The diversity of teleost fishes during the terminal Cretaceous and the consequences of the K/Pg boundary extinction event

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Abstract

The Late Cretaceous was a time of blossoming teleost diversification that came to a sudden restriction and partial termination during the extinction event at the Cretaceous–Paleogene (K/Pg) boundary. Among the dominant and diverse Late Cretaceous teleost groups prior to the K/Pg boundary event were certain pelagic Aulopiformes (e.g., Ichthyotringoidei and Enchodontoidei) and a large variety of basal Acanthomorpha whose relationships are difficult to determine. The skeletal record diminishes during the late Campanian and is low in the Maastrichtian and Paleocene, constituting the so-called 'Patterson's Gap'. Recent studies of fossil otoliths, however, have significantly increased the number of taxa recognised for this time inerval, but most of the putative extinct forms lack adequate calibration with otoliths found *in situ* in articulated skeletons. However, the otolith assemblages do confirm the presence of great morphological diversity among Aulopiformes and Acanthomorpha *incertae sedis* that became extinct at the K/Pg boundary. In the present review, we elucidate the effect of the K/Pg boundary from an otolith perspective and categorise extinct lineages and survivors. It is interesting to recognise that several of the surviving lineages are represented by groups that probably originated during the Late Cretaceous but were not particularly common up to the K/Pg boundary and began to expand rapidly and diversify during the early Paleogene. Such lineages probably took advantage to populate void ecospace that may have opened following the extirpation of previously dominant lineages. During the early Paleogene, the otolith record shows that the Ophidiiformes and perciforms s. lat. were the ones that diversified the most rapidly and became the most abundant, and in certain areas associated with the Gadiformes.

Introduction

The Late Cretaceous was a time of sustained diversification of bony fishes (e.g., Patterson, 1964, 1967; Cavin, 2008; Carnevale & Johnson, 2015; Poyata-Ariza & Martín-Abad, 2016). Numerous lineages of spiny-rayed fishes (Acanthomorpha) made their appearance in the fossil record from the Cenomanian onwards (see, e.g., Guinot & Cavin, 2018), suggesting that a major radiation took place at that time. Conversely, the time interval between the latest Cretaceous (Maastrichtian) and the early Paleogene (Paleocene) has been relatively meagre as far as the record of articulated fish skeletons is concerned; a pattern extensively discussed by Patterson (1993a). Patterson's comments have recently led Friedman et al. (2023) to refer to this time interval as 'Patterson's Gap' of teleost evolution. Therefore, 'Patterson's Gap' extends across a crucial time in Earth's history, namely the last of the 'big five' mass extinctions at the Cretaceous–Paleogene boundary (K/Pg extinction event). The K/Pg extinction event is generally believed to have been caused by the Chicxulub asteroid impact on Yucatán Peninsula at about 66 Ma, the largest documented extraterrestrial impact on our planet (e.g., Schulte et al., 2010; Lowery et al., 2019; Gulick et al., 2019). The impact is thought to have triggered a series of events of different duration ranging from few hours (mega-earthquake), to days (mega-tsunami, wild fires) to years, decades and periods of thousands of years (post-impact darkness, post-impact winter, disturbances of chlorophyll synthesis, partial collapse of food chains, acidic rain and ocean acidification, and reduction of biogenic carbonate sedimentation) (see discussion in Schwarzhans & Stringer, 2020, and references therein). In view of the paucity of articulated teleostean skeletons from the time interval represented by 'Patterson's Gap', the status of the teleost fauna prior to the K/Pg extinction event during the terminal Cretaceous and the effects of the extinction event itself on the bony fish fauna are not well understood (Friedman et al., 2023, and references therein).

However, there is another source of relevant data available for analysis and reconstructions of fossil bony fish faunas – otoliths. Otoliths had a relatively poor coverage across the Maastrichtian and Paleocene for a long time, but recent efforts have resulted in a comparatively
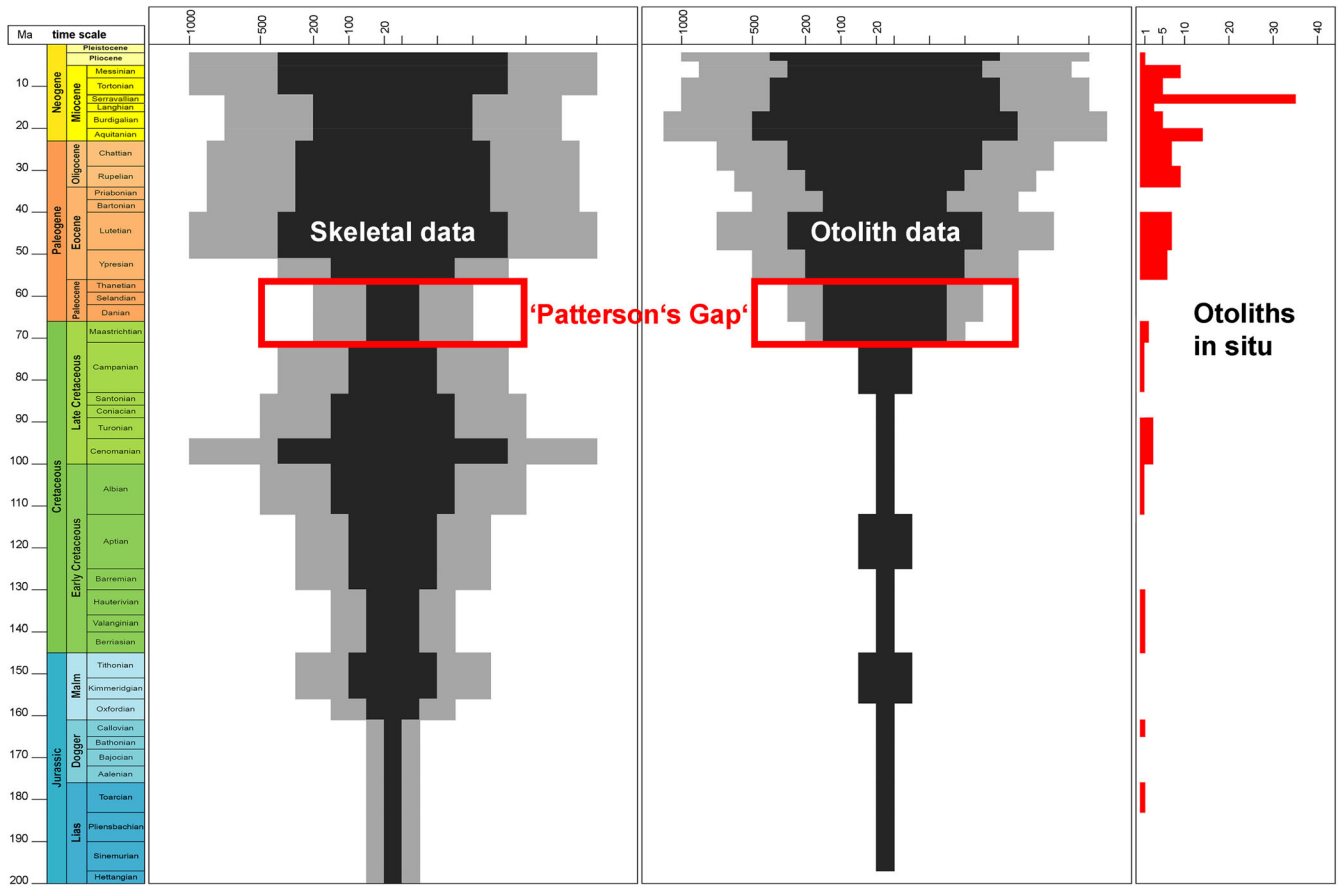
Figure 1. Bony fish diversity (genus level) estimates through time based on literature items available to the authors and updated from Schwarzhans et al. (2018a) for otoliths. Black bars represent counts and grey bars estimated upside considering ongoing research and a 50 per cent undiscovered margin.

dense dataset (Nolf & Stringer, 1996; Schwarzhans, 2010, 2012; Stringer et al., 2016, 2018, 2020; Schwarzhans et al., 2018a, b; Schwarzhans & Stringer, 2020; Schwarzhans & Jagt, 2021; Stringer & Schwarzhans, 2021; Stringer & Sloan, 2023). Consequently, when taking skeletal and otolith data into account, the meagre scenario evocated by 'Patterson's Gap' is no longer evident (Fig. 1). However, the use of otolith data for pre-Cenozoic reconstructions of teleost faunas comes with a major caveat; the taxonomy of isolated otoliths is based mostly on morphological comparisons with otoliths extracted from extant fishes. This practice becomes increasingly problematic with deep-time otoliths, for obvious reasons related to evolutionary changes or extinction of lineages. Therefore, calibration of isolated otoliths with otoliths found *in situ* in articulated skeletons is crucial in those deep-time finds, but unfortunately such finds are only rarely available (see Schwarzhans et al., 2018a; Fig. 1 here). Consequently, Cretaceous otoliths in particular must be interpreted using a rigorous quality control. On the other hand, otoliths are much more common in the fossil record and therefore allow for a more continuous assessment of teleost evolution in time and space. Moreover, otoliths and articulated skeletons have different taphonomic boundary conditions. The preservation of articulated skeletons depends on specific and rather rare taphonomic settings preventing the complete decay of the carcasses due to biological, chemical or physical factors. Preferential conditions for the fossilisation of articulated fish skeletons are, for instance, the presence of anoxic conditions on the sea floor, rapid sedimentation or mass mortality

events. Anoxic conditions on the sea floor favour fossilisation of neritic fishes and are disadvantageous for demersal taxa. In contrast, otoliths are thought to have mainly entered sediments through excretion of predators and scavengers having feasted on fish (Nolf, 1985; Schwarzhans, 2019). In addition, otoliths are primarily preserved in sedimentary rocks deposited under well-oxygenated conditions. Therefore, the fossil otolith record is dominated by small 'prey fish' and demersal fishes (Lin et al., 2019). In conclusion, the fossil otolith record provides an excellent complement to the record of fossil articulated skeletons, thereby allowing for a more complete understanding of the evolution of bony fishes and their faunal composition.

The purpose of the present study is to use the two complementary datasets relevant for extinct teleosts in order to elucidate the evolution and faunal composition of bony fishes during the Maastrichtian just prior to the K/Pg boundary extinction event and also assess the effects of the mass extinction event on teleosts, with particular emphasis on otoliths.

Filling 'Patterson's gap'

When Friedman et al. (2023) coined the expression 'Patterson's Gap', they also provided new data to complement those published by Patterson (1993a) and showed that a broad hiatus of knowledge still persisted. Because of the high information content of articulated fish skeletons, Friedman et al. (2023) exclusively discussed such finds and did not take the fossil otolith record into
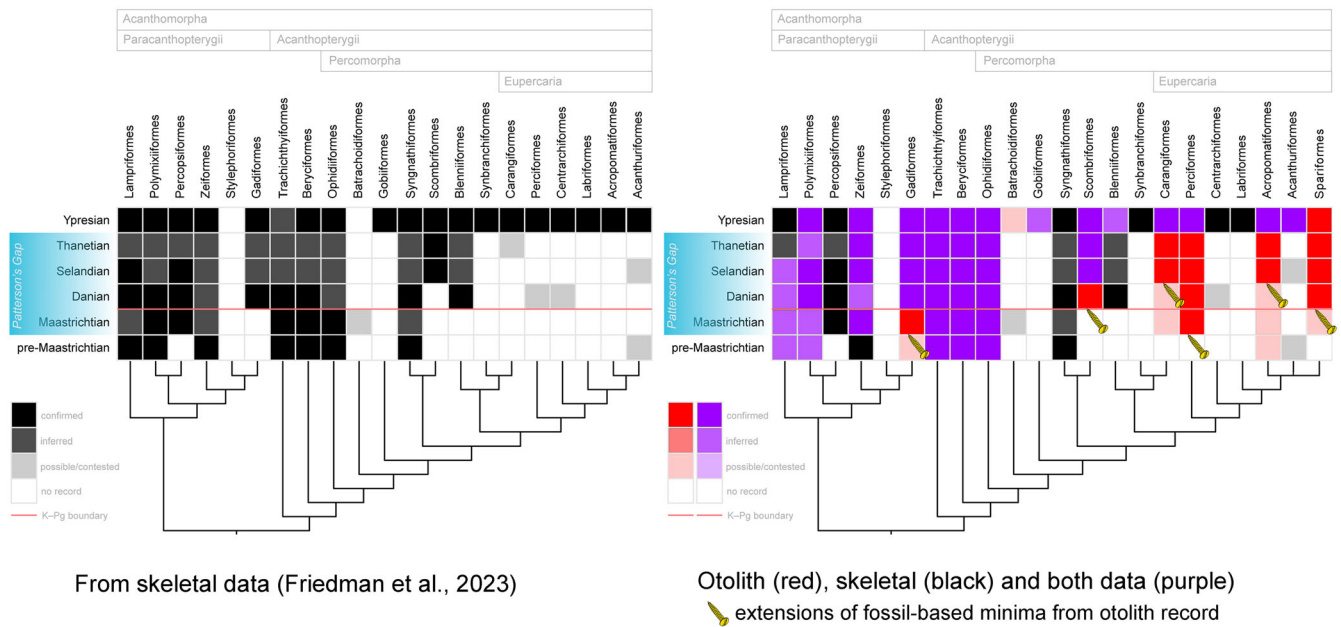
Figure 2. Summary of the fossil record of major acanthomorph lineages during the Late Cretaceous and early Paleogene; on the left-hand sideskeletal data from Friedman et al. (2023) are indicated; otolith data are shown on the right-hand side.

consideration. Those authors graphically summarised their assessment of acanthomorph skeletal findings across 'Patterson's Gap' in a figure reproduced here (Fig. 2, left-hand side). These findings are categorised in 'confirmed', 'inferred' and 'possible/contested' data, the last-named category indicating that the assessment of articulated skeletons in putative basal phylogenetic positions may be difficult or uncertain. We have here added information obtained from fossil otoliths onto their graph (Fig. 2, right-hand side), including the Spariformes (*sensu* Nelson et al., 2016) and using the same scheme of categories for the otolith finds (see discussion above). The combination of the two datasets shows how finds of articulated skeletons and otoliths complement each other, but that a high degree of overlap does also occur. The inclusion of the fossil otolith data results in a number of novel, earlier records among certain taxa such as the Gadiformes (at least since the Maastrichtian), Scombriformes (since the Danian), Carangiformes (at least since the Selandian), Perciformes (at least since the Maastrichtian), Acropomatiformes (at least since the Selandian) and Spariformes (at least since the Danian) (Fig. 2, right-hand side). Some of these findings result from the better fossilisation potential of otoliths of demersal fishes in comparison with articulated skeletons (Gadiformes), and others simply from the much denser record and higher abundance of otolith data compared to skeletal data. The details of these findings will be discussed below ('Case studies'). There are, however, also a number of groups that have been identified based on skeletons but have not been documented in the otolith record. The lack of fossil otolith data of the Percopsiformes, Synbranchiformes and Centrarchiformes is probably related to their occurrence in freshwater habitats and regions that have not been prospected for otoliths. Otoliths of the Syngnathiformes are generally very small and therefore rare in the fossil record. Finally, the Beloniformes and Labriformes inhabit settings with carbonate sedimentation that are less conducive for the fossilisation of isolated otoliths.

Case studies

The following is a discussion of selected groups of teleosts that were particularly abundant and/or diverse during the interval just prior to or after the K/Pg extinction event. We have selected groups with the emphasis on otolith-based data. Groups not specifically discussed here are listed in the summary. As far as skeleton-based data are concerned, reference is made to a variety of papers dealing with Late Cretaceous teleosts, such as Patterson (1964, 1967, 1993b), Cione & Prasad (2002), Fielitz (2004), Cavin (2008), Carnevale & Johnson (2015) and Friedman et al. (2023). The sequence of our discussion of the various groups below follows the systematic arrangement proposed by Nelson et al. (2016), unless indicated otherwise.

Siluriformes

The oldest fossil representative of the Ostariophysi known to date is *Tischlingerichthys viohli* from the Upper Jurassic (Arratia, 1997, 2018). Late Jurassic to Early Cretaceous is also the assumed origination age for the Otophysi (Chen et al., 2014). The earliest crown Otophysi are represented by the earliest Siluriformes from the Turonian–Santonian Adamantina Formation in Brazil (Alveş et al., 2016, 2019). The Otophysi are unique among teleosts in that the lapillus is the largest otolith (rather than the sagitta as in all other teleosts). The earliest ariid otoliths have been recorded from the upper Santonian of North America by Schwarzhans et al. (2018b), now identified as *Arius*? *danicus* Koken, 1891, indicating that it represents an ariid species of unknown relationships. A second ariid *incertae sedis* otolith-based species, *Arius*? *subtilis* Schwarzhans & Bratishko, 2011, was first recorded from the Maastrichtian. Both species are widely distributed during the Maastrichtian in Europe and North America and extend

apparently unaltered into the Paleocene in both regions (Schwarzhans & Stringer, 2020).

An occurrence of particular interest is that of *Vorhisia vulpes* Frizzell, 1965, an iconic lapillus otolith from the Maastrichtian of North America, assumed to represent a siluriform *incertae sedis* (see Schwarzhans & Stringer, 2020 and references therein). The analysis of δ^{18}O and δ^{13}C mapping across growth rings suggests that *V. vulpes* spawned in estuarine waters with otoliths of juveniles exhibiting brackish water signals, while adults occurred in shallow-marine environments (Carpenter et al., 2003). *Vorhisia vulpes* was very abundant in the Maastrichtian of North America, but unknown elsewhere. It represents one of the most prominent victims of the K/Pg extinction event among teleosts.

Aulopiformes (Fig. 3)

The Aulopiformes comprised highly diverse, specialised clades of pelagic predators during the Late Cretaceous; the extinct Ichthyotringoidei included the families Enchodontidae, Ichthyotringidae and Halecidae (Davis, 2010). The Ichthyotringoidea, Halecoidea and Enchodontoidea are currently placed within the Alepisauroidei (see Beckett et al., 2018). Otoliths of extant alepisauroids exhibit a highly derived morphological pattern that shows no similarities to that of *Apateodus* (Schwarzhans et al., 2018a); this contrasts with the putative alepisauroid relationship of ichthyotringoids suggested by Fielitz (2004) and Beckett et al. (2018). We therefore consider the Ichthyotringoidei to be an extinct aulopiform clade separate from the Alepisauroidei following the view expressed in Schwarzhans et al. (2018a) based on a morphological analysis of the otolith found *in situ* in *Apateodus corneti* (Forir, 1887).

The find of otoliths *in situ* in *Apateodus corneti* discovered by micro-CT-scanning (Schwarzhans et al., 2018a) proved crucial for the taxonomic calibration of these relatively common otoliths in the Santonian to Maastrichtian. Thus, many otolith-based taxa can now be attributed to *Apateodus* or at least to Ichthyotringoidei *incertae sedis* (Fig. 3) that had previously been linked to extant teleost groups. This serves as an example of how in the absence of *in situ* calibration with otoliths of extinct clades, isolated otoliths can be erroneously associated. The Ichthyotringidae and Enchodontidae constituted rich and diverse clades during the Late Cretaceous that became extinct at the K/Pg boundary, except for a few rare survivors of the Enchodontidae recorded on the basis of teeth from the lower Paleocene of Morocco (Patterson, 1993b). These finds, however, have been questioned as potentially reworked from underlying Cretaceous strata by Cavin (2001). Hopefully, future finds of additional otolith morphologies *in situ* can be associated with other ichthyotringoid or enchodontoid taxa.

In addition to the extinct ichthyotringoid and enchodontoid clades, another aulopiform clade, the Paraulopidae, occurs commonly in the otolith record from the Santonian onwards. The Paraulopidae comprises fishes of a smaller size and with a more generalised life habit in a lower position of the trophic chain. Today, this family contains but a single genus, *Paraulopus*, with 14 species (Nelson et al., 2016). Its otoliths are characterised by an upward and backward bend of the dorsal margin of the ostium; these are known to have remained nearly unaltered since the Maastrichtian or, possibly, the Campanian. Putatively related and extinct otolith-based taxa that occurred during the Late Cretaceous include *Archaulopus* and *Pseudotrichiurus* (Fig. 3). The Paraulopidae, and other aulopoid and alepisauroid clades that survived the K/Pg extinction event, were consequential for the

aulopiform radiation that occurred in the early Paleogene and led to the modern composition of this group.

Gadiformes (Fig. 4)

Compared to the Aulopiformes, the Gadiformes followed a completely different path in evolution. Until recently, they were only known from the Paleocene onwards. The earliest skeleton-based record is the still undescribed, informal genus 'Protocodus' from the Danian of western Greenland (Cohen, 1984; Friedman et al., 2023), which is here interpreted as a pan-Gadiformes (Fig. 4). A variety of gadiform otoliths were recorded from the Selandian of western Greenland by Schwarzhans (2004) and assigned to the extinct genera *Archaemacruroides* (here interpreted as a pan-Gadiformes), *Protocolliolus* (Gadidae) and *Palaeogadus* (Merlucciidae) (Fig. 4). It is likely that one of the isolated otolith-based taxa observed in the Selandian of western Greenland could be related to 'Protocodus'. Several taxa have been found with otoliths preserved *in situ*, including *Palaeogadus* by Fedotov (1976), *Rhinocephalus* by Schwarzhans et al. (2018a) and 'quasi in situ' in the early macrourid genus *Bobbitichthys* by Schwarzhans et al. (2021), thereby providing for a good calibration of isolated fossil gadiform otoliths (Fig. 4). Regardless even of this calibration, gadiform otoliths are indeed unmistakable because of their highly diagnostic and unique homosulcoid sulcus pattern (Schwarzhans, 1978).

Recent otolith studies have revealed the presence of multiple gadiform lineages present already during the latest Cretaceous and representing pan-gadiforms, gadids and merlucciids (Schwarzhans & Stringer, 2020; Schwarzhans & Jagt, 2021; Stringer & Schwarzhans, 2021; Stringer & Sloan, 2023), which occurred during the Maastrichtian and some possibly in the Campanian (Voigt, 1926; Schwarzhans & Stringer, 2020) (Fig. 4). Gadiform otoliths are mostly uncommon in the Maastrichtian except for *Dakotaichthys hogansoni* Schwarzhans & Stringer, 2020, which is the second most common species in the shallow, near-estuarine environments of the Fox Hill Formation in North Dakota, where *Vorhisia vulpes* is the most frequent. We conclude that the Gadiformes were already present during the Late Cretaceous, probably even since the Campanian, albeit probably with only a few lineages. They rapidly radiated and expanded during the Paleocene after the K/Pg extinction event and are therefore regarded as a group that benefitted from that event.

Ophidiiformes (Fig. 5)

The fate of the Ophidiiformes is very similar to that of the Gadiformes discussed above. Ophidiiforms are almost exclusively demersal fishes and therefore have a disadvantaged fossilisation potential as articulated skeletons. Indeed, articulated fossil ophidiiform skeletons are rare and therefore the find of an articulated skeleton of a stem-bythitid (*Pastorius*) in Campanian strata is remarkable (Carnevale & Johnson, 2015). In contrast, fossil ophidiiform otoliths are very common, particularly during the Eocene where they competed with perciforms in terms of abundance and diversity. Ophidiiform otoliths are relatively unmistakable and are uncommon during the Late Cretaceous, even though all the currently recognised families/lineages were represented, comprising the Ophidiidae with at least two lineages since the Maastrichtian (Schwarzhans, 2010; Schwarzhans & Stringer, 2020), Bythitidae since the Campanian (Voigt, 1926; Schwarzhans, 2010) and Dinematichthyidae since the latest Maastrichtian (Schwarzhans & Milàn, 2017) (Fig. 5).
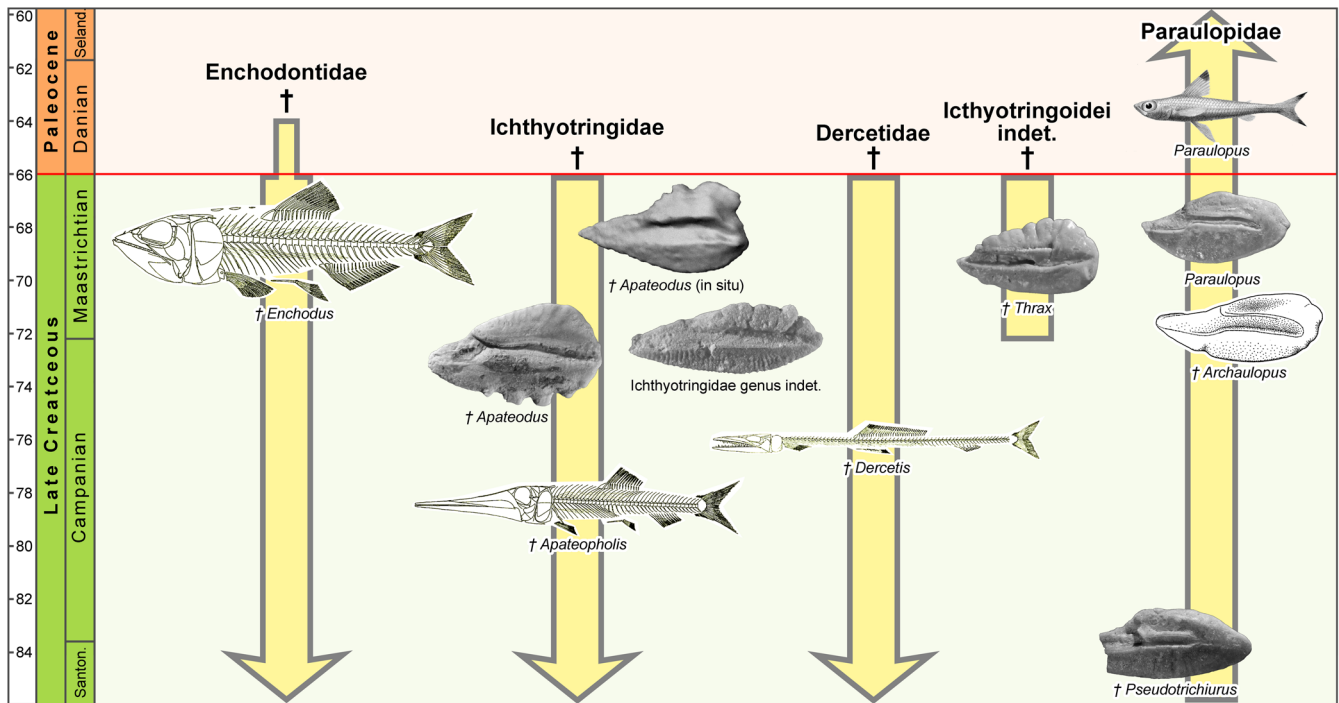
Figure 3. Stratigraphical ranges of selected lineages of the Aulopiformes across the Late Cretaceous and Paleocene. Skeletal reconstructions are based on Goody (1969); otoliths taken from Schwarzhans (2010), Schwarzhans et al., (2018a, b), Schwarzhans & Stringer (2020) and Schwarzhans & Jagt (2021).
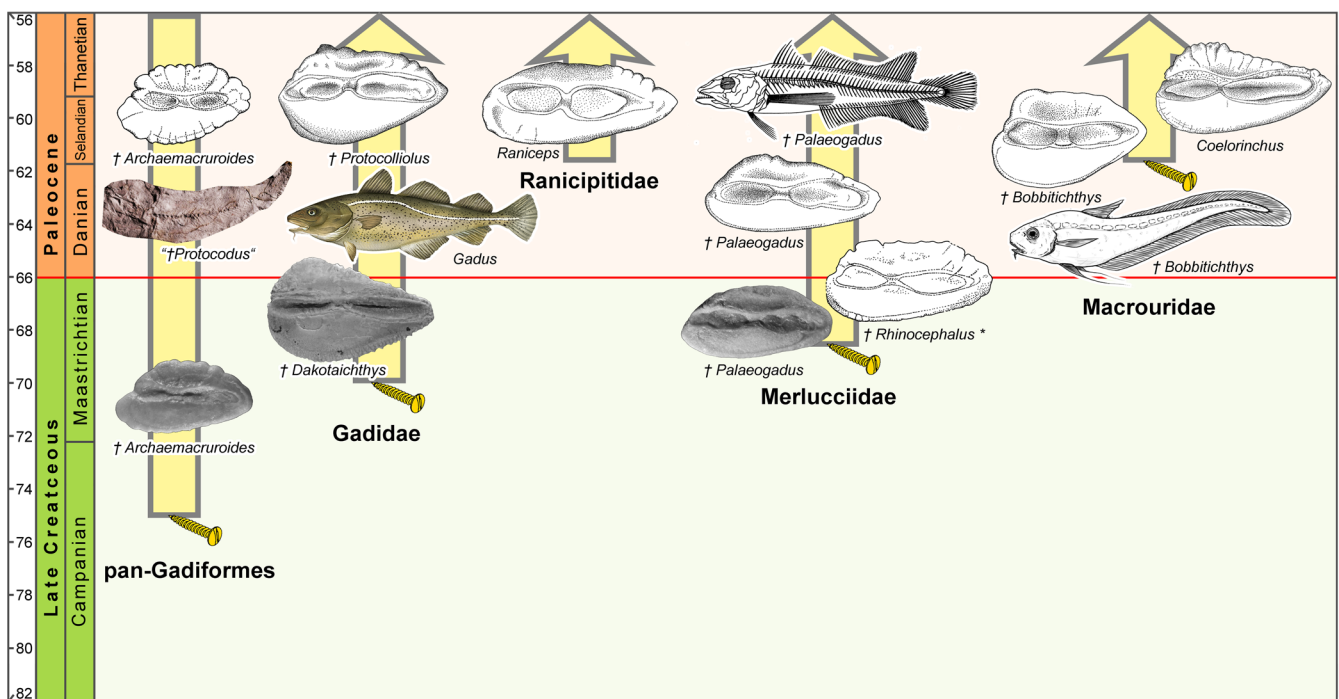

Figure 4. Stratigraphical ranges of gadiform lineages across the Late Cretaceous and Paleocene. Skeletal reconstruction is from Fedotov (1976); the reconstruction of *Bobbitichthys* is by Amanda McKeewer; the photograph of '*Protocodus*' is by G. Carnevale; otoliths are taken from Schwarzhans (2003, 2004), Schwarzhans & Stringer (2020) and Schwarzhans & Jagt (2021).
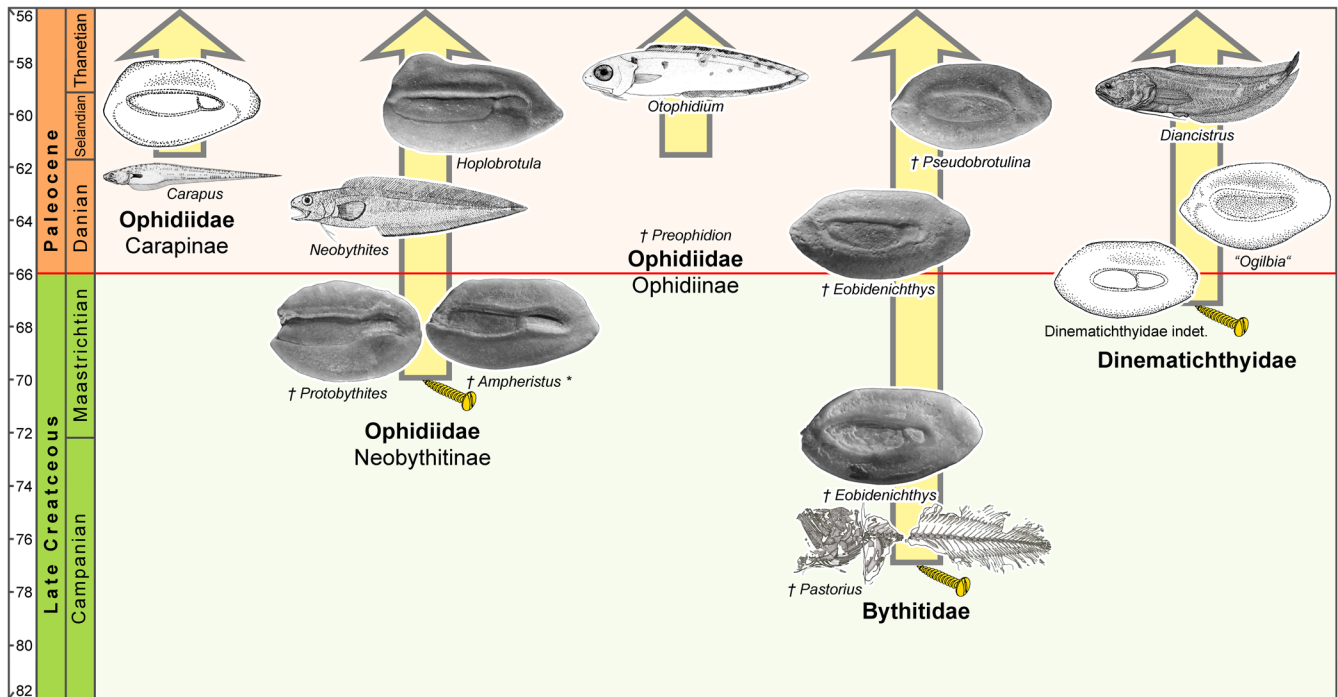
Figure 5. Stratigraphical ranges of ophidiiform lineages across the Late Cretaceous and Paleocene. Skeletal reconstruction is Carnevale & Johnson (2015); drawings of extant fishes are from Markle & Olney (1990), Nielsen (1995), Böhlke & Robins (1959) and Schwarzhans et al. (2005); otoliths are from Schwarzhans (2003) and Schwarzhans & Stringer (2020) and ongoing research.

We conclude that multiple ophidiiform lineages were already present in the Late Cretaceous, since at least the Campanian, and that all of the known extant families were in existence since the Maastrichtian, in some cases with more than one lineage per family. During the Paleocene (Danian to Selandian), additional ophidiiform lineages have been identified (Fig. 5). An explosive ophidiiform radiation took place during the late Paleocene and early Eocene. By the middle Eocene, as demonstrated by otoliths, Ophidiiforms competed with perciforms (s. lat.) in abundance and diversity (Schwarzhans et al., 2024).

Basal acanthomorpha (Fig. 6)

Under this informal category, we combine a relatively large number of highly specialised Late Cretaceous fishes, some of which are difficult to link to extant acanthomorph groups. From the skeletal record, we show examples of the genera *Aipichthys*, *Pycnosteroides*, *Berycopsis*, *Omosoma* and *Dinopteryx* (Fig. 6). They occur mostly in Cenomanian to Santonian rocks, rarely in Campanian ones, and have so far not been found in the Maastrichtian. We believe that their absence in the latest Cretaceous could be due to the lack of adequate data in 'Patterson's Gap'. These fishes have been associated with basal acanthomorph groups, and the Polymixiiformes and Lampriformes in particular (Patterson, 1964, 1967, 1993b; Davesne et al., 2016). However, it is likely that the Cretaceous acanthomorphs referred to polymixiiforms currently do not pertain to a natural group (see Murray, 2016) and should be in some cases regarded as acanthomorphs *incertae sedis* until a more comprehensive analysis of relationships becomes available.

Certain Late Cretaceous otoliths are also placed in this informal category as there are several highly derived/specialised morphologies that do not relate to any extant pattern and that became extinct at the K/Pg boundary. We here illustrate otoliths of the extinct genera *Beauryia*, *Argyroberyx*, *Ossulcus*, *Eutawichthys* and *Tippaha* (Fig. 6). They were formerly referred to perciforms, beryciforms or holocentriforms (e.g., Nolf & Stringer, 1996; Schwarzhans & Stringer, 2020; Stringer et al., 2020; Stringer & Sloan, 2023) but are here considered as basal acanthomorphs *incertae sedis*. They are known mostly from the Maastrichtian, except for *Eutawichthys*, which is known since the Santonian onwards. So far, no otoliths *in situ* have been found in any of the skeleton-based taxa and likewise none of the otolith-based taxa have been aligned with skeleton-based taxa by *in situ* finds. We consider it possible that future finds of otoliths *in situ* could show some kind of relationships of the mentioned skeleton- and otolith-based data.

The taxa informally placed here within the basal Acanthomorpha represent clades that are characterised by a significant radiation and diversification in the terminal stages of the Cretaceous, which went abruptly extinct at the K/Pg extinction event. Some otoliths, such as *Ossulcus* or *Tippaha,* show a morphology that is so peculiar that one could speculate that these fishes were characterised by an otophysic connection (see Schulz-Mirbach et al., 2020). For instance, *Tippaha* vaguely resembles otoliths of the extant gadiform family Moridae, which exhibit such a connection.

Genuine Lampriformes (Verliferidae and *Wettonius*) and Polymixiiformes (Polymixiidae and *Polyspinatus*) are known from the lower Eocene (Carnevale & Bannikov, 2018; Schröder et al., 2022), and there are also Late Cretaceous otolith records that suggest the presence of Lampriformes and Polymixiiformes of modern type (Fig. 6). These otoliths are less spectacular in morphology and well in line with extant morphotypes found in the Polymixiidae and Veliferidae.
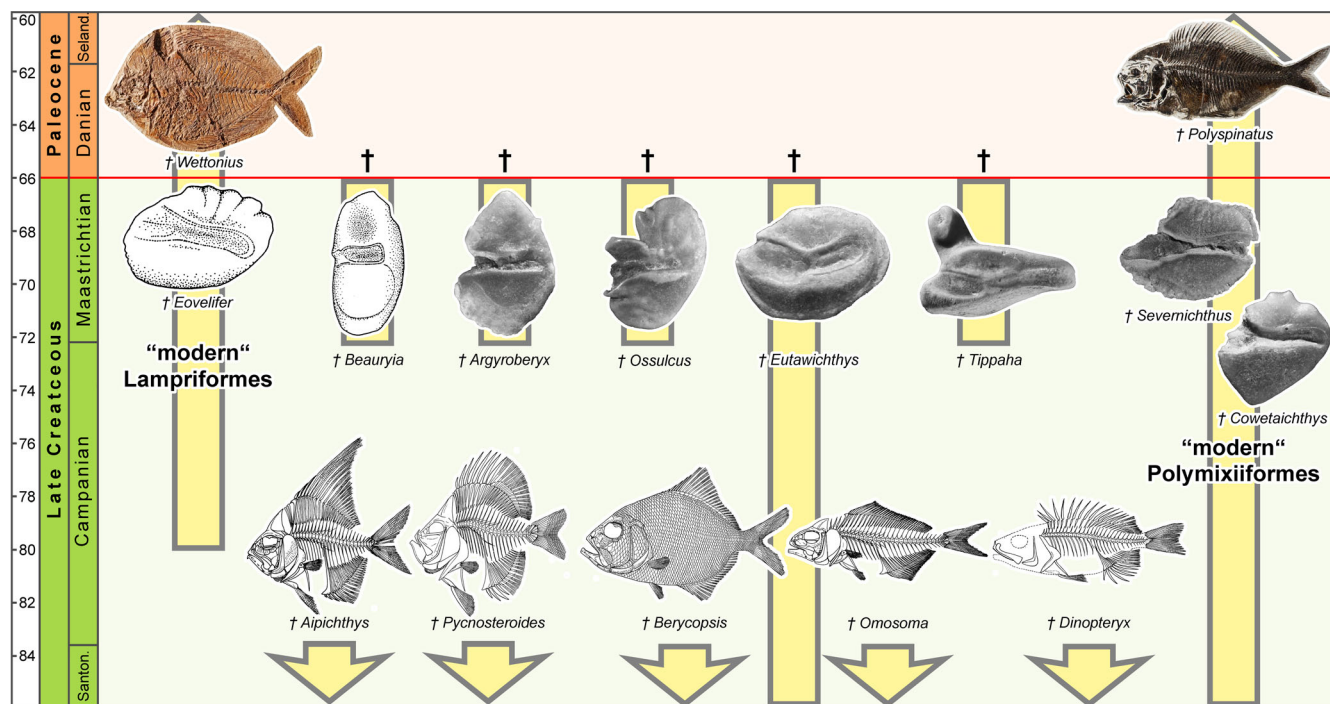
Figure 6. Stratigraphical ranges of selected lineages of basal acanthomorphs across the Late Cretaceous and Paleocene. Skeletal reconstructions are from Patterson (1964, 1967), photographs from G. Carnevale and Schröder et al. (2022); otoliths from Schwarzhans (2010), Schwarzhans et al. (2018b), Schwarzhans & Stringer (2020) and Stringer & Schwarzhans (2021).

Zeiformes (Fig. 7)

The Zeiformes are a relatively rare group in the fossil record but are known from the Late Cretaceous onwards on the basis of articulated skeletons (Tyler & Santini, 2005) and otoliths (Schwarzhans, 2010). Three otolith-based species are known from the Maastrichtian and Paleocene, all of them placed in the fossil genus *Isozen*, viz., *I. janni* Schwarzhans, 2003, *I. beateae* Schwarzhans, 2010 and *I. mareikeae* Schwarzhans, 2012. Morphologically, *Isozen* is in some ways intermediate between the Parazenidae/Zeniontidae and Oreosomatidae/Cyttidae clades (see Nolf & Tyler, 2006). The Cretaceous and Paleogene skeleton-based taxa *Cretazeus*, *Archeozeus* and *Protozeus*, and the relatively rare otolith-based occurrences of *Isozen* nevertheless indicate that zeiform lineages were present during the Late Cretaceous and survived the K/Pg extinction event.

Berycida (Fig. 7)

The Berycida (Beryciformes, Trachichthyiformes and Holocentriformes) represent a group of basal Acanthopterygii known by skeletal records since the Albian. There are two calibration points with otoliths *in situ* – the trachichthyid *Hoplopteryx* and an unidentified holocentrid (Schwarzhans et al., 2018a) (Fig. 7). Most of the taxa that survived the K/Pg extinction event experienced little morphological change until the present day, at least as far as otolith morphology is concerned. *Centroberyx* is a Cretaceous representative of the Berycidae, while the Trachichthyidae are represented by *Hoplostethus* and *Trachichthys*, and a putative diretmid are known from the Danian onwards (see Schwarzhans, 2010, 2012). Both holocentriform extant families, Holocentridae and Myripristidae, have been documented by otoliths since the Maastrichtian (Schwarzhans,

2010). However, there are also otolith morphologies known from the Maastrichtian that have not been found in sedimentary rocks younger than the K/Pg boundary, and these are only tentatively associated with the Berycida. These otolith-based taxa include *Traunichthys*, thought to be related to the Berycidae, and the genera *Pfeilichthys*, *Sillaginocentrus* and *Traubiella*, which are considered to represent extinct lineages of the Holocentriformes. All these lineages apparently became extinct at the K/Pg boundary.

Perciformes s. lat. (Fig. 8)

The most controversial group in terms of pre-Cenozoic origin is the Perciformes (*sensu* Nelson, 2006 = Perciformes s. lat. here) as for instance expressed in Patterson (1993a) when he described what is now coined 'Patterson's Gap'. There is no doubt that some perciforms s. lat. existed in the Paleocene, and there are convincing records since the Danian in the skeletal record (e.g., Cantalice & Alvarado-Ortega, 2017; Cantalice et al., 2018, 2019, 2020, 2022; Friedman et al., 2023), as well as from otoliths (e.g., Nolf, 1978, 2013; Nolf & Dockery, 1993; Schwarzhans, 2003, 2004, 2012; Schwarzhans & Bratishko, 2011). Many of these fishes show mostly very generalised morphologies, both with respect to articulated skeletons and otoliths, and are usually regarded as stem-forms in their respective families. The Paleocene otolith record comprises taxa of the Perciformes, Scorpaeniformes, Acropomatiformes, Carangiformes, Scombriformes and Spariformes (Fig. 8). Schwarzhans & Bratishko (2011, p. 108) interpreted the generalised morphologies seen in Paleocene perciform s. lat. otoliths as an expression of an early evolutionary phase at the base of an incipient radiation and concluded that 'it may serve as an indication that not much wealth of fossil Percoidei (= Perciformes s.l.) can be expected prior to the Tertiary'.
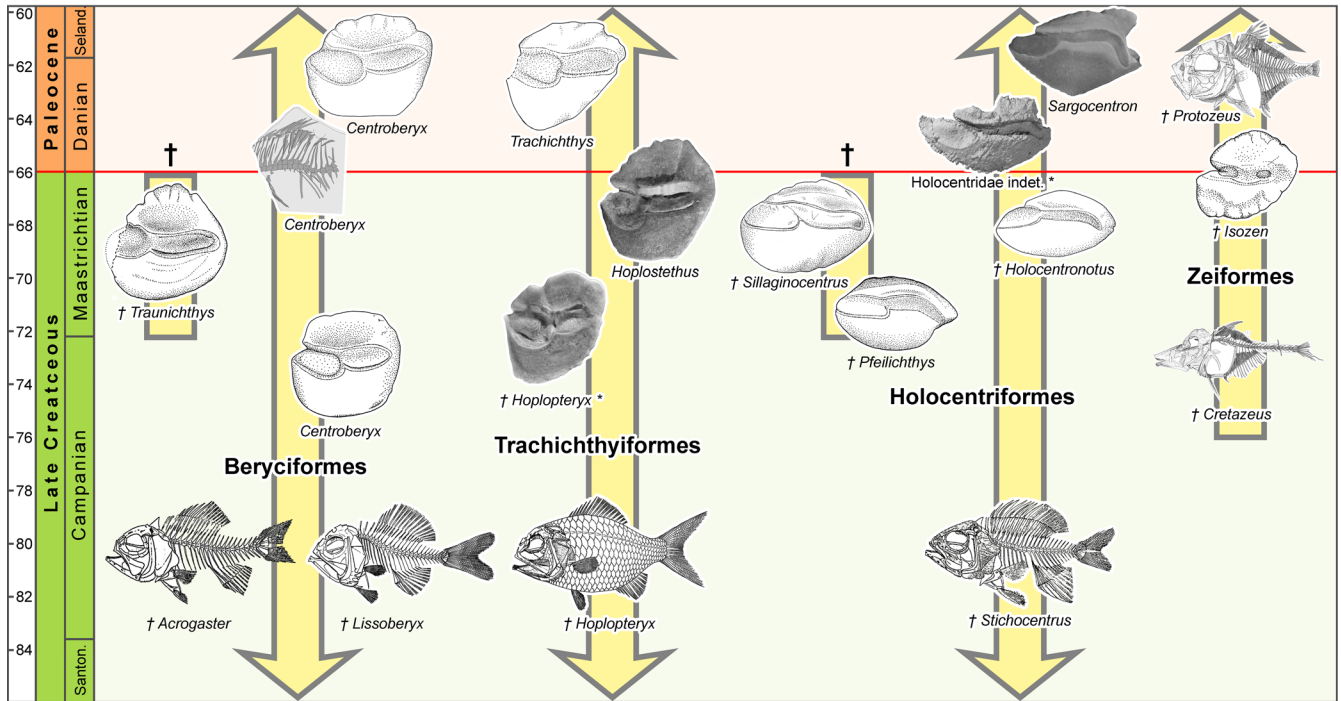
Figure 7. Stratigraphical ranges of selected lineages of the Beryciformes, Trachichthyiformes, Holocentriformes and Zeiformes across the Late Cretaceous and Paleocene. Skeletal reconstructions are from Patterson (1964, 1967), Tyler (2004); otoliths from Schwarzhans (2010, 2012), Schwarzhans et al. (2018a), Schwarzhans & Stringer (2020) and Stringer & Schwarzhans (2021).
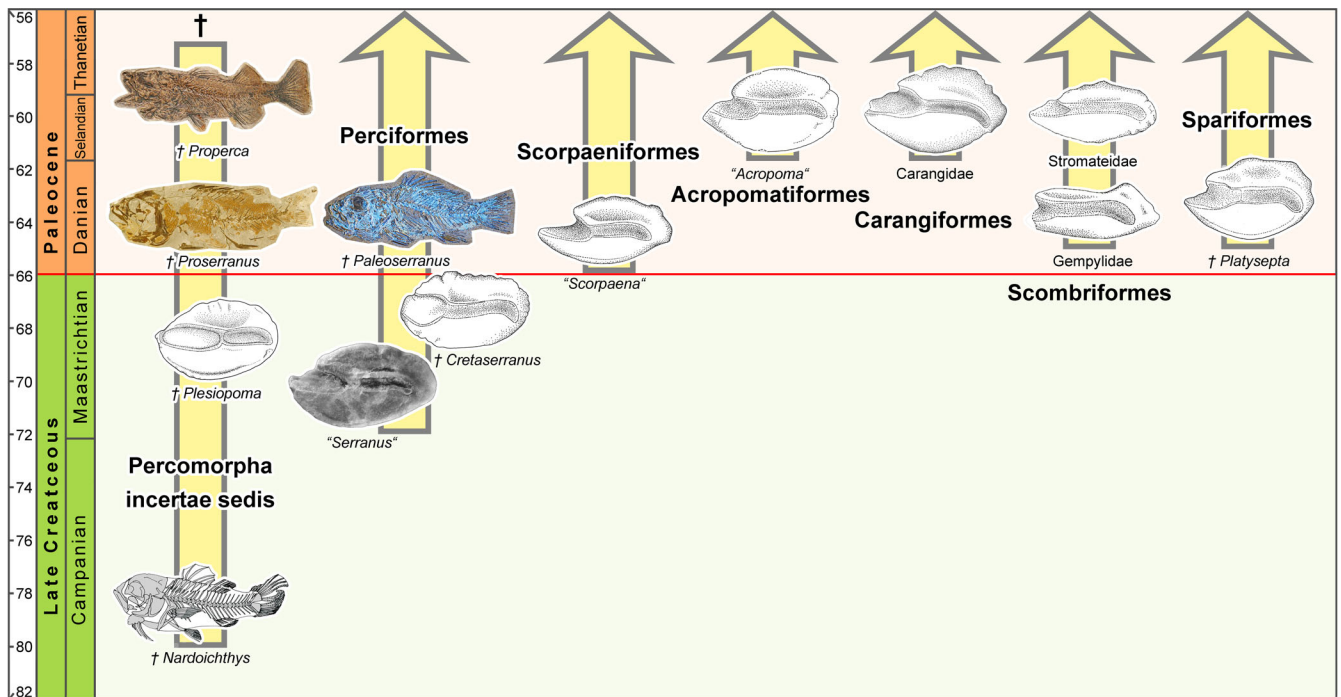

Figure 8. Stratigraphical ranges of selected lineages of the Percomorpha across the Late Cretaceous and Paleocene. Skeletal reconstructions are from G. Carnevale, photographs from Cantalice et al. (2018), Friedman et al. (2023); otoliths from Schwarzhans (2003, 2010, 2012), Schwarzhans & Stringer (2020) and Schwarzhans & Jagt (2021).

Some of the mentioned otolith records occur just above the impact event, for instance, *Scorpaena corallophilus* (Schwarzhans, 2003) at Stevns Klint in Denmark (Schwarzhans & Milàn, 2017). It is therefore unlikely that all these unambiguous perciform (s. lat.) otoliths only occurred just after the K/Pg boundary, and the

question of where their Maastrichtian forerunners are remains elusive. In the skeletal record, a few Maastrichtian finds have been associated with 'primitive' Perciformes (s. lat.) (see Arratia et al., 2004). In recent studies, all relevant Late Cretaceous skeletal finds are interpreted as Percomorpha *incertae sedis* (Friedman et al.,

2023) such as, for instance, *Nardoichthys* (Fig. 8). Conversely, a fair number of Late Cretaceous otoliths have been interpreted in the past as pertaining to some kind of perciforms (s. lat.) (Nolf & Dockery, 1990; Nolf & Stringer, 1996), the earliest dating back to the Cenomanian (Nolf, 2016). These taxonomic interpretations have subsequently been criticised (Schwarzhans, 2010; Stringer et al., 2020; Schwarzhans & Stringer, 2020), and only a few of them have remained tentatively associated with the perciforms (s. lat.).

Unlike otoliths of the Ophidiiformes and Gadiformes (see above), those of perciforms show only a few morphological features that may allow an unambiguous allocation. For the otolith morphotypes found in the Paleocene (Fig. 8), the combination of a moderately deep sulcus with an ostium that is shorter and wider than the cauda, anteriorly opening, and the cauda being slightly flexed towards its termination may be considered as typical of basal perciform (s. lat.) morphotypes. This morphology has been termed heterosulcoid (Schwarzhans, 1978), but it is also found in many other non-perciform groups such as certain Holocentriformes or Polymixiiformes. This has led to a rigorous reassessment of Cretaceous otoliths previously considered to represent perciforms (s. lat.) (Schwarzhans, 2010; Schwarzhans & Stringer, 2020). Some of those that were then still considered valid perciform (s. lat.) representatives should be more cautiously placed as *incertae sedis* within the Percomorpha, as for example is the case of *Plesiopoma* (Fig. 8). Only two otolith records from the Maastrichtian may indeed represent genuine Perciformes s. lat., namely *Cretaserranus* from Maastricht (Schwarzhans & Jagt, 2021) and *Serranus*? *caribbaeus* (Nolf & Dockery, 1993), a species that has been found across the K/Pg boundary.

We conclude that while early Paleocene finds strongly suggest that perciforms (s. lat.) were in existence in the Maastrichtian, the actual evidence prior to the K/Pg extinction event, however, remains small and, to a large part, problematic.

Bony fish life in Maastrichtian and Paleocene seas, and the K/Pg extinction event

The ocean configuration and circulation during the Late Cretaceous and early Paleogene was very different from today. Late Cretaceous/early Paleogene times were characterised by ice-free poles that resulted in a much lower temperature gradient and a more equable climate on land and in the sea (Hay, 2008, 2009; Uenzelmann-Neben et al., 2017). The large shelf settings along the Tethys, resulting from a very high sea level established in the Cenomanian (Hay, 2009), may have triggered a sustained radiation of neritic fishes (Cavin, 2008; Guinot & Cavin, 2016). Deep-water anoxic events occurred in ocean basins as a result of the combined effect of a halothermal deep-water circulation and the palaeogeographical configuration of the continents with the latest superregional anoxic event that took place in the Turonian (Ladant et al., 2020).

'A better-ventilated ocean triggered by Late Cretaceous changes in the continental configuration' (Donnadieu et al., 2016, title) and a consequential change in ocean circulation (Ladant et al., 2020) may have further enhanced the evolution of bony fishes during the Campanian and Maastrichtian. This Late Cretaceous oceanographical development probably resulted in the observed rich and diverse populations of the Maastrichtian seas with a more evolved bony fish assemblage in all known marine settings. It was the time of the blossoming of pelagic Aulopiformes and a variety of highly advanced, but difficult-to-place groups of basal acanthomorphs on the shelf (Fig. 9). Numerous still extant clades that originated prior

to the latest Cretaceous were present as well and also locally abundant, although not really diverse, for example, Elopiformes, Albuliformes, Anguilliformes, Siluriformes, Argentiniformes and Stomiiformes (Fig. 10). The Stomiiformes are probably the only deep-sea fishes with an Early Cretaceous origin that persisted until the present day (see discussion in Carnevale & Rindone, 2011, about the putative stem-stomiiform *Paravinciguerria*). However, the Maastrichtian (and possibly also part of the Campanian) was also a relevant time interval for the radiation of a number of modern teleost groups, which however remained relatively limited in diversity and abundance. The earliest records of the Gadiformes, Batrachoidiformes, Ophidiiformes and perciforms (s. lat.) all seem to fall in this time period (Fig. 9), and our current knowledge appears to suggest that their origin may not be placed much deeper in time.

The bustling and diverse Maastrichtian teleost fauna, however, came under severe stress from the catastrophic effects connected to the extraterrestrial impact that is thought to have triggered the K/Pg boundary extinction event (e.g., Schulte et al., 2010). The effects on the teleost communities were probably less severe than those that affected many other groups, yet were still substantial. Schwarzhans & Stringer (2020) discussed the otolith finds across the K/Pg boundary and the role of the events that had the most severe impact on teleost communities. They concluded that the (partial) collapse of the food chain, the post-impact winter that may have lasted several years or decades and a long-term retraction of biogenic carbonate environments may have had the severest impact on the teleost communities. Of course, perturbations of the food chain would have particularly impacted apex predators such as the aspidorhynchiforms, ichthyodectiforms, pachycormiforms, pachyrhizodontiforms and tselfatiiforms, but also the Ichthyotringoidei (Cavin, 2001; Friedman, 2009; Schwarzhans & Stringer, 2020). An extended post-impact winter could have influenced warm-water fishes that may have needed a certain water temperature level for spawning (Schwarzhans & Stringer, 2020). The long-term retraction of biogenic carbonate environments affected fishes that flourished during the Maastrichtian in warm carbonate settings, which we believe could have been the case for those highly specialised Late Cretaceous basal acanthomorphs. Finally, taxa with particularly complex reproduction strategies such as *Vorhisia* were also victims of these catastrophic events. We calculated that between 25 and 60 per cent of genera and 50 to 90 per cent of teleost species went extinct during the K/Pg boundary event (Schwarzhans & Stringer, 2020). The highest percentage of loss was observed in the Appalachian shore faunas and in the fauna in the Peninnic Ocean, while the lowest seems to have occurred in the cooler seas of the Western Interior Seaway in Texas, and in the North Sea Basin (Schwarzhans & Stringer, 2020).

Survivors are primarily located in groups that were still rather generalised in their lifestyle (?early perciforms s. lat.), adapted to cold waters (Gadiformes), living on muddy bottoms (Anguilliformes and Ophidiiformes), or in the deep-sea (Stomiiformes). A small faunal assemblage recovered from directly above the impact sediments in one of the iconic K/Pg boundary sections, Stevns Klint in Denmark, has revealed an unusual abundance of pterothrissid otoliths, which have been interpreted as 'disaster opportunists' (Schwarzhans & Milàn, 2017). The family Pterothrissidae and the genus *Pterothrissus* pertain to a basal teleost group, the Albuliformes, which may have originated during the Late Jurassic or Early Cretaceous (Filleul, 2001; Schwarzhans, 2018).

Figure 10 summarises the effects of the K/Pg boundary extinction event on teleosts as currently known from otoliths,
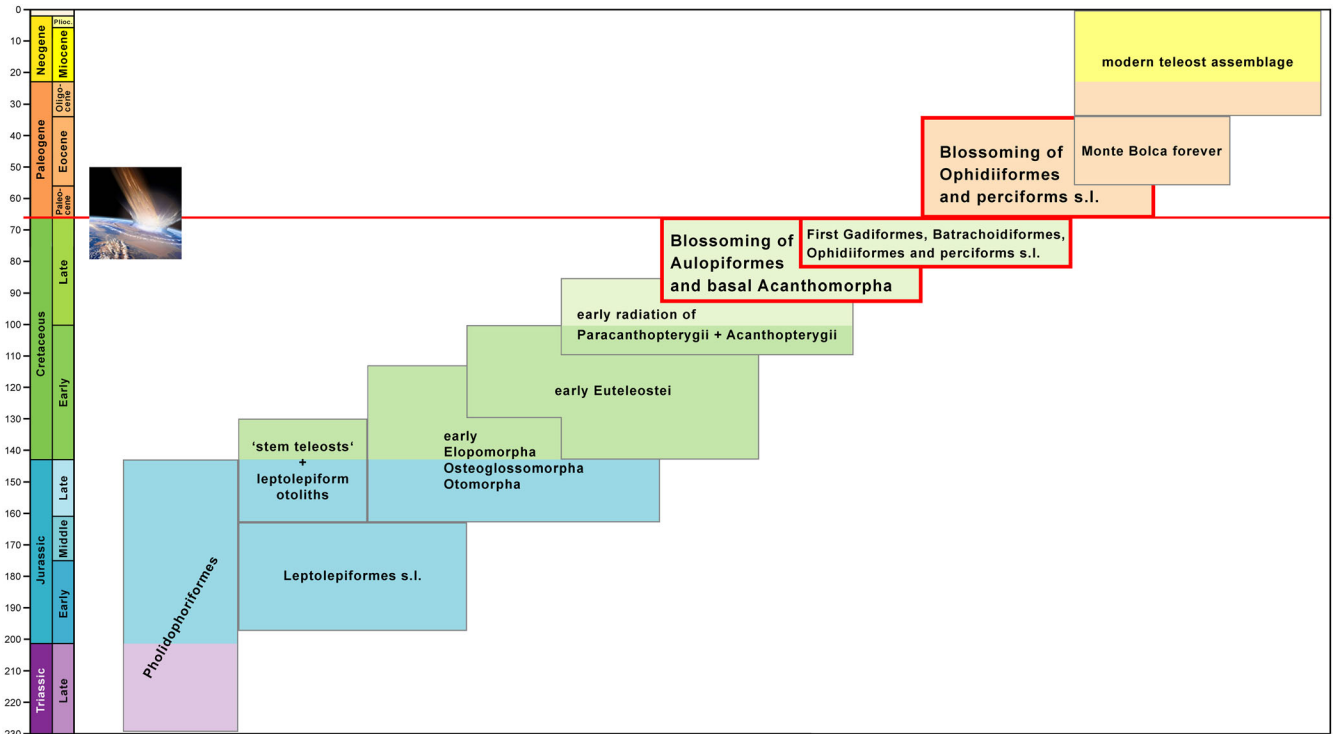
Figure 9. The 'evolutionary staircase' depicting major steps in the evolution of teleost fishes, highlighting events within the so-called 'Patterson's gap'.
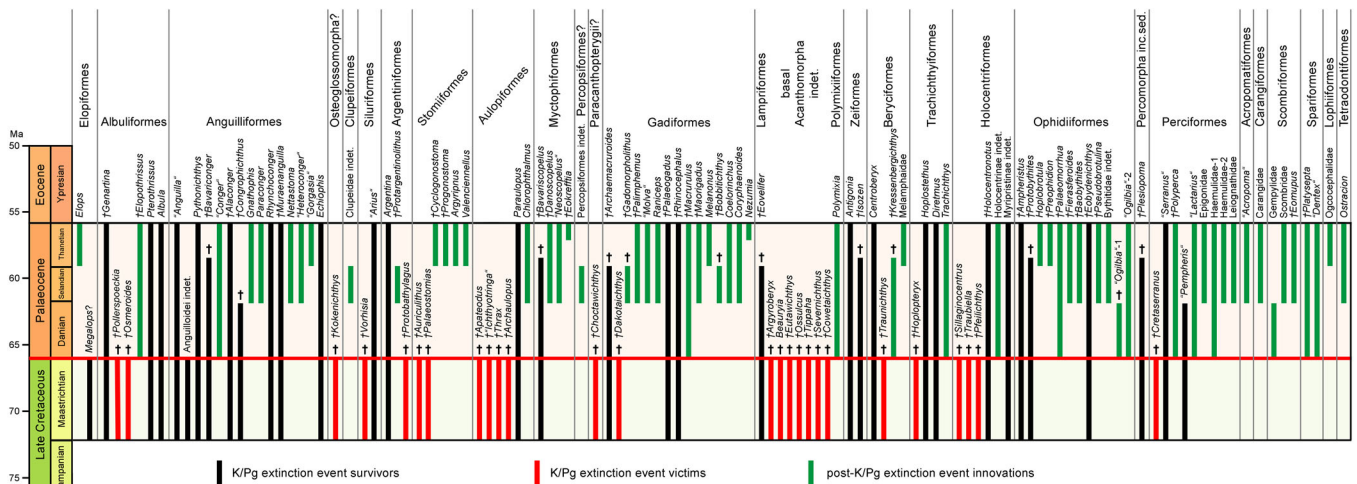

Figure 10. Stratigraphical range chart of otolith-based taxa (genus level) highlighting extinctions at the K/Pg boundary, survivors and the benefitters in the recovery from the extinction event.

depicting 120 genera or genera-like *incertae sedis* (together comprising about 200 species). Most extinctions are documented for the Aulopiformes (Ichthyotringoidei), basal Acanthomorpha *incertae sedis* and Berycida. Surviving taxa are common among the Albuliformes, Anguilliformes, Siluriformes, Zeiformes and Ophidiiformes. The most interesting groups are those that presumably originated in the Late Cretaceous and showed some low diversity during that period, but an explosive radiation and diversification in the early

Paleogene. These are primarily Gadiformes, Ophidiiformes and perciforms s. lat., the last-named represented by the orders Perciformes, Acropomatiformes, Carangiformes, Scombriformes and Spariformes. Clearly, these three major groups benefitted from the extinction of the earlier competitors. The Ophidiiformes and perciforms s. lat. competed in abundance and diversity during the Paleocene and Eocene, but during the Eocene, the perciforms s. lat. really began to become the dominant teleost group in shelf seas.

The way forward

Articulated fish skeletons have a high information content and are crucial for our understanding of teleost evolution. However, as stated above, they are also bound to very specific taphonomic settings. The meagre record of articulated fossil fishes from Maastrichtian and Paleocene strata has led to define 'Patterson's Gap' (Friedman et al., 2023). However, recent advances have also shown how much new important information can be gained when new Konservat-Lagerstätten with articulated fish skeletons are being discovered in this critical time interval, as for instance is the case in the recently recognised fish faunas from the Danian of Mexico (Cantalice & Alvarado-Ortega, 2017; Cantalice et al., 2018, 2019, 2020, 2022). A similarly rich Lagerstätte with fossil fishes of unquestionable Maastrichtian age is yet to be discovered.

In the otolith record, 'Patterson's Gap' is no longer relevant and a continuous coverage has now been achieved, albeit restricted to Europe and North America. We believe that there are many more regions across the globe that could harbour significant additional otolith data but are as yet to be investigated. The single most consequential issue with the otolith record, however, is a better connection with the skeletal record. This can only be achieved by searching for otoliths *in situ*, either by careful inspection of fossil fishes or by routine micro-CT-scanning of three-dimensional preserved skulls. Improvement of the calibration of isolated otoliths by *in situ* finds, particularly in the Late Cretaceous, is absolutely instrumental to tap into the tremendous wealth of information the fossil otoliths have to offer in ascertaining the evolution of fishes and reconstructing environments in deep time.

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