

Rising from the Ashes: The Biogeographic Origins of Modern Coral Reef Fishes

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During the excavation of Mayan tombs, little did the archaeologists know that the fossils they discovered in the tomb stones would fundamentally alter our understanding of the earliest origins of coral reef fishes. Located just 500 kilometers from the point where an asteroid impact reconfigured the world's biological systems 66 million years ago, we find the earliest origins of three typical reef fish groups. Their presence in Mexico just 3 million years after this impact finally reconciles the conflict between the fossil and phylogenetic evidence for the earliest origins of reef fishes. The incorporation of these fossils into a global reconstruction of fish evolutionary history reveals a new picture of the early biogeography of reef fishes, with strong Atlantic links. From locations associated with biological destruction and societal collapse, we see evidence of the origins of one of the world's most diverse and spectacular marine ecosystems: coral reefs.

Keywords: coral reef fishes, evolutionary biogeography, the Cretaceous–Paleogene boundary, asteroid impact, Mexico

Coral reefs are one of the most iconic high-diversity systems on the planet. Characterized by a global hotspot of exceptional biodiversity, they have been the focus of considerable ecological and evolutionary research (Myers 1997, Paulay and Meyer 2002, Bellwood and Meyer 2009, Parravicini et al. 2013, Pellissier et al. 2014). In recent years, there has been great progress in reconstructing the evolutionary history of coral reef organisms, including the origins of the marine biodiversity hotspot (Renema et al. 2008, Cowman and Bellwood 2011, Bowen et al. 2013, Leprieur et al. 2016, Siqueira et al. 2021). Arguably, it is in the fishes that most progress has been made, largely as a result of rapid developments in the size and quality of molecular phylogenies (Choat et al. 2012, Cowman and Bellwood 2013, Alfaro et al. 2018, Rabosky et al. 2018, Ghezelayagh et al. 2022). Today, most key reef fish families have a good representation in multitaxon phylogenies, and there is a growing consensus, among both fish families and studies, in the major patterns of diversification (Cowman and Bellwood 2013, Bellwood et al. 2017, Siqueira et al. 2020, Leprieur et al. 2021). This molecular evidence has been strongly underpinned by the fossil record, with key locations providing invaluable chronographic reference points (Bellwood 1996, Marramà et al. 2016, Friedman and Carnevale 2018). These fossils are used to turn phylogenies into robust time trees (chronograms). However, fossils

also have another major advantage. Unlike phylogenetic hypothesis, they can accurately place a taxon in a specific location and at a specific time (Bellwood et al. 2019). They are therefore invaluable in biogeographic reconstructions, acting as foundational, stabilizing facts in a sea of hypotheses.

In the early biogeographic reconstructions, fossils were used to date phylogenetic reconstructions (e.g., Bellwood et al. 2004, Choat et al. 2012), whereas subsequent biogeographic reconstructions of the distributions of ancestral lineages were inferred on the basis of a mapping and optimizing approach (e.g., Cowman and Bellwood 2013, Thacker 2015, Siqueira et al. 2019a, Santaquiteria et al. 2021). In essence, ancestral distributions were estimated on the basis of inferences drawn from modern distributions. There are, however, many problems with this approach. One of the foremost is movement. This may be especially problematic in marine systems where larvae can disperse widely and geographic ranges can span two-thirds of the global tropics (Hughes et al. 2002). This problem can be overcome, to some extent, if fossil taxa, and their locations, are included in the phylogenies (Dornburg et al. 2015, Siqueira et al. 2019b). The problem for reef fishes is that the fossil record of almost all families starts at the same time and in the same location: in the 50-million-year-old Eocene

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deposits in Monte Bolca, northern Italy (Bellwood 1996, Friedman and Carnevale 2018).

The Bolca fossils were deposited some 15 million years after the Cretaceous–Paleogene boundary, 66 million years ago. This boundary was the result of an asteroid impact that triggered a mass-extinction event, which was followed by the rise of modern marine systems. The Cretaceous–Paleogene mass extinction event marked the end of the Mesozoic (Cretaceous) and the beginning of the Cenozoic (Paleogene). On land, it is closely associated with the extinction of non-avian dinosaurs and the subsequent rise of mammals (Lyson et al. 2019, Chiarenza et al. 2020). However, its impact was arguably greatest in the marine realm, with the loss of the ammonites and numerous other swimming groups, including mososaurs, plesiosaurs, and many fish groups (Schulte et al. 2010, Friedman and Sallan 2012). In the resultant rebound, we see the rise of almost all major marine fish groups, including most reef fish families (Patterson 1993, Alfaro et al. 2018, Ghezelayagh et al. 2022). However, the timing and location of this rebound are poorly understood. For reef fishes, most work revolves around Monte Bolca. This site has been instrumental in our understanding of the ecology, evolution, and biogeography of coral reef fishes (Bellwood 1996, 2003, Bellwood et al. 2014, 2017, Friedman and Carnevale 2018, Marramà et al. 2016). Indeed, it plays a large role in placing Europe in the center of the early evolution of extant reef fish families (Renema et al. 2008). However, recently discovered fossils are beginning to shed new light on the 15–16 million year gap between the Cretaceous–Paleogene boundary, at 66 million years ago, and the Monte Bolca fossils, at 50 million years ago. These new fossils are from Mexico.

Mayan temples, a sarcophagus, and the Tenejapa–Lacandón formation

In the 2000s, archaeologists were studying the temples in the Mayan city of Palenque (figure 1a). Examination of the fossiliferous limestones inside the temples revealed fossil evidence of mass mortality events of fishes and invertebrates (Alvarado-Ortega et al. 2018). Closer examination of sarcophagi within the temple complex by anthropologists and paleontologists (figure 1b) found lithographic features that linked the limestones to a different location in the Tenejapa–Lacandón formation (Alvarado-Ortega et al. 2015, 2018). These limestones are of Danian (Lower Paleocene; 61.6–66 million years ago) age (Cuevas-García and Alvarado-Ortega 2009), and, remarkably, further examination of the Tenejapa–Lacandón formation deposits in nearby limestone quarries revealed exceptionally well-preserved fossil fishes (figure 1c–1e). These fishes included families that are typically found on modern coral reefs.

The age and geographic position of these Palenque fossil sites offers an exceptional opportunity to understand the response of reef fish lineages to the last great mass extinction event at 66 million years ago. These fishes

were living just 3 million years after the Cretaceous–Paleogene boundary (Cantalice and Alvarado-Ortega 2016, Cantalice et al. 2018, 2020) and offer a glimpse into the early formation of modern fish faunas at the beginning of the Cenozoic Era. Even more remarkable is the proximity of the Palenque deposits to the Chicxulub asteroid impact site (500 kilometers away)—that is, the site of the impact that triggered the Cretaceous–Paleogene boundary. The age and location of the fossils (figure 2), therefore, provide a unique setting to observe the dynamics of biodiversity accumulation shortly after the most recent global mass extinction event.

For a long time, there has been a question over the “missing” 16 million years between the end of the Cretaceous, at 66 million years ago, when we lose many marine groups, including some fishes, and the presence of a near complete reef fish assemblage, in terms of their taxonomic composition, in the Eocene, at 50 million years ago (figure 2; Bellwood et al. 2015, 2017). Where were the reef fishes during this time? The estimated age of origin of modern reef fish lineages, based on molecular phylogenies, varies widely, from the Eocene to the Cretaceous. These older estimates are clearly at odds with the fossil record, with no articulated fossils of any modern reef fish family prior to the Cretaceous–Paleogene boundary (Patterson 1993) and very few prior to 50 million years ago. This raises the question of when reef fish assemblages, or the fish lineages that occupy coral reefs today, first arose and where.

The Palenque fish fossils may hold the answer, with the presence of both pycnodonts, remaining vestiges of a once diverse and widespread Mesozoic fish group (Cawley et al. 2021), and the earliest representatives of a number of potentially nonmonophyletic acanthomorph fish groups (*sensu* Ghezelayagh et al. 2022) that are characteristic of modern coral reefs (i.e., coral reef fishes; cf. Bellwood and Wainwright 2002), including the flutemouths (Aulostomoidea), groupers (Serranidae) and damselfishes (Pomacentridae; Alvarado-Ortega et al. 2015, Cantalice and Alvarado-Ortega 2016, Cantalice et al. 2018, 2020). These discoveries promise to reshape our understanding of the early evolution and biogeography of coral reef fish families. Our goal in the present article, therefore, is to explore the impact of the fish fauna of Palenque on our understanding of the evolutionary biogeography of coral reef fishes and the formation of modern and historical biodiversity hotspots.

Reconciling molecules and fossils

Fortunately, for all three groups (the Aulostomoidea, Pomacentridae, and Serranidae), there is enough publicly available genetic data (Chang et al. 2019) to allow us to reconstruct their phylogenetic and biogeographic histories. By incorporating fossil taxa in the phylogenetic reconstructions through the fossilized birth–death process (Gavryushkina et al. 2014, Heath et al. 2014) and performing

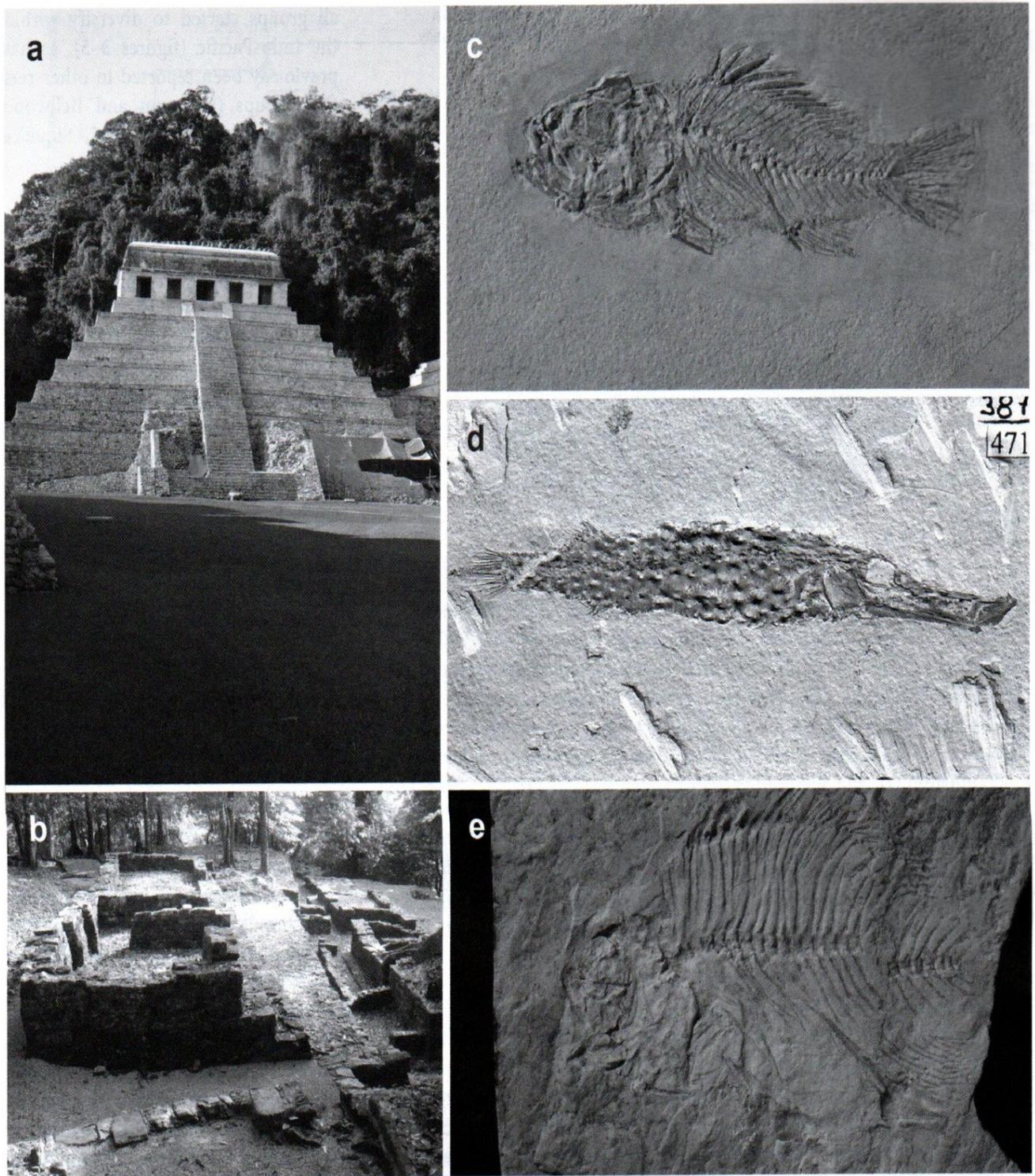


Figure 1. The Mayan city of Palenque contains numerous Mayan temples (a). The limestone slabs in these temples had traces of mass fish mortality events. These were particularly clear in the slabs from tombs in the bat group complex (b). Further examination of the quarries where these slabs came from revealed fossil fishes that may be part of the earliest modern reef fish assemblage—for example, *Paleoserranus lakamhae* (Serranidae; c), *Eekaulostomus cuevasae* (Aulostomoidea; d), and *Chaychanus gonzalezorum* (Pomacentridae). Photographs: Kleyton M. Cantalice

biogeographic reconstructions (Matzke 2014), we can evaluate the impact of the Palenque fishes on our understanding of the origins of modern reef fishes.

The Palenque fossil fishes offer a new view of the earliest origins of coral reef fishes and modern—after the Cretaceous–Paleogene boundary—acanthomorphs in general. Remarkably, this new perspective helps to resolve previously conflicting evidence in both the timing and geographic

origins of extant reef fish groups. In all three chronograms, the inclusion of the Palenque fossils resolves the long-standing questions of when and where the earliest representatives of these key reef fish families first arose. In all three cases, the inclusion of the Palenque fossils places the earliest origins of the families very close to the Cretaceous–Paleogene boundary. The origin of the superfamily Aulostomoidea was dated at 65.5 million years ago (63–73 million years ago,

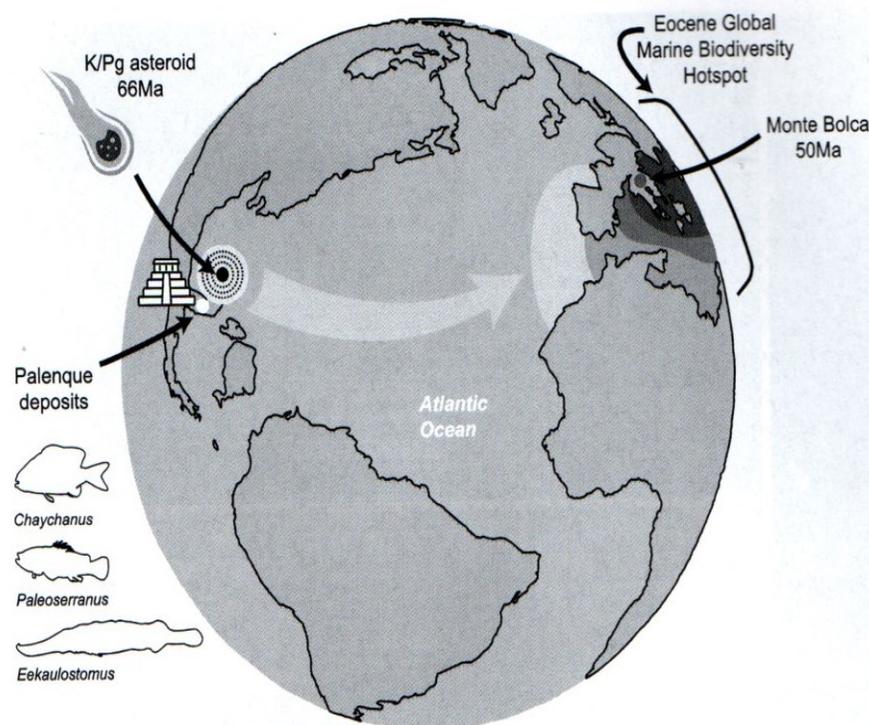


Figure 2. The Palenque fish fossils, Mexico, were deposited in the Lower Paleocene (62–66 million years ago). This site lies approximately 500 kilometers from the site of the Chicxulub asteroid impact that triggered the Cretaceous–Paleogene mass extinction event at 66 million years ago. Fish species described from these fossil deposits belong to groups that are typical of modern coral reefs, such as the Pomacentridae (*Chaychanus*), Aulostomoidea (*Eekaulostomus*), and Serranidae (*Paleoserranus*). The arrow indicates the likely contribution of these lineages to the later Eocene (56–33.9 million years ago) marine biodiversity hotspot (cf. Bellwood et al. 2017) and highlighting the key location of Monte Bolca, approximately 9000 kilometers to the east. The continental configuration is a representation of the mid-Paleocene; not the Eocene, when Monte Bolca was the hotspot for marine biodiversity.

highest posterior density interval; figure 3). The origins of Serranidae and Pomacentridae were also dated to be very close to the Cretaceous–Paleogene boundary at 65.1 million years ago (63–76 million years ago, highest posterior density interval) and 63 million years ago (62–70 million years ago, highest posterior density interval), respectively (figures 4 and 5).

The biogeographic reconstructions all, again, clearly emphasize the importance of the Atlantic in the early evolution of the three reef fish groups, either alone (Serranidae) or as part of the central Tethys (Aulostomoidea, Pomacentridae). In the case of Serranidae, the ancestral reconstructions suggest that the origin of the family (crown group) is more likely to have happened in the Western Atlantic region (figure 4). The Pomacentridae (figure 5) and Aulostomoidea (figure 3) reconstructions also support the Western Atlantic as part of the ancestral area of origin of these groups. However, in this case, the models suggest a more widespread distribution, with the root lineage also being present in the central Tethys region. The biogeographical reconstructions also suggest that it was only during the Oligocene–Miocene that lineages in

all groups started to diversify within the Indo-Pacific (figures 3–5), as has previously been reported in other reef fish groups (Cowman and Bellwood 2013, Bellwood et al. 2017, Siqueira et al. 2019b).

Temporal implications

In regards to the time of origin of coral reef fish families, and most other percomorph fishes (*sensu* Ghezelayagh et al. 2022), there have been confusing disparities between studies. Some phylogenies place the origins of crown reef fish families in the Eocene at 50–55 million years ago (e.g., Sorenson et al. 2013, McCord et al. 2021); these studies mainly use Bolca fossils as a calibration point. Larger phylogenies, looking at deeper timeframes, often place the origins of some reef fish families in the Cretaceous from 65 to 95 million years ago (Rabosky et al. 2018). However, these latter estimates conflict with both the earlier phylogenies and the fossil record (Patterson 1993). There is currently no fossil evidence of any reef fish family before the Cretaceous–Paleogene boundary. Evidence of any percomorph family before the boundary (based on articulated fossils, or clear synapomorphies) is equally scarce (cf. Carnevale and Johnson 2015).

By combining the Palenque fossil evidence with molecular data, we are finally able to reconcile the fossil and molecular evidence. The Palenque fossils provide a more realistic scenario, with families arising in the Paleocene—that is, earlier than Bolca and much closer to the Cretaceous–Paleogene boundary but not in the Cretaceous. Indeed, the temporal appearance of modern reef fish families in the fossil record seems to be closely associated with the Cretaceous–Paleogene boundary—that is, no modern families prior to the Cretaceous–Paleogene boundary and some appearing shortly after it (e.g., Cowman et al. 2009, Dornburg et al. 2015). This scenario is strongly supported by the phylogenies containing Palenque fossils, which place the origins of the three focal groups, the superfamily Aulostomoidea at 65.5 million years ago, the Serranidae at 65.1 million years ago, and the Pomacentridae at 63 million years ago, all very close to the Cretaceous–Paleogene boundary at 66 million years ago. It is important to note that the upper bounds of these estimates still include the end of the Cretaceous. Cretaceous origins, therefore, cannot be discounted. However, the evidence points strongly to

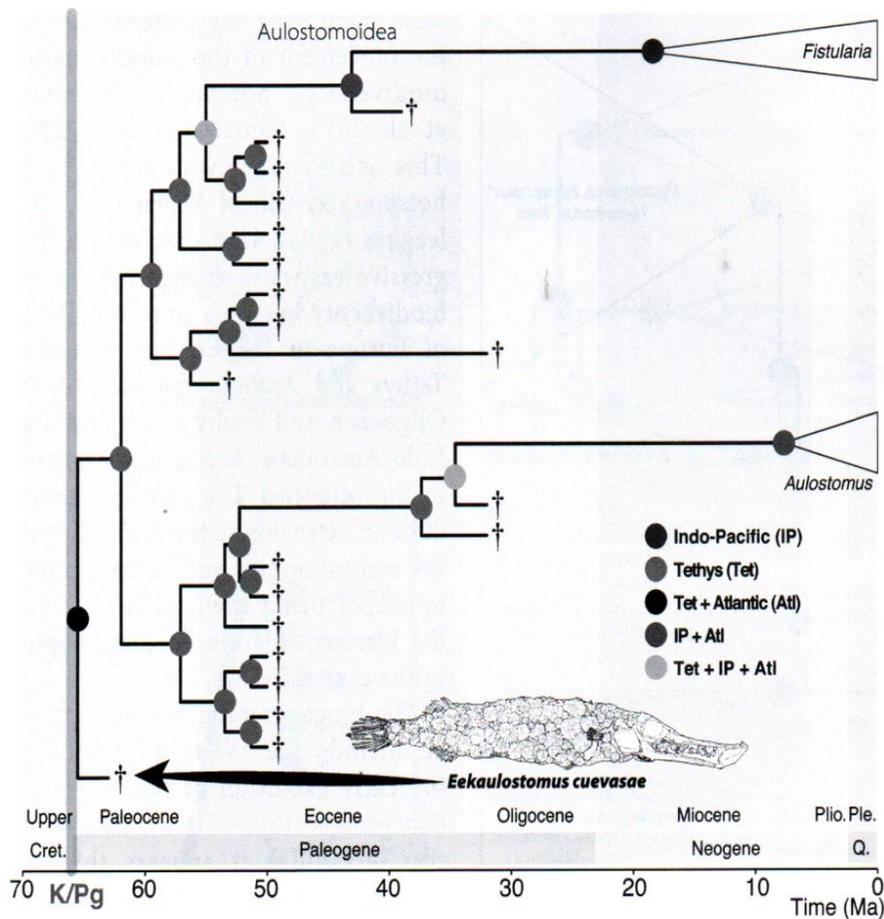


Figure 3. Chronogram of the superfamily Aulostomoidea built with the fossilized birth–death model. The vertical stripe depicts the Cretaceous–Paleogene boundary. The dagger signs denote extinct lineages and we highlight the position of the Palenque species described from the Tenejapa–Lacandón deposits. The nodes are coded according to the best fit model for ancestral biogeographical reconstructions. The triangles are proportional to the number of extant species in each clade.

post Cretaceous–Paleogene boundary origins of all three lineages.

This rapid rise of groups after the mass extinction event accords well with previous accounts of the speed of the rebound after mass extinction events, which has been reported in both acanthomorph fishes (Friedman 2010, Alfaro et al. 2018, but see Ghezelayagh et al. 2022), and in terrestrial taxa (Lyson et al. 2019). It appears that the Cretaceous–Paleogene boundary was closely associated with, and probably triggered, the formation and subsequent expansion of the three fish groups analyzed in the present article. The estimated ages of origin of the three focal taxa (at 65–63 million years ago), therefore, considerably predates the Eocene biodiversity hotspot in the central Tethys (by about 15 million years ago), the formation of modern wave-resistant coral reefs (which first appear at about 30 million years ago, in the Oligocene and early Miocene; Bellwood et al. 2017), and the characteristic *Acropora*-dominated coral reefs seen today (which only arose in the last 5 million years, in the Plio-Pleistocene; Renema et al. 2016, Siqueira et al. 2022).

Biogeographic implications

The location of the Palenque fossil fishes also has biogeographic implications. The proximity of the fossiliferous beds in Palenque, Mexico, to the epicenter of the asteroid impact might suggest that the area was a specific source of evolutionary novelty. But the Cretaceous–Paleogene boundary was a global phenomenon that rapidly reconfigured the biological landscape (Lyson et al. 2019). The proximity may therefore simply be a remarkable coincidence. However, the location may have had some specific attributes. Being close to the impact site, the speed and extent of the destruction may have created an extensive area of new habitat devoid of life, and offering opportunities for marine groups that could colonize rapidly. Although modern day biogeographic distributions attest to the inability of some species to colonize areas over millennia, even when connected by the sea (Cowman et al. 2017), the low latitudes had global circulation at this time. Therefore, the Palenque region, and Central America in general, would have been the final downstream refuge for all the tropical larvae, and lineages, from the Tethys before they pass into the vast openness and oblivion of the Pacific (which would have acted like a giant East Pacific biogeographic barrier;

cf. Bellwood and Wainwright 2002). The Central American region at this time is therefore likely to have acted as a site of lineage accumulation, in exactly the same manner as the Indo-Australian Archipelago when the current global marine biodiversity hotspot first started to develop in that location in the Eocene (Cowman and Bellwood 2013). The Chicxulub meteorite impact location and the surrounding areas may therefore have presented a particularly well placed clean slate with which to redraw the future of marine fish assemblages.

Indeed, the location of the Palenque fossils has far-reaching implications for our understanding of the possible locations where reef fish lineages first arose and subsequently diversified. The biogeographic setting of the Palenque fossils calls for a reinterpretation of the location of marine biodiversity hotspots through time. Although it is not yet known whether the central Tethys region was also a hotspot during the Paleocene, the fossils from Mexico suggest that the Western Atlantic was at least as important as the Tethys (if not more so) as a marine hotspot during the Paleocene. Early

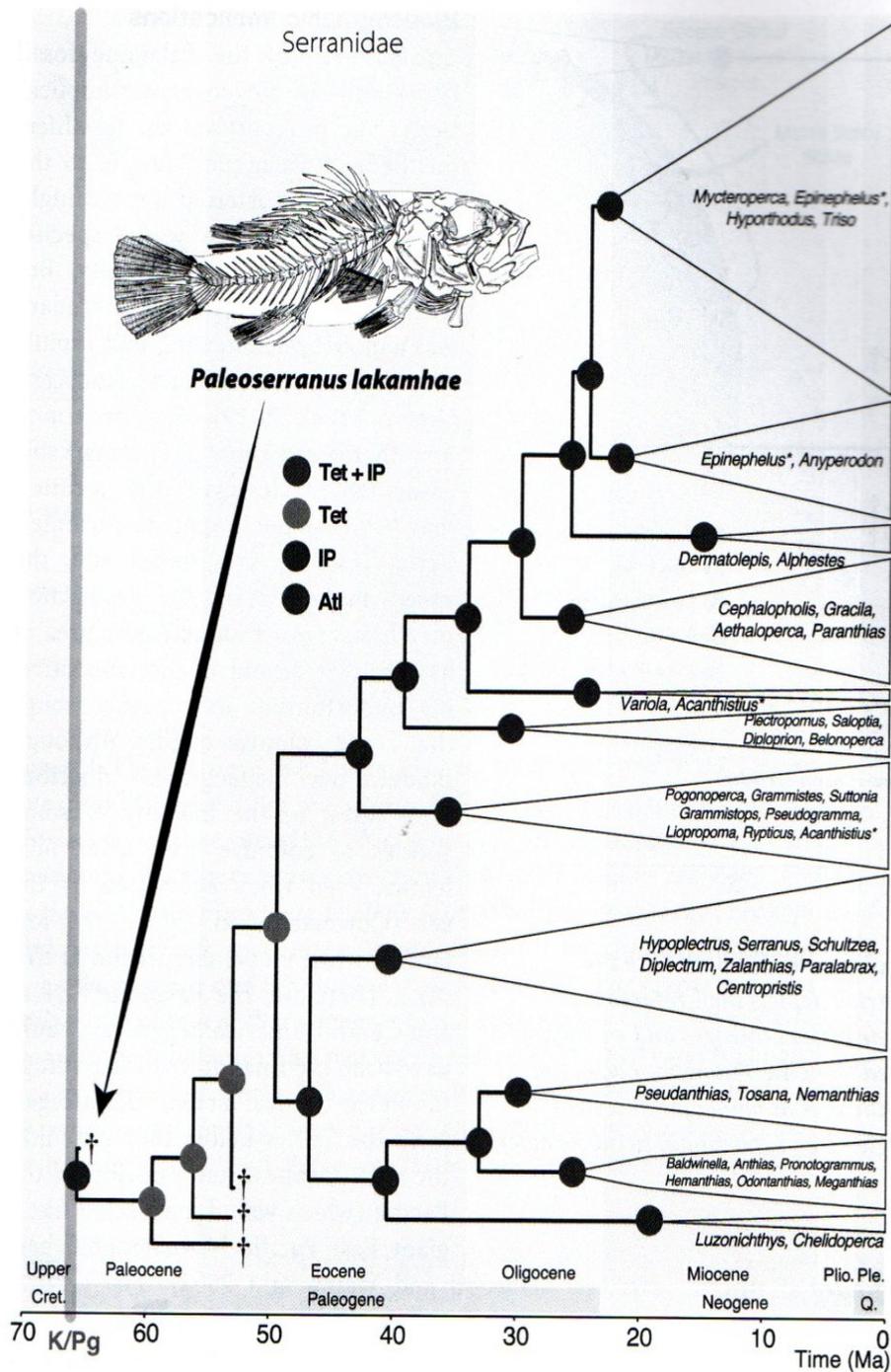


Figure 4. Chronogram of the family Serranidae built with the fossilized birth–death model. The vertical stripe depicts the Cretaceous–Paleogene boundary. Dagger signs denote extinct lineages and we highlight the position of the Palenque species described from the Tenejapa–Lacandón deposits. The nodes are coded according to the best fit model for ancestral biogeographical reconstructions. Triangle sizes are proportional to the number of extant species in each clade. Abbreviations: IP, Indo-Pacific; Tet, Tethys; Atl, Atlantic.

reconstructions of the biogeographic origins of reef fish families have been stymied by the overwhelming preponderance of lineages in the Indo-Australian Archipelago biodiversity hotspot. It is therefore almost inevitable that biogeographic reconstructions place the origins of families in the Indo-Australian Archipelago (e.g., Cowman and Bellwood 2013, Thacker 2015). The fossil evidence clearly indicates that this is not the case and the inclusion of Bolca fossils shifts the origins to the

west, paralleling the patterns seen in the movement of the world’s marine biodiversity hotspots (Dornburg et al. 2015, Siqueira et al. 2019b). This accords well with the hopping hotspot scenario of Renema and colleagues (2008), who described a progressive eastward shift in the marine biodiversity hotspots from the Tethys of Europe in the Eocene, to paired Tethys and Arabian hotspots in the Oligocene, and finally to a single large Indo-Australian Archipelago hotspot in the Miocene. The Palenque fossils offer an extension to this scenario with the earliest origins and perhaps a protohotspot being even further west in the Western Atlantic—before hopping to the central Tethys.

The biogeographic reconstructions all include the Western Atlantic in the early evolution of the three reef fish groups (figures 3–5). Indeed, in the Serranidae it appears that the early expansion of the family (i.e., the crown group) probably did occur in the Western Atlantic region (figure 4), the first hints of a possible Western Atlantic protobiodiversity hotspot. However, the early diversification of the Pomacentridae (figure 5) and Aulostomoidea (figure 3) probably already included the central Tethys, suggesting that geographic expansion was already occurring before the Western Atlantic hotspot was fully formed. The hotspot spread before it could hop. Interestingly, the other fossils in all three groups were found in the central Tethys, which underpins the early expansion of taxa and the importance of the central Tethys as a marine biodiversity hotspot during the Eocene–Oligocene (figures 3–5). This pattern is most evident in the Aulostomoidea, which has a richer fossil record when compared to the other families. Out of 20 extinct taxa, only the Palenque Paleocene fossil *Eekaulostomus cuevasae* is described from the Western Atlantic region. It therefore plays a central role in illuminating the early biogeographical history of this iconic group of fishes, although later diversification is predominantly Tethyan. Finally, the biogeographical reconstructions also suggest that it was only during the Oligocene–Miocene that lineages in all three groups started to diversify within

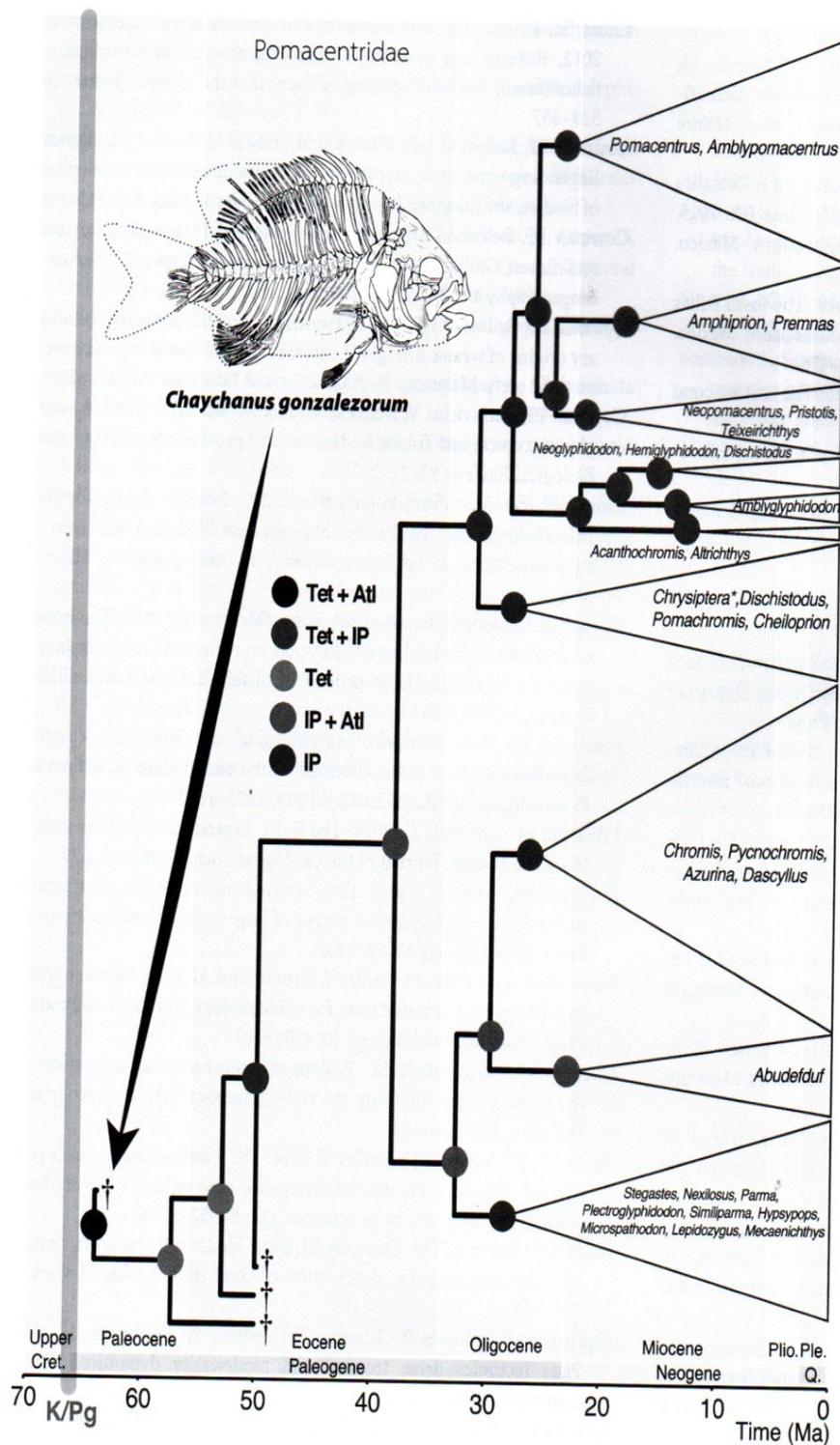


Figure 5. Chronogram of the family Pomacentridae built with the fossilized birth–death model. The vertical stripe depicts the Cretaceous–Paleogene boundary. The dagger signs denote extinct lineages, and we highlight the position of the Palenque species described from the Tenejapa–Lacandón deposits. The nodes are coded according to the best fit model for ancestral biogeographical reconstructions. The triangles are proportional to the number of extant species in each clade. Abbreviations: IP, Indo-Pacific; Tet, Tethys; Atl, Atlantic.

the Indo-Pacific (figures 3–5)—that is, the location of the present hotspot for marine biodiversity. The pattern is, therefore, entirely consistent with previous studies describing the origins of the Indo-Australian Archipelago hotspot (Renema et al. 2008, Cowman and Bellwood 2013).

Conclusions

Overall, the Palenque fossil fishes most clearly reveal the early origins of coral reef fishes. After the collapse of many major marine groups at the Cretaceous–Paleogene mass extinction event, there was a rapid rebound, with the appearance of the three focal reef fish groups within just 500,000 (Aulostomoidea) to 3 million years (Pomacentridae). Early diversification within these groups probably laid the foundations for a protohotspot in the Western Atlantic. However, rapid geographic expansion in most groups probably led to diversification over a broader geographic extent, that encompassed the Western Atlantic and central Tethys. Notably, the Western Atlantic remained an important location for the earliest origins and initial diversification of all three fish groups. It is remarkable that the study of a collapsed human society (the Mayans), led to the discovery of the origins of modern reef fish assemblages. All this happened in a location a few hundred kilometers from the asteroid impact that reset the world’s biological systems, triggering the events that led to the ecosystems we see today. However, it may be the ability of the Palenque fishes to reconcile the molecular and fossil evidence—and to open a new arena of research—that is their greatest legacy.

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Conflict of interest

The authors declare no competing interests.

Supplemental material

Supplemental data are available at BIOSCI online.