauria.

2. Results and Discussion

2.1. Ichthyosaur Genera in the Cretaceous

2.1.1. *Platypterygius*

The genus *Platypterygius* was the first (and until recently, sole) ichthyosaur known from the Cretaceous, and is a geographically widespread and geologically long-lived genus. Its status as a wastebasket taxon has been noted by many authors [11]. Previously, it was thought that all members of this group may eventually be synonymized into fewer species [14], or that they may belong to a single supraspecific taxon [5]—this is in contrast to the more recent theory that the genus may eventually be split into additional genera, supported by the morphological disparity noted by Fischer [15]. Indeed, the genus as it currently stands may be polyphyletic [9–11]. Pending further revision, eight species of *Platypterygius* are discussed here: five previously recognized by McGowan and Motani [2], *Platypterygius hauthali*, *Platypterygius platydactylus*, *Platypterygius australis*, *Platypterygius americanus*, and *Platypterygius campylodon*; *Platypterygius hercynicus*, synonymized with *P. campylodon* by McGowan and Motani [2], but considered a separate valid species by Kolb and Sander [16]; an additional species from South America not considered in McGowan and Motani's [2] extensive review, *Platypterygius sachicarum*; and *Platypterygius ochevi*, a species erected subsequent to McGowan and Motani's [2] review by Arkhangelsky *et al.* [17].

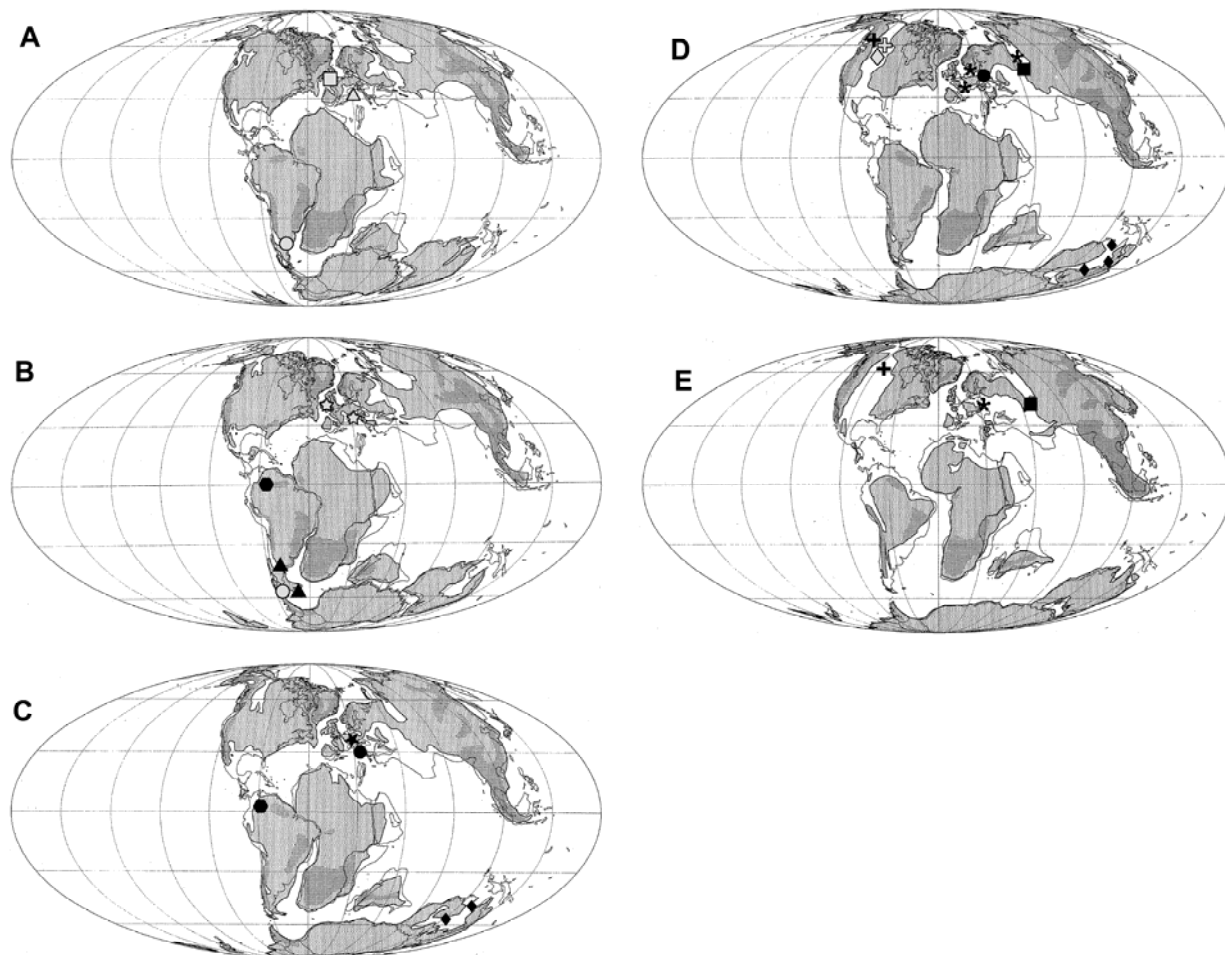
Platypterygius hauthali—Originally described as *Myobradypterygius hauthali*, von Huene [18] erected this South American ichthyosaur on forelimb material from the Barremian [19] of Argentina (Figure 1)—McGowan [13] referred the specimen to the genus *Platypterygius*. McGowan and Motani [2] retained the species, but thought it might prove synonymous with the contemporaneous *Platypterygius platydactylus*. However, Fernández and Aguirre-Urreta [19] undertook a revision of the holotype material, and considered it a valid species based on its carpal pattern. Hauterivian-Barremian occurrences of this species have been reported in southern-most Chile [20,21], but descriptions are currently limited to a single forefin considered *Platypterygius* sp [22]. Description of this relatively complete material may aid in distinguishing the two contemporaneous South American species, the holotypes of which do not share comparable elements.

Platypterygius platydactylus—*Platypterygius platydactylus* was first described by Broili [7] from the Aptian of Germany (Figure 1), and is the type species for the genus *Platypterygius*. Unfortunately,

the holotype was destroyed during World War II [2], and additional material for this species has not yet been reported.

Platypterygius australis—Australia’s species of *Platypterygius*, *Platypterygius australis*, include the best preserved, most abundant, and most complete remains of this genus [23]. Originally described in the nineteenth century from the Albian of Queensland [24,25], the erection of this species on non-diagnostic material has led to confusion surrounding the taxonomic identity of Australian specimens (as summarized—and resolved—by Zammit [26])—*Platypterygius marathonsensis* [27] and *Platypterygius longmani* [28] have been synonymized with this taxon [2,13,29]. Remains attributable to this species have also been reported from the Aptian–Albian of South Australia and the Northern Territory [29] (Figure 1).

Figure 1. Cretaceous ichthyosaur occurrences for the (A) Berriasian-Valanginian; (B) Barremian-Hauterivian; (C) Aptian; (D) Albian; and (E) Cenomanian. Base maps from Smith *et al.* [30]. Symbols: *Acamptonectes densus*, grey star; *Aegirosaurus leptospondylus*, grey triangle; *Athabascasaurus bitumineus*, grey diamond; *Caypullisaurus bonapartei*, grey circle; *Maiaspondylus lindoei*, grey ‘plus’ symbol; *Ophthalmosaurus* sp., grey square; *Platypterygius americanus*, black ‘plus’ symbol; *Platypterygius australis*, black diamond; *Platypterygius campylodon*, black asterisk; *Platypterygius hauthali*, black triangle; *Platypterygius hercynicus*, black circle; *Platypterygius ochevi*, black square; *Platypterygius platydactylus*, black star; *Platypterygius sachicarum*, black hexagon.



Platypterygius campylodon—Originally referred to *Ichthyosaurus*, *Platypterygius campylodon* was first described in 1846 from Cambridge, UK [31]. The brief type description was followed by a slightly longer report later in the same year [32]. This species is now known from the Albian-Cenomanian of England [33], France [6], and Russia [2,34,35], and the Cenomanian of Germany [36] (Figure 1). However, the taxonomy of several Russian species is uncertain—Storrs *et al.* [35] provisionally retained *Platypterygius bedengensis*, *Platypterygius birjukovi*, *Platypterygius bannovkensis*, and *Platypterygius kiprijanoffi*, while McGowan and Motani [2] considered all four taxon *nomen dubium* and synonymized the latter two taxa with *P. campylodon*. The revision of McGowan and Motani [2] is followed here as (a) Storrs *et al.* [35] were uncertain regarding the validity of *P. bannovkensis*, *P. bedengensis*, and *P. birjukovi* holotypes for taxonomic diagnosis, and (b) McGowan and Motani [2] demonstrated that the characteristic features of *P. kiprijanoffi* are not diagnostic.

Platypterygius americanus—*Platypterygius americanus* was first described from the upper Albian [23] of Wyoming [37]—originally described as a new genus, *Myopterygius*, it was later referred to *Platypterygius* [13]. It also occurs in the Lower Cenomanian of Wyoming [23,38] (Figure 1).

Platypterygius hercynicus—Though *Platypterygius hercynicus* was originally described in 1946 [39], it was synonymized with *P. platydactylus* [2] before being resurrected by Kolb and Sander [16]. Resurrection of the species was further supported by Fischer [15], based on the cranial characters of a referred specimen. The species occurs in the Aptian and upper Albian sediments of Lower Saxony, Germany, and north-western France, respectively [15] (Figure 1).

Platypterygius sachicarum—*Platypterygius sachicarum* is the second species of *Platypterygius* known from South America. The holotype, consisting of a nearly complete skull, was identified as being derived from the Barremian-Aptian Paja Formation of Colombo [40] (Figure 1). Cranial features suggested a closer affinity with the North American species than the Australian or Eurasian forms [40], but this is yet to be tested in a phylogenetic analysis. Currently, the holotypes of the two South American *Platypterygius* do not share comparable elements, and thus, may eventually be synonymized—however, Fernández and Aguirre-Urreta [19] point out that there is a conspicuous difference in size.

Platypterygius ochevi—Described by Arkhangelsky *et al.* [17], *Platypterygius ochevi* was erected on features of the forelimb, specifically the large size of the humeral facet for the extra zeugopodial element anterior to the radius—however, the taxonomic utility of this character requires assessment (an opinion shared by Fischer *et al.* [11]). It is provisionally retained here pending re-examination of the material. The remains of this species of *Platypterygius* occur in the Albian-Cenomanian strata of the Voronezh Region, Russia [17] (Figure 1).

Additional *Platypterygius* remains—Several other occurrences attributed to *Platypterygius* also need to be considered. This includes Lydekker's [41] *Ichthyosaurus indicus*, which was erected on fifteen associated vertebrae from the Cretaceous of India. This material was considered indeterminate by McGowan and Motani [2]—despite this, Underwood *et al.* [42] tentatively referred teeth to Lydekker's [41] species, placing the material in *Platypterygius indicus*. The teeth were placed in this genus based on similarity to *Platypterygius*, and the proximity to Lydekker's [41] locality. However, the tooth form in other Cretaceous ichthyosaurs, such as *Brachypterygius*, is similar to *Platypterygius* [8]—thus, a more detailed comparison is required to conclusively show the teeth can be referred to *Platypterygius*.

Specimens from Italy [43], New Zealand [44], and Bavaria [45] have also been referred to *Platypterygius*. Bardet *et al.* [45] considered the robustness of the Bavarian remains (and the inferred large size) and tooth morphology consistent with *Platypterygius* sp. However, the fragmentary specimens from Italy and New Zealand were assigned to *Platypterygius* in part because no other Cretaceous genus was known at the time of discovery. Further examination may provide additional support for referral to this genus, particularly for the largest, well-preserved rostral fragment figured by Sirotti and Papazzoni [43].

Each species of *Platypterygius* appears to be endemic to a given region (Figure 1), though this may in part be due to geographic criteria being used in taxonomic assignment, e.g., [44]. However, *Platypterygius* remains have been described from both North America and Australia that appear inconsistent with the endemic species. The specimens described by Maxwell and Caldwell [46] and Adams and Fiorillo [47] appear to show more similarity with the European or Australian forms of this genus—however, while the forefin figured by Adams and Fiorillo [47] is consistent with the forelimbs of *P. hercynicus* and *P. australis*, the atlas-axis complex lacks the suture at the base of the neural canal exhibited by these two species [48,49]. Choo [50] described a fragmentary humerus that was more comparable with European rather than Australian or North American forms. Due to the incomplete nature of the material, the affinities of this humerus are uncertain—however, if this interpretation is upheld, the potential implication of this find is the possibility of two ichthyosaur dispersal events into Australia, as mentioned by Kear [51].

2.1.2. *Maiaspondylus*

Maiaspondylus consists of a single species, *Maiaspondylus lindoei*, recovered from the Albian of the Northwest Territories, Canada [8] (Figure 1). The holotype of *M. lindoei* was found associated with ichthyosaur remains referred to *Platypterygius* [46], indicating that the two genera occurred together.

2.1.3. *Athabascasaurus*

Athabascasaurus consists of a single species, *Athabascasaurus bitumineus*, described from the earliest Albian of Alberta, Canada [9] (Figure 1). The holotype consists of a nearly complete skull and partial postcranial skeleton that was collected in 2000 [9]. *Platypterygius* remains have been reported from the same formation containing *Athabascasaurus* [9].

2.1.4. *Sveltonectes*

Described from the upper Barremian of western Russia (Figure 1), the genus *Sveltonectes* contains a single species, *Sveltonectes insolitus*, erected on a nearly complete skeleton [10]. As a result, the authors have been able to identify many unique features, some of which relate to diet and swimming style that were also used to establish the generic name (see Etymology of Fischer *et al.* [10]).

2.1.5. *Acamptonectes*

The most recently described Cretaceous genus, *Acamptonectes*, is monotypic, only containing the species *Acamptonectes densus*. It occurs in the basal Hauterivian—upper Hauterivian of north

Yorkshire, UK, and Lower Saxony, Germany [11] (Figure 1). Specimens attributable to the genus have also been identified from the Albian-Cenomanian of Cambridge, UK, but show features that differ from the already described species [11]. The preserved section of the snout is slender, exhibiting one of the lowest snout depth ratios in all known ophthalmosaurid ichthyosaurs, though the relative length of the rostrum is unknown [11]. Together with the tooth morphology described by Fischer *et al.* [11], this may indicate a different diet and thus lifestyle to previously known Cretaceous ichthyosaurs.

2.1.6. Ichthyosaurs Crossing the Jurassic–Cretaceous Boundary

Ophthalmosaurus—*Ophthalmosaurus* is a well-known Jurassic ichthyosaur. The extension of this genus into the Cretaceous has been suggested by several authors [2,52,53], but a recent study [11] considers these reports to be ambiguous as the elements may belong to other genera now known from the Cretaceous. However, the same study refers a basioccipital and humerus from the Berriasian of the UK (Figure 1) to cf. *Ophthalmosaurus*, indicating survival across the Jurassic-Cretaceous boundary.

Caypullisaurus—Previously thought to be limited to the Upper Jurassic [1], the monotypic genus *Caypullisaurus* has since been shown to extend into the Berriasian (Lower Cretaceous) of Argentina [54] (in Reference [19]) (Figure 1). Additional material that may be attributed to *Caypullisaurus* has been recovered from the Hauterivian-Barremian of Chilean Patagonia, and occurs with *P. hauthali* [20,21].

Aegirosaurus—the anterior part of a rostrum is the only record of *Aegirosaurus* from the Cretaceous. Found in late Valanginian strata of southeastern France (Figure 1), the snout was referred to this genus based on four characters: anterior-posterior order in which the cranial bones emerged; slenderness of the snout; tooth morphology; and tooth density [55]. This species was previously only known from the upper Jurassic [2]. Like *P. platydactylus*, holotype material was destroyed during World War II (though syntype material, thin sections of the teeth, survived, [56]), but comparable material was referred to the genus at the beginning of the 21st Century [57].

Additional Genera—In addition to *Ophthalmosaurus*, *Caypullisaurus*, and *Aegirosaurus*, *Brachypterygius* may also have crossed the Jurassic–Cretaceous boundary. Ensom *et al.* [58] redescribed and dated an indeterminate ichthyosaur specimen that had affinities with *Brachypterygius*. Pending comparison with additional Cretaceous genera (such as *Maiaspondylus*), this material indicates that another Jurassic ichthyosaur may have survived into the Cretaceous.

2.2. Diversity and Evolution of Cretaceous Ichthyosaurs

The review of Cretaceous ichthyosaur occurrences demonstrates that five genera are currently known only from the Cretaceous, while at least three (and possibly four) additional Jurassic genera cross the Jurassic-Cretaceous boundary. The majority of this increased diversity has been recognized only recently (e.g., Maxwell and Caldwell [8] (p. 1043) state that “All Cretaceous ichthyosaurs are referred to a single genus, *Platypterygius* Huene, 1922”), and dispute the hypothesis of low taxonomic diversity within the Ichthyosauria prior to their extinction, though Cenomanian occurrences remain extremely rare. Further, some faunas include ichthyosaur fossils referred to two genera (e.g., *Platypterygius* and *Maiaspondylus*, [8])—this may have been possible through different adaptations (*i.e.*, morphological diversity) that allowed the ichthyosaurs to exploit different ecological niches.

One feature that has been linked to diet, and thus ecological niche, is tooth form. Massare [59] proposed seven predatory guilds (condensed to six in Massare [60]) based on tooth morphology and tooth wear in Jurassic marine reptiles. However, placing some Cretaceous ichthyosaurs within this framework is difficult when (a) their teeth exhibit characters that are present in several different guilds (e.g., [55]), or (b) when inferences of diet cannot be supported by stomach contents [10]. Despite these concerns, diet has been inferred for Cretaceous ichthyosaurs with some success. Fischer *et al.* [10] considered the slender, pointed teeth of *Sveltonectes* intermediate between the ‘pierce I’ and ‘pierce II/generalist’ guilds of Massare [59], thus inferring a diet of soft to very soft prey or small bony prey. *Aegirosaurus* exhibits tooth morphologies that are present in both the ‘pierce I’ and ‘pierce II/generalist’ guilds of Massare [59], but was most consistent with the ‘pierce II/generalist’ guild [55], indicating a diet of fleshy prey that lacked a hard exterior. As pointed out by Fischer *et al.* [55], this guild was previously restricted to some pliosauroids, plesiosauroids, and thalattosuchians, and *Aegirosaurus* was included within this guild on the provision that it likely fed on smaller prey than the other predators. The slender tooth crown with longitudinal ridges observed in *Acamptonectes* [11] and *Athabascasaurus* [9] may also correspond to the ‘pierce II/generalist’ guild of Massare [59], though the ridges in the latter are less prominent. The four ichthyosaurs considered probably impaled prey rather than grasping it, or, for *Sveltonectes*, used the teeth as a sieve [59].

Though previously considered edentulous [61], teeth are not firmly attached in *Ophthalmosaurus* and generally lost [2]. This genus has been described as having small, conical teeth [55,62] with a pointed apex bearing fine longitudinal ridges [63]. The size of the teeth suggests inclusion within Massare’s [59] ‘smash’ guild, while the crown morphology is consistent with the ‘general’ guild. This indicates a diet consisting of fleshy prey that may have contained some internal hard parts, but the method of prey capture may have been either grasping or impaling [60]. Similarly, *Caypullisaurus* is currently considered edentulous [64], though a single specimen figured by Fernández [65] has teeth in the anterior section of the jaws. The preserved teeth are described as having a similar shape to *Ophthalmosaurus*, and bear striations on the crown [65]. Apices of the teeth are not preserved. Thus, tooth morphology tentatively indicates a similar method of prey capture and diet to *Ophthalmosaurus*—however, the edentulous nature of most *Caypullisaurus* individuals suggests either ontogenetic variation in diet [65], or post-mortem loss of teeth resulting from weak attachment to the jaws (as in *Ophthalmosaurus*).

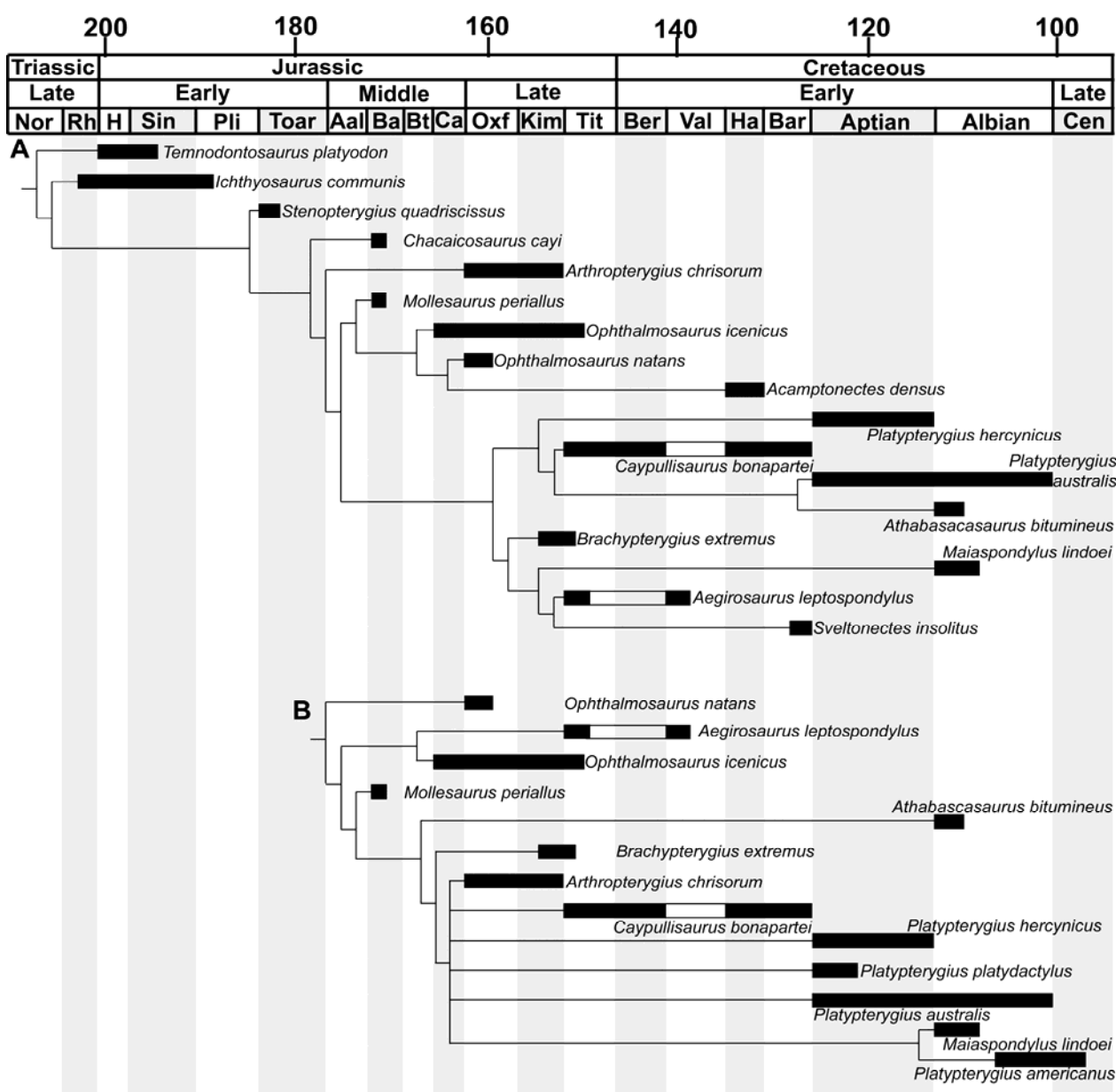
Platypterygius (and *Maiaspondylus*, which as a similar tooth morphology but more weakly developed enamel ornamentation, [8]) is more complex. The large robust teeth of *P. campylodon* were figured as an example of the ‘smash’ guild that fed on soft prey with some internal hard parts [59,60], and the tooth form described by Fischer [15] for *P. hercynicus* also corresponds to the morphology of this guild. However, as discussed by Fischer *et al.* [10], stomach contents of *P. australis*, which shares the ‘smash’ guild tooth morphology [66], indicated a less restricted diet that included scavenging and opportunistic feeding on vertebrates [67]. In addition, Kear and Barrett [68] hypothesized that the robust teeth of *P. campylodon* may have been an adaptation to feed on hard-shelled invertebrates, which would place this species within the ‘crunch’ guild of Massare [60]. Placing the genus *Platypterygius* in the ‘crunch’ guild would also be more consistent with the stomach contents described from *P. australis*. However, the slender, moderately long teeth described for *P. americanus* by Nace [38] are difficult to place in Massare’s [59] guilds, but may correspond to the ‘smash’ or

‘general’ guilds. This suggests that either prey preference varies between species of *Platypterygius*, or the teeth of *Platypterygius* can be adapted to several different potential diets and prey handling strategies. The tooth form in *Maiaspondylus* is similar to *Platypterygius* [8], and is thus consistent with the ‘smash’ guild of Massare [60]—however, stomach contents, if discovered, may indicate a less restricted diet, as for *P. australis*. Regardless of the prey consumed, all but one of the predator guilds considered for *Platypterygius* and *Maiaspondylus* use the same handling technique—grasping prey rather than impaling it (the general guild is the only one considered that was thought to incorporate impaling rather than grasping, Massare [60]). Thus, while there is some dietary overlap between Cretaceous ichthyosaurs, the differences in tooth morphology would also have likely allowed exploitation of different resources.

While the morphological diversity present in Cretaceous ichthyosaurs can no longer be denied, how this diversity evolved has not yet been investigated. Relationships between Cretaceous ichthyosaurs have only recently come under scrutiny [9–11]. Results vary between analyses, though the minor differences exhibited by Fischer *et al.* [10] and Fischer *et al.* [11] possibly result from the inclusion of additional taxa (*i.e.*, *Ophthalmosaurus natans* and *Acamptonectes*). The only consistent result found in these analyses is that the genera *Ophthalmosaurus* and *Platypterygius* as currently defined are polyphyletic, and thus a reanalysis of these two genera is warranted [9,11]—however, the additional taxa included within the two genera varies (Figure 2). In Fischer *et al.* [11], the two *Ophthalmosaurus* species were separated by *Acamptonectes*, and were located at the crown of one clade. The relationship between *Ophthalmosaurus natans* and *Ophthalmosaurus icenicus* was more complicated in Druckenmiller and Maxwell [9]—*O. icenicus* and *Aegirosaurus* were recovered as sister taxa, and separated *O. natans* from the rest of the Ophthalmosauridae. The difference here may in part result from the inclusion of the new taxon *Acamptonectes*. Druckenmiller and Maxwell [9] found a polytomy containing a *Maiaspondylus*-*P. americanus* sister-group, *P. australis*, *P. hercynicus*, *P. americanus*, *Caypullisaurus*, and *Arthropterygius*. In contrast, Fischer *et al.* [11] recovered a four-taxon clade where *Caypullisaurus* separated a *P. australis*-*Athabascasaurus* sister-relationship and *P. hercynicus*. This could be related to the exclusion of *P. platydactylus* in the study of Fischer *et al.* [11].

Tree topology varies greatly between the analyses (Figure 2). Druckenmiller and Maxwell [9] recover a ‘classic’ branching pattern with a crownward polytomy. Fischer *et al.* [11], on the other hand, splits the Ophthalmosauridae into two major radiations, the Ophthalmosaurinae and the Platypterygiinae, the latter containing two branches. Both phylogenetic hypotheses indicate a ghost lineage for *Platypterygius* extending into the Late Jurassic—either through the origin of *P. hercynicus* in the Kimmeridgian prior to the first appearance of *Caypullisaurus* [11], or *P. australis*, *P. platydactylus*, and *P. hercynicus* occurring with the first appearance of *Caypullisaurus* in the Tithonian [9]. Inclusion of the oldest known *Platypterygius*, *P. hauthali* and *P. sachicorum*, may further change these results. The positions of several taxa also vary greatly between the phylogenetic analyses. Several taxa are recovered in both stem- and crown-ward positions (*e.g.*, *Athabascasaurus*, *Aegirosaurus*, and *Arthropterygius*). Different taxa also separate species of the problematic genus *Platypterygius*—*Athabascasaurus* and *Caypullisaurus* [11], or *Maiaspondylus*, *Arthropterygius*, and *Caypullisaurus* [9].

Figure 2. Stratigraphy-related phylogenetic trees. (A) modified from Fischer *et al.* [11]; (B) modified from Druckenmiller and Maxwell [9]. *Ichthyosaurus communis* and *Ophthalmosaurus icenicus* now extend into the Pliensbachian [69] and Tithonian [62], respectively. Black bars indicate species occurrence within an epoch. White bars indicate a species is not known from this epoch, but occurs in surrounding epochs. Abbreviations: Aal, Aalenian; Ba, Bajocian; Bar, Barremian; Ber, Berriasian; Bt, Bathonian; Ca, Callovian; Cen, Cenomanian; H, Hettangian; Ha, Hauterivian; Kim, Kimmeridgian; Nor, Norian; Oxf, Oxfordian; Pli, Pliensbachian; Rh, Rhaetian; Sin, Sinemurian; Tit, Tithonian; Toar, Toarcian; Val, Valanginian.



So, what do the divergent phylogenetic hypotheses tell us about the origins and evolution of Cretaceous ichthyosaurs? The radiation of *Platypterygius* [9] or the emergence of the Platypterygiinae [11] during the Late Jurassic could coincide with the opening of the Atlantic Ocean [70], or new dispersal routes through the breakup of Gondwana [71]. With the exception of the *Maiaspondylus*-*P. americanus* sister

relationship recovered by Druckenmiller and Maxwell [9], the phylogenetic positions of Cretaceous genera do not appear to correlate with stratigraphic position or proximity—for example, *P. australis* and *Athabascasaurus* were recovered as sister-taxa [11], yet are found in strata of the same age from different continents (Figure 1). Further, sister relationships were not recovered between *Platypterygius* species collected from similar localities (i.e., *P. hercynicus* and *P. platydactylus*, Druckenmiller and Maxwell [9]), suggesting the absence of phylogeographic structuring (i.e., widespread panmixia), and possibly dispersal between non-adjacent regions—this is perhaps unsurprising given that *Platypterygius* material inconsistent with the endemic species (i.e., most likely belonging to a non-endemic species) has been found in North America [46]. To more fully understand the origins and evolution of Cretaceous ichthyosaurs, the phylogenetic position of some of the stratigraphically oldest specimens (e.g., *P. hauthali* and *P. sachicarum*, the former of which contains a newly referred, complete specimen, Pardo Perez *et al.* [21]) needs to be investigated.

3. Conclusions

A total of eight genera are known from the Cretaceous—*Platypterygius*, *Maiaspondylus*, *Athabascasaurus*, *Sveltonectes*, and *Acamptonectes* are found only in the Cretaceous, while *Ophthalmosaurus*, *Aegirosaurus*, and *Caypullisaurus* cross the Jurassic-Cretaceous boundary. The different genera likely occupied different, though overlapping, ecological niches. This is supported by different tooth morphologies, indicating different diets, and sympatry of two genera (e.g., *Caypullisaurus* and *Platypterygius*, and *Maiaspondylus* and *Platypterygius*). Phylogenetic relationships between Cretaceous ichthyosaurs remain problematic, with tree topology varying between analyses. As a result, little can be stated with certainty regarding the radiation and dispersal of these ichthyosaurs, though the emergence of some forms in the Late Jurassic may have coincided with the opening of the Atlantic Ocean or the breakup of Gondwana. Inclusion of the stratigraphically oldest species (e.g., *Platypterygius hauthali* and *Platypterygius sachicarum*) may shed additional light on the evolution of the group.

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