Remarkable dominance of myctophid otoliths in Upper Miocene Chagres Formation, Caribbean Panama

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Abstract

Marine fossils from the Upper Miocene Chagres Formation in northern Panama offer critical insights into the paleoenvironmental conditions and ecological responses prior to the separation of the Atlantic from the Pacific by the formation of the Isthmus of Panama. Here we present a systematic study based on more than 6,200 otoliths collected from a coastal exposure near the town of Piña, Colón. This assemblage is remarkable for the extraordinary dominance of the family Myctophidae, constituting over 96% of specimens. The otolith density in the sediments is among the richest known globally (278.80 ± 135.59 otoliths/kg). The taxonomic composition is represented by 31 taxa across 12 families, including four new species: namely *Chiloconger aflorens* sp. nov., *Dasyscopelus inopinatus* sp. nov., *Hoplostethus boyae* sp. nov., and *Malakichthys schwarzhansi* sp. nov. Taphonomic evidence, combined with abundant predatory marine vertebrate fossils and extensive burrow ichnofossils, indicates a dynamic and highly productive nearshore ecosystem. The dominance of myctophids and multiple lines of evidence support the existence of a Late Miocene coastal upwelling system in the region, highlighted by efficient trophic transfer channeled from high primary production to apex predators. These findings provide a nuanced understanding of Neogene marine ecosystems prior to the final emergence of the Isthmus of Panama.

Introduction

The formation of the Isthmus of Panama is recognized as a critical event that fundamentally shaped modern ocean circulation, biogeographic patterns, and the evolutionary history of both terrestrial and marine organisms (Haug & Tiedemann, 1998; O'Dea et al., 2016; Stigall et al., 2017; Domingo et al., 2020; Jackson & O'Dea, 2023; Titus et al., 2024). Localized tectonic fracturing, faulting and extension, as well as subduction-driven uplift during the formation of the isthmus resulted in numerous marine sedimentary basins to develop initially as interconnected fore- and back-arc basins along an extended archipelago (Farris et al. 2011). Continued uplift and volcanic "infilling" (Buchs et al. 2019) eventually led to the isthmus forming a complete marine barrier in the Late Pliocene around 2.8 Ma (O'Dea et al., 2016). These sedimentary basins are crucial repositories of Neogene fossils, which have been helpful in revealing patterns of change

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in the diversity, ecology and evolution of marine faunas through a major environmental transition (Jackson & O'Dea, 2023).

Marine sedimentary archives often contain fish otoliths which offer unique insights into the spatiotemporal distribution, community structure, and evolutionary history of fishes (Nolf, 2013). In Tropical America, multiple studies have been conducted on Neogene otolith, including Schubert (1908), Fitch (1984), and Martin & Dunn (2000) in Panama, Nolf (1976) in Trinidad, Nolf & Stringer (1992) in the Dominican Republic, Stringer (1998) in Jamaica, Nolf & Aguilera (1998) and Aguilera & Rodrigues de Aguilera (2001, 2003) in Venezuela, and Aguilera et al. (2014) in Brazil. Studies by Schwarzhans & Aguilera (2013, 2016, 2024) and Aguilera et al. (2016, 2020) have comprehensively described otoliths of multiple families from tropical America, including material from Panama. Nonetheless, the Upper Miocene Chagres Formation, one of the significant fossil-yielding strata associated with the final stages of isthmus formation (Stiles et al., 2022), has not been investigated in its entirety with respect to its otolith assemblage at the community level.

The depositional environment of Chagres Formation was originally interpreted as a deep-water setting with notable Pacific influence (Collins & Coates, 1993; Coates & Obando, 1996), based primarily on the composition of benthic foraminifera (Collins et al., 1996, 1999), elasmobranch teeth (Carrillo-Briceño et al., 2015), and teleost otoliths (Aguilera & Rodrigues de Aguilera, 1999). Conversely, a recent study of ichnofossils and sedimentological data has proposed a relatively shallow-water depositional environment (Stiles et al., 2022).

In this study, we present results from quantitative otolith sampling from the Chagres Formation on the Caribbean coast of Panama. Based on the collection of over 6,200 otoliths, we document the richest fish records from the Late Miocene of the Panama Canal Basin. We provide detailed taxonomic remarks and assess taphonomic conditions which bring greater insights into the paleoenvironmental conditions and marine trophic dynamics of the region during the Late Miocene.

Geological setting

The Panama Canal Basin is underlain primarily by Cretaceous volcanic and plutonic rocks, which reflects its volcanic arc origins (Coates & Obando, 1996; Coates, 1999). Overlying this basement is a series of Cenozoic sedimentary formations, and the extensive Neogene transisthmian marine sediments (i.e. deposits spanning across the Isthmus of Panama) were exposed during the construction of the Panama Canal (Woodring, 1957). Sediment deposition within the basin is structurally controlled by the Gatun Fault Zone, which separates the Chorotega Block in western Panama and the Choco Block in the east (Coates & Obando, 1996; Coates, 1999).

On the Caribbean side of Colón Province, Panama, the Neogene deposits are primarily represented by the Gatun Formation and the overlain Chagres Formation (Coates, 1999). The Gatun Formation is of late Middle to Late Miocene age (Hendy, 2013), consists of approximately 500 m of massive, blue-gray, marine fine sandstone to siltstone, notable for its rich and diverse marine fossils, particularly the mollusk fossils (Woodring, 1957; Jackson et al., 1999). Fossil evidence indicates deposition occurred at relatively shallow marine depths, typically less than 40 m (Coates & Obando, 1996; Collins et al., 1999).

The Chagres Formation, deposited between approximately 6.4 and 5.8 Ma (Late Miocene; Collins et al., 1996), is predominantly exposed in the northern part of the Panama Canal Zone and extends southwestward along the Caribbean coast (Fig. 1). The formation is

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about 250 m thick and is primarily comprised of marine, blue-gray volcaniclastic sandstone derived from volcanic arcs (Collins et al., 1996; Coates, 1999). It is subdivided into three members: the lower Toro Limestone, the middle Rio Indio Siltstone, and the upper Chagres Sandstone members. The Toro Limestone Member is characterized by calcareous beds rich in coquina composed of echinoid, mollusk, and barnacle fragments (Coates, 1999; Stiles et al., 2022). The Rio Indio Siltstone is characterized by gray-brownish silts with scattered mollusk fossils (Stiles et al., 2022). The Chagres Sandstone Member consists of gray, quartzose, volcanic-derived silty sandstones that exhibit extensive bioturbation, predominantly from arthropod burrows (Collins et al., 1996; Stiles et al., 2022). These sandstones yield abundant marine fossils and are prominently exposed along the Caribbean coast (Aguilera & Rodrigues de Aguilera, 1999; Carrillo-Briceño et al., 2015; Pyenson et al., 2015; Velez-Juarbe et al., 2015; Stiles et al., 2022; Benites-Palomino et al., 2023; Cadena, Gracia & Combita-Romero, 2023), particularly near the town of Piña (see below).

Materials & Methods

Sampling

The fossil site is located about ~500 m northeast of Piña town, Colón, Panama (Fig. 1; 9°17'09.11"N, 80°02'41.28"W). This locality corresponds to the Piña Norte site described by Stiles et al. (2022) and the STRI site 650009 in Pyenson et al. (2015). The Chagres Sandstone Member of the Chagres Formation is exposed along the Caribbean shoreline, especially at low tide (Fig. 2B). Fragments of echinoids, mollusks, and fish otoliths, as well as trace fossils, are easily visible on the surface of the siltstone (Stiles et al., 2022). Surface sediments are yellowish to brownish, contrasting with fresh sediments located several centimeters below the surface, which are darker and have a distinct blue-gray color. We collected thirty-three bulk sediment samples laterally from the same stratigraphic level in this fresher, blue-grey material in 2018 and 2024 (Fig. 2A). Samples weighed on average 0.6 kg each (Table S1). An additional larger bulk sample (unweighted but less than 2 kg, CH18-1-1) was also collected from this fresh sandstone layer for otolith extraction (Tables S1, S2). Permits for collecting and exporting paleontological samples were issued by the Ministerio de Comercio e Industrias (MICI, SE/AO-4-18) in Panamá.

Otolith preparation, imaging, and identification

Bulk sediment samples were disaggregated using freeze-thaw cycles and Glauber's Salt (saturated sodium sulfate solution) methods (Hanna & Church, 1928; Herrig, 1966), then wet-sieved through a 500-µm mesh. After sieving, sediments were dried overnight in an oven at 40°C. Otoliths larger than this 500-µm mesh were carefully hand-picked under a stereomicroscope. In this study, the term "otolith" refers to the saccular otolith (sagitta). Representative otoliths were photographed using a digital camera adapted to a Nikon SMZ1270 stereomicroscope, and image stacking was performed using Helicon Focus software. Final figures were prepared using Adobe Photoshop.

For otolith identification and terminology, we followed key references, including Rivaton & Bourret (1999), Lin & Chang (2012), Schwarzhans (2013), Schwarzhans & Aguilera (2013, 2016), Nolf (2013), and Haimovici et al. (2024). In addition, direct comparisons were made with a reference collection of extant otoliths housed at the Biodiversity Research Museum, Academia Sinica, Taiwan (BRCAS) under the code CHLOL. Whenever possible, otoliths were identified to the species level. All collected specimens are stored at BRCAS, and figured specimens are archived under the registration code ASIZF.

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Sampling completeness and biodiversity analysis

Due to the overwhelming number of otoliths in each sample, we conducted biodiversity analysis to assess sampling completeness and diversity. Otolith abundances were quantified by dividing otolith counts by the corresponding dry sediment weight (kg) for each sample (except CH18-1-1). Family-level abundances were calculated by summing otolith counts across all samples, and families were ranked by total abundance. To evaluate statistical uncertainty in these abundance estimates, binomial 95% confidence intervals were computed using Wilson's method. We computed these with and without the unweighted sample CH18-1-1. Diversity was estimated using Hill numbers (Hill, 1973) calculated at three different orders: $q = 0$ (^{0}D, species richness), $q = 1$ (^{1}D, Shannon diversity), and $q = 2$ (^{2}D, Simpson diversity), representing total (alpha) species richness, abundant species diversity, and dominant species diversity, respectively (Chao, Chiu & Jost, 2014; Chao et al., 2020; Lin et al., 2023a). Rarefaction and extrapolation methods were applied to create species accumulation curves, with 1,000 bootstrap resampling iterations used to estimate 95% confidence intervals. Specimen-based abundance data was analyzed to evaluate sample coverage comprehensively. All analyses were conducted using the R package iNEXT (Chao, Chiu & Jost, 2014; Hsieh, Ma & Chao, 2016).

Nomenclatural acts for new species

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:996A25D1-9CB7-4AAD-9041-0ABCF49710C5. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Results

Systematic Paleontology

A list of identified taxa and their abundances is presented in Table 1. Classification scheme follows Nelson et al. (2016). Morphometrics and measurements include otolith length (OL), otolith height (OH), sulcus length (SuL), ostium length (OsL), and cauda length (CaL). Descriptions and discussions for common or previously described taxa are provided briefly under remarks, while new species include detailed descriptions and diagnostics.

Order Anguilliformes
Family Congridae
Genus *Chiloconger* Myers & Wade, 1941
Chiloconger aflorens sp. nov.
(Figs. 3A–3B)

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Holotype: ASIZF 0100943 (Fig. 3A), Piña Norte, Panama. Upper Miocene, Chagres Formation. OL = 5.48 mm, OH = 4.23 mm.
Paratype: One specimen: ASIZF 0100944 (Fig. 3B), same data as holotype. OL = 1.85 mm, OH = 1.52 mm.
Etymology: The species name *aflorens* is derived from the Spanish word "afloramiento", meaning "upwelling." It refers to the flourishing productivity and dynamic marine conditions of the coastal upwelling system in which this species lived. It also symbolically reflects the scientific blossoming of paleontological research in Panama.
Diagnosis: OL/OH = 1.20–1.30, OL/SuL = 1.55–1.80. Otoliths oval with thick profile. Dorsal rim dome-shaped, evidently elevated anterior to midline; ventral rim smoothly curved. Sulcus moderately wide, poorly differentiated into ostium and cauda. Cauda short with an obtuse posterior tip.
Description: Otoliths oval to elliptic, thick; inner and outer faces highly convex. Anterior and posterior rims pointed in holotype, blunt to nearly vertical in juvenile paratype. Dorsal rim dome-shaped, elevation just anterior to midline. Ventral rim smoothly curved. Sulcus median, very slightly inclined (~15°), with ostium and cauda only faintly differentiated due to the indistinct collum, resulting in a nearly continuous sulcus. Ostial channel nearly indiscernible in holotype, but narrow, vertical, and ending just before dorsal elevation in paratype. Cauda short, extending slightly posterior to dorsal elevation; bears obtuse, truncated posterior end.
Remarks: *Chiloconger* is distinguished from other congrids by the notably short cauda, a character state considered plesiomorphic (Schwarzhans 2019; Schwarzhans & Nielsen, 2021). Although based on small and not fully morphologically mature specimens, the new species differs from the two extant species, *C. dentatus* (Garman, 1899) and *C. philippinensis* Smith & Karmovskaya, 2003, by having a less pronounced, more anteriorly positioned dorsal elevation (Schwarzhans, 2019). Additionally, compared to the Early Miocene *Chiloconger chilensis* Schwarzhans & Nielsen, 2021 from Chile (Schwarzhans & Nielsen, 2021), *C. aflorens* exhibits a more compact and rounded shape.
Occurrence: Currently known only from the Piña Norte locality, Panama (Upper Miocene, Chagres Formation).

Genus *Rhynchoconger* Jordan & Hubbs, 1925
Rhynchoconger sp.
(Fig. 3C)

Remarks: A single, fragmentary otolith exhibiting key *Rhynchoconger* characteristics is identified to the genus level. The preserved portion shows a discernible ostial channel and anterior ostium outline, diagnostic for *Rhynchoconger* (Schwarzhans, 2019). Due to the incomplete preservation, further species-level identification is not possible.

Order Argentiniformes
Family Argentinidae
Genus *Argentina* Linnaeus, 1758

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Gelöscht: poorly divided into ostium and cauda.
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Gelöscht: a subadult specimen
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Argentina sp.
(Fig. 3D)

Remarks: A single thin otolith is assigned to the genus *Argentina* based on a strong, nearly orthogonal posterodorsal angle, a straight posterior rim, a curved ventral rim, and a median, horizontally oriented sulcus. The anterior portion of the specimen is missing, preventing confident assignment to species level.

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Order Stomiiformes
Family Sternoptychidae
Genus *Polyipnus* Günther, 1887
Polyipnus sp.
(Figs. 4A–4B)

Remarks: *Polyipnus* otoliths are distinctive by their tall, compressed shape, indistinctive sulcus outline, thin, slender rostrum bearing most of the ostium, elevated colliculum crest along the crista inferior, and a considerable thickness in the posterior rim. However, species-level identification is challenging due to extensive interspecific overlap and the limited availability of modern otolith reference material from the region, and the rostrum is very fragile and usually broken off in the fossil record, seriously hampering species definitions and recognition. Additionally, most specimens from the Chagres Formation are poorly preserved, with only the thick posterior rims preserved. The better-preserved specimens are depicted here.

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Order Myctophiformes
Family Myctophidae

Remarks: The abundance of myctophid otoliths in the Chagres Panama is extraordinary. Most identifications are based on large subadult to adult individuals; tentative assignments for juvenile or poorly preserved specimens were conservative, resulting in a significant number of otoliths classified as Myctophidae indet. Consequently, the true myctophid diversity is likely underestimated in this collection. Significant advances in myctophid otolith taxonomy, sourced by the development of comprehensive global reference collections (Rivaton & Bourret, 1999; Schwarzhans, 2013), have greatly improved identification in fossil assemblages (Schwarzhans et al., 2022; Lin et al., 2023b). We primarily follow Schwarzhans & Aguilera (2013) for taxonomic treatment and species-level identification of the myctophid otoliths in this study.

Genus *Benthosema* Goode & Bean, 1896
Benthosema pluridens Schwarzhans & Aguilera, 2013
(Fig. 4C)
2013 *Benthosema pluridens*; Schwarzhans & Aguilera: pl. 1, figs. 8–12.

Remarks: Otoliths of *B. pluridens* are relatively common in the collection. They are characterized by a sub-rectangular outline, a relatively flat dorsal rim, and multiple ventral denticles. However, juvenile myctophid otoliths often display intermediate outlines between rounded and sub-rectangular forms. To ensure accuracy, only specimens closely matching those illustrated by Schwarzhans & Aguilera (2013: pl. 1, figs. 8–12) were assigned to *B. pluridens*; other, less definitive specimens were conservatively classified under Myctophidae indet. Therefore, the true abundance of *B. pluridens* may be underestimated.

Genus *Bolinichthys* Paxton, 1972
Bolinichthys sp.
(Fig. 4D)

Remarks: A single, juvenile otolith is assigned to *Bolinichthys* based on its prominent rostrum and gently curved, oblique posterior rim, consistent with diagnostic features of the genus (Rivaton & Bourret, 1999). Notably, *Bolinichthys* otoliths have not been previously reported from the Neogene of tropical America (Schwarzhans & Aguilera, 2013).

Genus *Dasyscopelus* Günther, 1864

Remarks: Following the molecular phylogenetic revision by Martin et al. (2018), seven species previously assigned to *Myctophum* (*M. asperum*, *M. brachygnathos*, *M. lychnobium*, *M. obtusirostre*, *M. orientale*, *M. selenops*, and *M. spinosum*) were reallocated to *Dasyscopelus*. We adopt this updated classification herein, although we note that, in our view, otolith morphology among these species does not consistently show clear differentiation from other *Myctophum* species or internally within *Dasyscopelus* itself (see Schwarzhans & Aguilera, 2013: pl. 3). Otoliths attributed to *Dasyscopelus* are typically characterized by a pronounced posterior extension and a pointed ventral rim, giving them a more angular appearance compared to the generally rounded and often deeper-bodied otoliths of *Myctophum*. Exceptions include *D. brachygnathos* and *D. selenops*, which possess a much shorter posterior rim and a taller overall shape (Schwarzhans & Aguilera, 2013; Ng et al., 2024a).

Three closely related species—*Dasyscopelus degraciai* (Schwarzhans & Aguilera, 2013), *Dasyscopelus jacksoni* (Aguilera & Rodrigues de Aguilera, 2001), and the newly described *Dasyscopelus inopinatus* sp. nov. (see below)—are here allocated to the genus *Dasyscopelus* due to their otoliths having a protruding posterior part, a relatively flat dorsal rim, and general similarity to extant *Dasyscopelus* species, such as *D. asper* and *D. lychnobius*.

Dasyscopelus degraciai (Schwarzhans & Aguilera, 2013)
(Figs. 5A–5F)
2013 *Myctophum degraciai*; Schwarzhans & Aguilera: pl. 5, figs. 1–5.

Remarks: The otoliths of *D. degraciai* are distinguished by their compact outline, less pronounced posterior extension, gently curved dorsal rim, and narrower sulcus. They differ from the co-occurring *D. inopinatus* sp. nov. and the Pliocene *D. jacksoni* by their shorter posterior tip, more compact, less angular shape, narrower ostium, and the more delicate crenulation of the otolith rims.

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Dasyscopelus inopinatus sp. nov.
(Figs. 5G–5L)

Holotype: ASIZF 0100962 (Fig. 5I), Piña Norte, Panama. Upper Miocene, Chagres Formation. OL = 3.61 mm, OH = 2.43 mm.

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Paratypes: Five specimens: ASIZF 0100957–0961 (Figs. 5G–5H, 5J–5L), same data as holotype. OL = 3.28–4.06 mm, OH = 2.31–2.66 mm.
Additional material: 57 specimens, unfigured, same data as holotype.
Etymology: From Latin *inopinatus* (feminine *inopinata*) = unexpected, alludes to the surprising and remarkable discovery of this new species, which exhibits a mosaic of morphological features shared with closely related congeners.
Diagnosis: OL/OH = 1.40–1.65 (mean = 1.48, n = 10), OL/SuL = 1.15–1.25 (mean = 1.23, n = 6), OsL/CaL = 1.45–2.10 (mean = 1.76, n = 10). Elongate otoliths with thin profile. Dorsal rim flat, nearly horizontal, with slight or no posterior elevation and a postero-dorsal angle. Ventral rim curved, bearing around eight lobes or denticles. Posterior rim short, nearly vertically straight. Sulcus very wide, with large, rectangular ostium and squarish cauda.

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Description: Otoliths elongate, thin; both inner and outer faces are relatively flat. Anterior rim bearing large, protruding rostrum and shorter but conspicuous antirostrum, separated by clearly defined notch (excisura), varies from shallow to deep. Dorsal rim nearly horizontally flat, occasionally slightly elevated posteriorly, forming postero-dorsal angle just anterior to marked postero-dorsal concavity. Posterior rim short and nearly vertically straight. Ventral rim broadly curved, bearing ~8 lobes or denticles. Sulcus wide, median-positioned. Ostium large, deep, rectangular; cauda short, squarish.
Remarks: The otoliths of the new species exhibit an intermediate morphology between *D. degraciai* and *D. jacksoni*. They share with *D. degraciai* a compact, deep-bodied outline and a less elongate posterior part, but resemble *D. jacksoni* in having a horizontal dorsal rim, wide sulcus, and a postero-dorsal concavity. Notably, the original illustrations of *D. jacksoni* (as *Lampadena jacksoni* in Aguilera & Rodrigues de Aguilera, 2001: figs. 7.15–7.22) suggest a more elongated and posteriorly extended shape compared to the ones documented in Schwarzhans & Aguilera (2013: pl. 5, figs. 6–10), as also indicated by differences in OL/OH ratios (1.60–1.85 vs. 1.50–1.65), although this may reflect ontogenetic variation.

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Schwarzhans & Aguilera (2013) proposed a species turnover from the Late Miocene *D. degraciai* to the Pliocene *D. jacksoni* at the boundary between Messinian and Zanclean and further suggested a linear relationship between the two species. However, the finding of *D.*

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inopinatus suggests a more complex evolutionary history, with this new species likely representing a transitional or closely related lineage to *D. jacksoni*.
Occurrence: Currently known only from the Piña Norte locality, Panama (Upper Miocene, Chagres Formation).

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Genus *Diaphus* Eigenmann & Eigenmann, 1890

Remarks: *Diaphus* represents the most abundant and diverse taxon in our collection. A total of seven species, *D. aequalis*, *D. apalus*, *D. barrigonensis*, *D. dumerilii*, *D. multiserratus*, *D. pedemontanus*, and *D. rodriguezi*, are recorded. Our identifications are primarily based on larger, more mature specimens, which exhibit sufficient diagnostic characters to allow confident assignment (see remarks under the family). The otolith taxonomy of *Diaphus* has been extensively revised by Schwarzhans & Aguilera (2013), whose detailed descriptions and high-quality images serve as the primary references for this study. Therefore, only brief remarks distinguishing among similar co-occurring species are presented here.

Diaphus aequalis Schwarzhans & Aguliera, 2013
(Figs. 6A–6C)
1992 *Diaphus* aff. *D. brachycephalus* Tåning, 1928; Nolf & Stringer: pl. 10, figs. 11–13.
?1992 *Diaphus* sp. 1; Nolf & Stringer: pl. 10, fig. 19.
1998 *Diaphus brachycephalus* Tåning, 1928; Stringer: pl. 2, fig. 2.
2013 *Diaphus aequalis*; Schwarzhans & Aguilera: pl. 13, figs. 13–25.

Remarks: The species is common but never abundant within the Piña assemblage. Its otoliths are morphologically most similar to smaller individuals of the co-occurring *D. apalus* and, to a lesser extent, *D. barrigonensis* (see below). It differs from *D. apalus* by its very rounded and compact outline, and by possessing only a subtle postero-dorsal concavity (vs. a pronounced, deeply indented concavity). Compared to *D. barrigonensis*, *D. aequalis* is distinguished by its shorter rostrum and gently curved dorsal and posterior rims (vs. steeply inclined dorsal rim and sharp posterior rim).

Diaphus apalus Schwarzhans & Aguliera, 2013
(Figs. 6D–6F)
2013 *Diaphus apalus*; Schwarzhans & Aguilera: pl. 13, figs. 1–10.

Remarks: See remarks under *D. aequalis*.

Diaphus barrigonensis Schwarzhans & Aguliera, 2013
(Figs. 6G–6K)
2001 *Diaphus* sp. 2; Aguilera & Rodrigues de Aguilera: fig. 7.7–7.8.
2013 *Diaphus barrigonensis*; Schwarzhans & Aguilera: pl. 7, figs. 1–9.

Remarks: See remarks under *D. aequalis*.

Diaphus dumerilii (Bleeker, 1856)
(Figs. 6L–6O)
?1976 *Diaphus dumerilii* (Bleeker, 1856); Nolf: pl. 3, figs. 8–14.
1992 *Diaphus* sp. 1; Nolf & Stringer: pl. 10, figs. 18, 20–21, 23 (non figs. 19, 22).
1998 *Diaphus* sp. 1; Stringer: pl. 2, fig. 3.
2001 *Diaphus dumerilii* (Bleeker, 1856); Aguilera & Rodrigues de Aguilera: figs. 7.1–7.2.
2013 *Diaphus dumerilii* (Bleeker, 1856); Schwarzhans & Aguilera: pl. 10, figs. 18–23.

Remarks: The otoliths of *D. dumerilii* are most recognizable by their slightly elevated antero-dorsal rim and the narrow antero-ventral part of the rostrum. However, as noted by Schwarzhans & Aguilera (2013), these otoliths are morphologically inconspicuous and, in our view, confident identification is generally limited to larger, well-preserved specimens. Some otoliths assigned to *D. dumerilii* by Nolf (1976) from Neogene deposits in Trinidad display a more compact outline (e.g., pl. 3, figs. 8, 11–12), suggesting they may actually belong to different species. Nevertheless, distinguishing such variations based solely on the available figures remains difficult.

Diaphus multiserratus Schwarzhans & Aguliera, 2013
(Figs. 7A–7B)

2013 *Diaphus multiserratus*; Schwarzhans & Aguilera: pl. 12, figs. 4–11.

Remarks Otoliths of *D. multiserratus* are readily distinguished by their elongate outline, wide sulcus, and, most conspicuously, the presence of numerous minute denticles along the ventral rim. Although not a frequent species in the collection, it is typically represented by larger, well-preserved specimens.

Diaphus pedemontanus (Robba, 1970)
Fig. 7C–F

1970 *Porichthys pedemontanus*; Robba: pl. 16, fig. 8.
2013 *Diaphus pedemontanus* (Robba, 1970); Schwarzhans & Aguilera: pl. 9, figs. 1–4.

Remarks: *Diaphus pedemontanus* closely resembles the co-occurring and most abundant species *D. rodriguezi* but can be distinguished by a high, more undulating dorsal rim and a short, nearly vertically straight posterior rim, whereas *D. rodriguezi* has a gently curved dorsal rim, a deeper and wider excisura, and a larger rostrum (see below). Otoliths of *D. pedemontanus* are widely

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recorded from the Miocene and Pliocene of the Mediterranean (Girone, Nolf & Cavallo, 2010; Lin, Girone & Nolf, 2015; Lin et al., 2017) and have also been documented in the coeval Caribbean assemblages (Schwarzhans & Aguilera, 2013). Ontogenetic variation in *D. pedemontanus* is considerable (Brzobohatý & Nolf, 2000), although we note that Caribbean specimens tend to be smaller than their European counterparts.

Diaphus rodriguezi Schwarzhans & Aguliera, 2013
(Figs. 7G–7J)

2013 *Diaphus rodriguezi*; Schwarzhans & Aguilera: pl. 9, figs. 5–12.

Remarks: See remarks under *D. pedemontanus*.

Genus *Diogenichthys* Bolin, 1939
Diogenichthys sp.
(Fig. 7K)

Remarks: A single otolith, characterized by a rounded outline (OL/OH = 1.05) and a thick profile, is assigned to the genus *Diogenichthys* (see Schwarzhans & Aguilera, 2013). However, due to partial damage along the anterior rim and the absence of additional material for comparison, species-level identification was not attempted.

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Genus *Lepidophanes* Fraser-Brunner, 1949
Lepidophanes inflectus Schwarzhans & Aguliera, 2013
(Fig. 8I)

2001 *Lampanyctus* aff. *latesulcatus* Nolf & Stringer, 1992; Aguilera & Rodrigues de Aguilera: figs. 7.13–7.14. (note: the authorship of *L. latesulcatus* should be Nolf & Steurbaut, 1983).
2013 *Lepidophanes inflectus*; Schwarzhans & Aguilera: pl. 6, figs. 16–19.

Remarks: Otoliths of this species are very small, but highly diagnostic within the assemblage. They are particularly recognized by a subtle ventral inflection along the ostial crista inferior, although this feature is variably preserved among specimens. These otoliths also resemble much to those of *Lampanyctus latesulcatus* from the Tortonian Mediterranean; however, *L. latesulcatus* displays a more compact outline and lacks the ventral inflection characteristic of *L. inflectus* (Nolf & Steurbaut, 1983).

Genus *Lobianchia* Gatti, 1904
Lobianchia johnfitchi Schwarzhans & Aguliera, 2013
(Figs. 8A–8C)

2013 *Lobianchia johnfitchi*; Schwarzhans & Aguilera: pl. 14, figs. 10–15.

Remarks: *Lobianchia johnfitchi* is readily distinguished from other myctophid otoliths by its wide sulcus, prominently elevated antero-dorsal rim, and strongly depressed postero-dorsal rim. A closely related extant congener, *L. dofleini* (Zugmayer, 1911), exists during the Miocene–Pliocene in the NE Atlantic and Mediterranean (Lin et al., 2017). We follow Schwarzhans & Aguilera's (2013) interpretation that *L. johnfitchi* persisted in the Caribbean until the Middle Pliocene, whereas *L. dofleini* continued its presence into the modern Atlantic and Mediterranean.

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Gelöscht: middle

Genus *Myctophum* Rafinesque, 1810
Myctophum affine (Lütken, 1892)
(Figs. 8G–8H)

1992 *Myctophum* sp.; Nolf & Stringer: pl. 10, figs. 14–15.
2013 *Myctophum affine* (Lütken, 1892); Schwarzhans & Aguilera: pl. 4, figs. 9–12.

Remarks: *Myctophum affine* is recognized by its very rounded and relatively flat otolith outline. The specimens from the Piña assemblage agree well with extant *M. affine* otoliths (Nolf & Stringer: pl. 10, figs. 16–17; Schwarzhans & Aguilera: pl. 3, figs. 17–18). It differs from the closely related fossil species *Myctophum arcanum* Schwarzhans & Aguliera, 2013 by having a shorter posterior extension and a slightly curved dorsal rim (see below).

Myctophum arcanum Schwarzhans & Aguliera, 2013
(Figs. 8D–8F)

2013 *Myctophum arcanum*; Schwarzhans & Aguilera: pl. 4, figs. 13–17.

Remarks: See remarks under *M. affine*.

Order Gadiformes
Family Macrouridae
Genus *Coelorinchus* Giorna, 1809
Coelorinchus sp.
(Figs. 9A–9B)

Remarks: Two incomplete otoliths are assigned to *Coelorinchus* based on the presence of the characteristic pince-nez-shaped sulcus (homosulcoid-type) and the presence of a collicular crest at the collum. However, due to the fragmentary preservation, further identification beyond the genus level is not possible.

Family Bregmacerotidae

Genus *Bregmaceros* Tompson, 1840

Bregmaceros sp.

(Figs. 9C–9E)

Remarks: *Bregmaceros* otoliths are representatives of the third most common family in the Piña assemblage, although nearly all specimens are poorly preserved. They typically show a heavily abraded inner surface, such that the ostial and caudal depressions are not preserved (Figs. 9C–9D), while the general outline remains intact, complicating detailed taxonomic assignment. The best-preserved specimen is illustrated in Fig. 9E. Due to their preservation state, the specimens are conservatively identified only to the genus level.

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Order Trachichthyiformes

Family Trachichthyidae

Genus *Hoplostethus* Cuvier, 1829

Hoplostethus boyae sp. nov.

(Figs. 10A–10D)

Holotype: ASIZF 0101006 (Fig. 10A), Piña Norte, Panama. Upper Miocene, Chagres Formation. OL = 5.54 mm, OH = 5.38 mm.

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Gelöscht: Late

Paratypes: Three specimens: ASIZF 0101007–1009 (Figs. 10B–10D), same data as holotype. OL = 2.60–6.24 mm, OH = 2.52–5.67 mm.

Etymology: Named in honor of Brígida De Gracia (Boya in Ngäbere, the language of the Ngäbe-Buglé people) for her outstanding contributions to scientific research, public communication, and outreach activities in Panamá. The Ngäbe and their ancestors have inhabited the Isthmus of Panama for millennia, developing traditional ecological knowledge deeply connected to marine productivity cycles. Historical records demonstrate the Ngäbe's reliance on seasonal fish abundance driven by upwelling systems along Panama's Caribbean coast (Cybulski et al., 2025), creating a meaningful temporal bridge between the ancient upwelling ecosystem preserved in the Chagres Formation and the traditional knowledge systems that have recognized and depended upon these productive marine environments through time.

Diagnosis: OL/OH = 1.00–1.15, OL/SuL = 1.15–1.25, OsL/CaL = 0.70–0.90. Tall, sole-shaped otoliths with thick profile. Dorsal rim dome-shaped, evidently elevated posterior to midline; ventral rim either horizontally straight or smoothly curved, occasionally with large undulations. Sulcus very broad, shallow, median, well-differentiated into ostium and cauda. Ostium subtriangular, opening widely antero-dorsally. Cauda broad, rectangular.

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Description: Otoliths tall, sole-shaped, thick; outer face strongly convex, inner face nearly flat. Dorsal rim curved, markedly elevated posterior to midline. Anterior rim with obtuse, upward-directed rostrum. Posterior rim straight, strongly inclined between postero-dorsal and posteroventral angles, especially pronounced in larger specimens. Ventral rim horizontally straight to smoothly curved, occasionally with large undulations. Sulcus shallow, very broad, median; ostium subtriangular, opening widely antero-dorsally with shallow colliculum; cauda rectangular, broad, shallow. Dorsal depression fan-shaped, moderately deep.

Remarks: Among the six extant *Hoplostethus* species inhabiting the pan-Caribbean and East Pacific (*H. atlanticus*, *H. fragilis*, *H. mediterraneus*, *H. mento*, *H. occidentalis*, and *H. pacificus*), *H. boyae* most closely resembles juvenile otoliths of *H. occidentalis* (Haimovici et al., 2024: p. 139; but see (Conversani et al., 2017): pl. 8). Other extant species typically exhibit a more variable dorsal rim, including flattened or undulating forms, often with digitiform projections, which may be a reflection of ontogenetic variation (Kotlyar, 1996). The new species differs by its consistently gently curved, dome-shaped dorsal rim, observed across both juvenile and adult stages. Compared to fossil congeners, such as the European Miocene species *Hoplostethus praemediterraneus* Schubert, 1905, and the Pliocene *Hoplostethus pisanus* Koken, 1891, *H. boyae* exhibits a more elevated dorsal profile and a shorter posterior rim, making the overall outline more compact and erect.

Occurrence: Currently known only from the Piña Norte locality, Panama (Upper Miocene, Chagres Formation).

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Gelöscht: type locality

Order Ophidiiformes

Family Carapidae

Genus *Carapus* Rafinesque, 1810

Carapus sp.

(Figs. 10E–10F)

Remarks: All *Carapus* otoliths in the Piña assemblage are small and represented by juvenile specimens. They closely resemble an undescribed fossil *Carapus* otolith illustrated by Schwarzhans & Aguilera (2016: fig. 12), although preservation quality in our material is poorer. Given the incomplete preservation and small size, the specimens are conservatively assigned to the genus level. Schwarzhans & Aguilera (2016) further referred to a larger specimen from the Pliocene of Jamaica, depicted by Stringer (1998), but in our view, confirming such a connection requires additional material.

Family Ophidiidae

Genus *Lepophidium* Gill, 1895

Lepophidium limulum Schwarzhans & Aguliera, 2016

(Fig. 10G)

Remarks: A comprehensive review on the otolith taxonomy of fossil Ophidiidae from the region, and particularly the genus *Lepophidium*, has been provided by Schwarzhans & Aguilera (2016). The juvenile otoliths assigned to *Lepophidium limulum* closely match the type material illustrated by Schwarzhans & Aguilera (2016: fig. 56). The species is characterized by a gently declining dorsal rim, a moderately proportioned sulcus with a slight ventral notch at the posterior of cauda.

Order Gobiiformes
Family Opistognathidae
Genus *Opistognathus* Cuvier, 1816
Opistognathus sp.
(Fig. 11A)

Remarks: A peculiar, thickset otolith is assigned to *Opistognathus* based on its distinctive sulcus morphology. The ostium curves sharply upward anteriorly, while the cauda initially bends slightly upward before flexing ventrally in its posterior portion. This sulcus configuration matches the pattern seen in extant *Opistognathus* otoliths (see Nolf & Stringer, 1992: pl. 15, fig. 10). Due to limited material, identification is restricted to the genus level.

Order Carangiformes
Family Carangidae
Carangidae indet.
Fig. 11B)

Remarks: Two thin otoliths are assigned to the family Carangidae based on their pronounced concavity of the outer face and the presence of a typical percomorph-type sulcus. However, due to incomplete preservation, particularly of the anterior regions, further identification to genus or species level was not attempted.

Order Acropomatiformes
Family Malakichthyidae
Genus *Malakichthys* Döderlein, 1883
Malakichthys schwarzhansi sp. nov.
(Figs. 12A–12F)

?1999 *Epigonus denticulatus* Dieuzeide, 1950; Aguilera & Rodrigues de Aguilera: pl. 1.

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Gelöscht: , 1999)

Holotype: ASIZF 0101015 (Fig. 12A), Piña Norte, Panama. Upper Miocene, Chagres Formation. OL = 2.78 mm, OH = 2.29 mm.

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Gelöscht: Late

Paratypes: Five specimens: ASIZF 0101016–1020 (Figs. 12B–12F), same data as holotype. OL = 1.89–4.55 mm, OH = 1.53–4.14 mm.
Additional material: Nine specimens, unfigured, same data as holotype.

Etymology: Named in honor of Werner Schwarzhans (Natural History Museum of Denmark) for his outstanding contributions to the study of fossil and extant fish otoliths, particularly in tropical America.

Diagnosis: OL/OH = 1.10–1.30 (mean = 1.20, n = 6), OL/SuL = 1.05–1.15 (mean = 1.10, n = 4), OsL/CaL = 0.60–0.90 (mean = 0.61, n = 6). Pentagonal otoliths with thick profile. Dorsal rim gently angled, highest anterior to midline; ventral rim gently angled or curved, deepest slightly anterior to midline; posterior rim nearly vertically straight. Sulcus broad, median, shallow, clearly divided into ostium and cauda. Ostium oblong, filled with colliculum, opening widely antero-dorsally. Cauda horizontally straight, narrow, slightly flexed at tip, nearly reaching posterior rim.

Description: Otoliths pentagonal, thick; thickness mostly from convex outer face umbo, inner face slightly convex. Dorsal rim gently angled, highest point anterior to midline, ending in postero-dorsal angle (most manifest in larger specimens). Ventral rim curved or subtly angled, deepest point slightly anterior to midline. Posterior rim nearly vertically straight. Sulcus broad, median, bounded by well-developed cristae. Ostium oblong, filled with colliculum, opening widely antero-dorsally; ostial crista superior markedly bent antero-dorsally, crista inferior gently curving upward. Cauda horizontally straight, narrow, nearly reaching posterior rim, slightly flexed at tip. Dorsal depression shallow, wide.

Remarks: The pentagonal outline of *M. schwarzhansi* is superficially similar to otoliths of several other families, such as Lactariidae and Epigonidae. However, none of these possess the markedly upward-directed ostium and sharply bent ostial crista superior observed in *Malakichthys* (Lin et al., 2023b; Ng et al., 2024b) (Fig. 13). Small specimens of *M. schwarzhansi* also resemble otoliths of *Ambassis* (Ambassidae), but *Ambassis* otoliths differ by having a more pointed posterior rim and a slightly widened caudal tip, features not observed in *Malakichthys* (see Fig. 14).

A large otolith previously illustrated by Aguilera & Rodrigues de Aguilera (1999: pl. 1) may belong to this species, although it shows a more strongly elevated dorsal area, possibly reflecting ontogenetic variation. Additional specimens are needed to confirm this assignment.

The genus *Malakichthys* comprises eight extant species distributed in the Indo-Pacific (Yamanoue & Matsuura, 2004; Ng, Liu & Joung, 2023). Other members of the order Acropomatiformes, such as *Parascombrops*, display much wider geographic and stratigraphic distributions (Schwarzhans & Prokofiev, 2017). The occurrence of *M. schwarzhansi* in the Late Miocene of Panama suggests that the genus had a broader Neogene distribution than it does today.

Occurrence: Panama: Upper Miocene, Chagres Formation in Piña Norte locality, Colon. ?Venezuela: Lower Pliocene, Cubagua Formation, northwestern Venezuela.

Otolith density, sample coverage, and diversity indices

A total of 6,211 otoliths were collected from 34 bulk sediment samples, yielding an average otolith density of 278.80 ± 135.59 otoliths/kg (Table S1). Our otolith collection was represented by 31 taxa belonging to 12 families, plus nine additional specimens remaining indeterminate

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Gelöscht: late

(Table 1; Fig. 15). Rank abundance of otolith families remains stable with or without the unweighted sample CH18-1-1 (Fig. 15). Sample coverage, based on specimen counts, reached 99.87%, indicating a high level of sampling completeness. Rarefaction curves based on species richness (^0D) suggested that the estimated diversity could increase to approximately 35 taxa with additional sampling effort, with or without the unweighted sample (Fig. 16). However, rarefaction curves for Shannon (^1D) and Simpson (^2D) diversity indices approached asymptotes, indicating that the most abundant and dominant taxa were successfully captured (Fig. 16). This pattern suggests that any additional taxa would likely be rare and of low-abundance.

Discussion

Taphonomy and preservation

Otoliths are exceptionally abundant at the Piña site and are readily visible on the surface of the exposed sediments. Closer examination reveals that the otoliths are not randomly or evenly distributed but instead exhibit distinct clustering patterns within the sediment layers (Figs. 2C–2D). This clustered distribution suggests that otolith burial was not continuous, but occurred episodically.

Piscivorous predation, digestion, and subsequent excretion are important processes in the formation of otolith assemblages in marine sediments (Schäfer, 1972; Nolf, 1985; Welton, 2015; Lin et al., 2019; Agiadi et al., 2022). Predator feeding events can result in the accumulation of thousands of otoliths, especially by large predators such as whales, dolphins, and tunas (Fitch & Brownell, 1968; Lin et al., 2020). At Piña, fossils of marine predatory mammals (dolphins and predatory whales) as well as piscivorous billfishes and sharks are common (Fierstine, 1978; Vigil and Laurito, 2014; Carrillo-Briceño et al., 2015; Pyenson et al., 2015; De Gracia et al., 2022), supporting a predation-mediated accumulation model. Therefore, the clustered distribution of otoliths in the sediments is consistent with deposition from predator excretions rather than from background mortality or mass mortality events.

Moreover, otoliths appear closely associated with ichnofossils attributed to *Ophiomorpha* (Stiles et al., 2022; Figs. 2C–2D). This suggests that burrowing organisms may have contributed to the local redistribution and concentration of otoliths within their burrow systems, either by incorporating otoliths during their activities or perhaps by selectively concentrating organic-rich material containing otoliths (Fig. 2D). While this burrowing activity does not increase the overall abundance of otoliths in the sediment, it may create localized zones of higher otolith density within and around burrow structures.

Surface-exposed otoliths are, on the whole, heavily weathered, often cleaving in half and exposing their whitish internal structure. Better-preserved otoliths were obtained from excavated blue-grey sediments found around 1–10 cm deep into the exposed sediments, which is where we focused sampling. In cases where lower taxonomic assignment was not possible, this was usually due to specimens being juveniles rather than from poor preservation. Nonetheless, a substantial proportion of specimens are moderately eroded, resulting in loss of outline details, resulting in taphonomic scores of 2 or 3 following Agiadi et al. (2022). This, combined with the prevalence of juvenile specimens, contributed to a relatively high number of otoliths being assigned only to the family level (Table 1).

Paleoenvironmental and paleoecological implications

The otolith assemblage at Piña is extraordinary in both abundance and composition, providing compelling evidence for a unique paleoenvironmental setting. Otolith densities in the

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Gelöscht: , likely linked to biological processes

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Gelöscht: likely

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Gelöscht: otolith

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Gelöscht: feeding on fish or fecal material and subsequently incorporating otoliths into their burrows, as reported in other fossil contexts (Schwarzhans & Carnevale, 2021)

Werner Schwarzhans 17.7.2025 18:24
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Gelöscht: resulted

Chagres Sandstone at Piña are exceptionally high, with individual sediment samples frequently exceeding 300 otoliths/kg, and one sample exceeding 775 otoliths/kg (Table S1). Similarly, Stringer et al. (2020) reported that a clay interbed of the Oligocene Glendon Limestone in Mississippi, USA, yielded 811 otoliths/kg, which they suggest may reflect enrichment driven by piscivorous predators. In this context, the densities observed at Piña rank among the highest otolith densities ever recorded from fossil assemblages for which sediment weight was systematically measured (c.f. Leonhard & Agiadi, 2023). This unprecedented abundance coincides with a unique taxonomic dominance, where mesopelagic lanternfishes (Myctophidae) constitute over 96% of otoliths and represent more than 50% of the taxa (18 out of 31). Other mesopelagic fishes, such as hatchetfishes (*Polyipnus*) and codlets (*Bregmaceros*), were also present, albeit at much lower frequencies (each approximately 1.5% of the total otolith counts). Nevertheless, these three mesopelagic families (Myctophidae, Sternoptychidae, and Bregmacerotidae) were the top three most abundant families (Fig. 15) at the site, demonstrating the importance of mesopelagic fauna in what we now understand to be relatively shallow-water deposits.

The depositional environment of the Chagres Formation has been debated, with interpretations ranging from bathyal depths based on benthic foraminifera and fish assemblages (Collins et al., 1999) to shallow near-shore settings based on ichnofossils and sedimentological evidence (Stiles et al., 2022). A more nuanced interpretation emerges when considering multiple lines of evidence together.

Collins et al. (1999) proposed upper bathyal depths based on benthic foraminifera and the presence of deep-water fish taxa. However, the current geographic position of the Chagres Formation outcrops, located approximately 20 km from the modern shelf edge, would require exceptional tectonic uplift and/or eustatic sea level changes to reconcile with an original bathyal depositional setting. A more parsimonious interpretation suggests deposition occurred at middle to outer neritic depths.

To explore this question further, we analyzed the proportion of mesopelagic planktivorous (principally myctophids) otoliths relative to all other otoliths in 187 modern Caribbean shelf sediment dredge samples (data from O'Dea et al., 2007; Jackson & O'Dea, 2023). When plotted against depth (Fig. 17), these data reveal that modern myctophid otolith assemblages increase from near-shore environments, peaking at around 120–150 m, before declining towards the shelf edge at 200 m. These modern analogues demonstrate that high abundances of myctophid otoliths can accumulate in neritic rather than bathyal environments, and actually favor a mid- to outer neritic setting for the Chagres Formation (c.f. Lin et al., 2016, 2019). The extensive bioturbation observed in the Chagres Formation suggests deposition occurred at the shallower end of this range—i.e., middle neritic depths (~100–120 m).

The extremely shallow, near-shore depths proposed by Stiles et al. (2022) are therefore as unlikely as bathyal depths. Further supporting this interpretation is the total absence of ariid lapilli in our assemblage, which near-ubiquitous in many Neogene shallow-marine otolith assemblages in the Caribbean (Aguilera et al., 2020). The absence here strongly suggests a depositional setting distal from the coast, consistent with a middle neritic environment. A middle neritic depositional setting can be reconciled with moderate post-depositional tectonic uplift, which is consistent with the tectonically active setting during isthmus formation (O'Dea et al., 2016). This interpretation places the Chagres Formation at Piña at an intermediate depth between the demonstrably shallow-water Gatun Formation and true bathyal environments, consistent with the progressive deepening documented during the late stages of inter-oceanic connectivity (O'Dea et al., 2016).

user 25.6.2025 22:31
Gelöscht: To our knowledge

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Gelöscht: , these represent

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Gelöscht:

Werner Schwarzhans 17.7.2025 18:36
Kommentar [1]: This is not a valid observation since it has occurred in shorter times across a wide array of localities. I would simply delete these two sentences. too much unnecessary speculation.

Werner Schwarzhans 17.7.2025 19:08
Kommentar [2]: None of these cited articles contain anything about myctophid otoliths let alone their abundance.
However, Fig. 17 included in this article shows the distribution of myctophids from samples of the captioned two articles. Myctophid otoliths in Fig. 17 do not exceed 20% of all otoliths at any depth. The depths reach from 0 to 210 m, i.e., is entirely on the shelf. The vast majority of myctophids are oceanic mesopelagic fishes undertaking dial migration between the surface at night and about 1000 m and more during the day (e.g., Robison et al., 2020). So this interval is hardly relevant to estimate myctophid abundances in sediments. See also next comment below.

Werner Schwarzhans 17.7.2025 19:13
Kommentar [3]: This is simply wrong! There are two studies of otoliths from ocean bottom dredges relevant for this. 1.- Schwarzhans (2013) from multiple transects from 30 to over 3000 m in the gulf of Guinea and deepwater of the Azores and, 2. Lin et al. (2017) from the Mediterranean Sea. Both studies show that myctophid otoliths can occur indeed in relatively shallow water starting at ab ... [1]

Werner Schwarzhans 17.7.2025 19:17
Kommentar [4]: Yes, unlikely. Where is the reference to Miguel-Salas et al. (2021).
I consider these entire paragraphs as evidence picking and requiring more scrutinity.

Werner Schwarzhans 17.7.2025 19:18
Kommentar [5]: All biota point to a bathyal environmental setting, may be upper bathyal at 300 to 500 m but certainly below shelf break.

user 30.6.2025 21:26
Gelöscht: Indeed, sedimentological evidence and the pervasive presence of ichnofossils at Piña strongly favour a more shallow-water paleoenvironmental interpretation (Stiles et al., 2022) than had previously been assigned ... [2]

Many Caribbean coastal systems experienced strong seasonal upwelling during the Late Neogene. This is observed in the isotopic fluctuations within fossil shells and intracolony variations in module size in bryozoans from Florida and the Dominican Republic to Costa Rica and the Isthmus of Panama (O'Dea et al., 2007; Grossman et al., 2019; Jones & Allmon 1995; Anderson et al., 2017). Additionally, the ecological composition of other nearshore fossil assemblages around the Caribbean during this period strongly support high levels of upwelling and productive coastal ecosystems, many of which contain abundant otoliths from fishes indicative of high productivity (Allmon, 1992; Jackson & O'Dea, 2023) and taxa shared with the Chagres Formation (Aguilera & Rodrigues de Aguilera, 2001). These productive ecosystems subsequently collapsed at the end of the Pliocene, giving rise to the modern, aseasonal and oligotrophic Caribbean (Jackson & O'Dea, 2023).

The tropical upwelling system observed at Piña differs substantially from modern temperate upwelling systems like the colder Humboldt and California Currents, where anchovies, sardines, and other small epipelagic fishes typically dominate (Chavez et al., 2003)—taxa almost entirely missing from the Piña assemblages. Instead, we argue that the Piña ecosystem was shaped by three key factors: warm tropical temperatures, high productivity from seasonal upwelling, and intense predation pressure. High tropical temperatures would have increased metabolic rates, which when combined with elevated primary productivity from upwelling, would have created conditions where predation rates can be extremely high (c.f. Kordas et al., 2022). This would, in turn, favor the selective survival of predator-avoiding planktivorous fishes like myctophids, whose diel vertical migrations (feeding at the surface at night and retreating to deeper waters during the day) serve as a principal mechanism of predator avoidance. Despite these adaptations, a substantial proportion of myctophids still fell prey to predators. However, the extraordinary productivity, and rapid demographic turnover of these small fishes, would have sustained large prey biomass. This rapid turnover, supported by highly productive waters, resulted in the high abundances of myctophid otoliths preserved in the sedimentary record.

Evidence for high predation pressure at Piña is substantial. The locality has yielded numerous predatory shark taxa, including *Otodus megalodon* (Carrillo-Briceño et al., 2015), and the frequent occurrence of large predatory vertebrates (e.g., dolphins, billfishes) and abundant elasmobranch teeth at the Piña locality (Fierstine, 1978; Vigil & Laurito, 2014; Carrillo-Briceño et al., 2015; Pyenson et al., 2015; De Gracia et al., 2022). Particularly striking, but as yet unremarked, is the extraordinary abundance of cookiecutter shark teeth (*Isistius*). While such teeth have been observed in Neogene tropical American sediments, their frequency at the Piña Chagres site is exceptional (see Table S1). As *Isistius* is a facultative ectoparasite that often feeds on large marine mammals, fishes, and sharks (Papastamatiou et al., 2010), their abundance testifies to a remarkably high density of large-bodied animals. The Piña scenario parallels tropical upwelling systems in the modern Arabian Sea, where primary production predominantly channels relatively directly into mesopelagic fish communities (Gjøsaeter, 1984). In these systems, high planktonic productivity supports dense aggregations of myctophids, bypassing some of the longer and more complex food chains, and efficiently transferred to higher trophic levels, particularly to apex predators.

The combination of warm temperatures, strong coastal upwelling, extremely high planktivore abundance, and intense predation pressure thus explains the ecological observations at Piña. The Piña assemblage therefore represents a fossil example of a middle neritic, upwelling-driven, mesopelagic fish-dominated ecosystem during the Late Miocene, providing

user 3.7.2025 21:51
Gelöscht: We account for this apparent discrepancy by accounting for the presence of strong tropical upwelling which has been documented in contemporaneous formations to west in Bocas del Toro and to the east in the Darien using the d^{18}O variation in fossil shells alongside intracolony variation in cupuladriid bryozoans (O'Dea et al., 2007; Grossman et al., 2019; Jackson & O'Dea, 2023). A contemporaneous upwelling system whose fossil otolith assemblages have been identified from near-shore deposits in northern Venezuela (Aguilera & Rodrigues de Aguilera, 2001) share many taxa with the Piña assemblages, further supporting this interpretation.

user 3.7.2025 21:55
Gelöscht: The ecological pattern

user 3.7.2025 21:57
Gelöscht: u

Werner Schwarzhans 17.7.2025 19:20
Kommentar [6]: May be so, but it would still not lead the myctophids to live in shallow water.

kurosa 25.6.2025 12:33
Gelöscht: preferentially

kurosa 25.6.2025 12:30
Gelöscht: parasitizes

user 3.7.2025 22:01
Gelöscht: predator

user 3.7.2025 22:05
Gelöscht: . In such ecosystems, primary production is also

user 3.7.2025 22:05
Gelöscht: through mesopelagic fishes

Werner Schwarzhans 17.7.2025 19:23
Kommentar [7]: No evidence for that (see above). At minimum upper bathyal.

user 3.7.2025 22:06
Gelöscht: The absence of other planktotrophic diurnal taxa further suggests that predation must have been high.

user 30.6.2025 21:43
Gelöscht: shallow-water

user 25.6.2025 21:08
Gelöscht: late

valuable insights into trophic dynamics and ecosystem structure just prior to the final formation of the Isthmus of Panama (Fig. 18).

Conclusions

The exceptionally abundant fossil otolith assemblage from the Chagres Formation at Piña reveals an extraordinary dominance of mesopelagic myctophid fishes during the Late Miocene in Caribbean Panama. Our otolith collection, based on over 6,200 specimens, consists of 31 taxa belonging to 12 families, and the otolith densities are among the highest ever documented from fossil deposits. Taphonomic observations, including clustered otolith distributions and close associations with ichnofossils, indicate that otoliths entered the sediments mainly through predator-prey interactions with additional preservation facilitated by burrowing organisms. Although the dominance of mesopelagic taxa typically implies deeper-water settings (Nolf & Brzobohatý, 1992; Lin et al., 2016, 2017, 2018), the co-occurrence of shallow-water taxa and sedimentological evidence (Stiles et al., 2022) indicate deposition in a highly dynamic, middle neritic depositional setting influenced by coastal upwelling. Our findings reveal previously unrecognized ecological dynamics in ancient tropical coastal ecosystems, where mesopelagic fishes aggregated near-shore in response to nutrient-rich conditions supporting high populations of apex predators. The Piña assemblage, therefore, represents a rare fossil record of a middle neritic, mesopelagic fish-dominated ecosystem linked to coastal upwelling during the Late Miocene (Fig. 18).

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References

Agiadi K, Azzarone M, Hua Q, Kaufman DS, Thivaiou D, Albano PG. 2022. The taphonomic clock in fish otoliths. *Paleobiology* 48:154–170.

Aguilera O, Lopes RT, Rodriguez F, dos Santos TM, Rodrigues-Almeida C, Almeida P, Machado AS, Moretti T. 2020. Fossil sea catfish (Siluriformes; Ariidae) otoliths and in-skull otoliths from the Neogene of the Western Central Atlantic. *Journal of South American earth sciences* 101:102619.

Aguilera O, Rodrigues de Aguilera D. 1999. Bathymetric distribution of Miocene to Pleistocene Caribbean teleostean fishes from the coast of Panama and Costa Rica. *Bulletins of American paleontology* 357:251–269.

user 25.6.2025 21:08
Gelöscht: late

Werner Schwarzhans 17.7.2025 19:25
Kommentar [8]: Should be mentioned somewhere in the Conclusions that Myctophidae make up 96% of all otoliths.

user 25.6.2025 21:48
Gelöscht: ,

Werner Schwarzhans 17.7.2025 19:26
Kommentar [9]: what shallow water taxa? Didn't find anything to that extend in the manuscript.

Werner Schwarzhans 17.7.2025 19:27
Kommentar [10]: Please review and cite Miguel-Salas et al. (2021), which gives a very different explanation to that extend.

Werner Schwarzhans 17.7.2025 19:27
Kommentar [11]: no, see above.

Werner Schwarzhans 17.7.2025 19:29
Kommentar [12]: Have you thought about contourites? This is what can happen in highly dynamic deep-water settings and here again Miguel-Salas et al. is a relevant article.

user 30.6.2025 21:44
Gelöscht: shallow-marine environment

user 25.6.2025 21:49
Gelöscht: ,

user 30.6.2025 21:45
Gelöscht: shallow

user 25.6.2025 21:09
Gelöscht: late

user 10.7.2025 10:52
Gelöscht: and

Aguilera O, Rodrigues de Aguilera D. 2001. An exceptional coastal upwelling fish assemblage in the Caribbean Neogene. *Journal of paleontology* 75:732–742.

Aguilera O, Rodrigues de Aguilera D. 2003. Two new otolith-based sciaenid species of the genus *Plagioscion* from the South American Neogene marine sediments. *Journal of paleontology* 77:1133–1138.

Aguilera O, Schwarzhans W, Béarex P. 2016. Otoliths of the Sciaenidae from the Neogene of tropical America. *Palaeo Ichthyologica* 14:7–90.

Aguilera O, Schwarzhans W, Moraes-Santos H, Nepomuceno A. 2014. Before the flood: Miocene otoliths from eastern Amazon Pirabas Formation reveal a Caribbean-type fish fauna. *Journal of South American Earth Sciences* 56:422–446.

Allmon WD. 1992. Role of nutrients and temperature in extinction of turritelline gastropods in the northwestern Atlantic and northeastern Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 92:41–54Anderson BM, Hendy A, Johnson EH, Allmon WD. 2017. Paleoecology and paleoenvironmental implications of turritelline gastropod-dominated assemblages from the Gatun Formation (Upper Miocene) of Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology* 470:132–146. https://doi.org/10.1016/j.palaeo.2017.01.026.

Benites-Palomino A, Vélez-Juarbe J, De Gracia C, Jaramillo C. 2023. Bridging two oceans: small toothed cetaceans (Odontoceti) from the Late Miocene Chagres Formation, eastern Caribbean (Colon, Panama). *Biology letters* 19:20230124.

Brzobohatý R, Nolf D. 2000. *Diaphus* otoliths from the European Neogene (Myctophidae, Teleostei). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 70:185–206.

Buchs DM, Irving D, Coombs H, Miranda R, Wang J, Coronado M, Arrocha R, Lacerda M, Goff C, Almengor E, Portugal E, Franceschi P, Chichaco E, Redwood SD. 2019. Volcanic contribution to emergence of Central Panama in the Early Miocene. *Scientific reports* 9:1417.

Cadena E-A, Gracia CD, Combita-Romero DA. 2023. An Upper Miocene marine turtle from Panama that preserves osteocytes with potential DNA. *Journal of vertebrate paleontology* 43. DOI: 10.1080/02724634.2023.2254356.

Carrillo-Briceño JD, De Gracia C, Pimiento C, Aguilera OA, Kindlimann R, Santamarina P, Jaramillo C. 2015. A new Late Miocene chondrichthyan assemblage from the Chagres Formation, Panama. *Journal of South American earth sciences* 60:56–70.

Chao A, Chiu C-H, Jost L. 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual review of ecology, evolution, and systematics* 45:297–324.

Chao A, Kubota Y, Zelený D, Chiu C-H, Li C-F, Kusumoto B, Yasuhara M, Thorn S, Wei C-L, Costello MJ, Colwell RK. 2020. Quantifying sample completeness and comparing diversities among assemblages. *Ecological research* 35:292–314.

Chavez FP, Ryan J, Lluch-Cota SE, Niquen C M. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science (New York, N.Y.)* 299:217–221.

user 4.7.2025 09:43
Gelöscht:

Coates AG. 1999. Lithostratigraphy of the Neogene strata of the Caribbean Coast from Limon, Costa Rica, to Colon, Panama. *Bulletins of American paleontology* 357:17–38.
Coates AG, Obando JA. 1996. The geologic evolution of the Central American Isthmus. In: Jackson JBC, Budd AF, Coates AG eds. *Evolution and Environment in Tropical America*. Chicago: The University of Chicago Press, 21–56.
Collins LS, Aguilera OA, Borne PF, Cairns SD. 1999. A paleoenvironmental analysis of the Neogene of Caribbean Panama and Costa Rica using several phyla. *Bulletins of American paleontology*:81–87.
Collins LS, Coates AG. 1993. Marine paleobiogeography of Caribbean Panama: last Pacific influences before closure of the Tropical American Seaway. *Geological Society of America Annual Meeting, Abstracts with Programs* 25:A–428.
Collins LS, Coates AG, Berggren WA, Aubry M-P, Zhang J. 1996. The late Miocene Panama isthmian strait. *Geology* 24:687.
Conversani VRM, Brenha-Nunes MR, Santificetur C, Giaretta MB, Siliprandi CC, Rossi-Wongtschowski CLDB. 2017. Atlas of marine bony fish otoliths (sagittae) of Southeastern-Southern Brazil Part VII: Atheriniformes, Beloniformes, Beryciformes, Zeiformes, Syngnathiformes, Scorpaeniformes and Tetraodontiformes. *Brazilian journal of oceanography* 65:400–447.
Cybulski JD, Sharpe AE, Carvajal-Contreras DR, De Gracia B, Dillon EM, García I, Isaza-Aizpurúa II, Núñez-Cortés Y, Monge-Blanco S, Smith-Guzmán NE, O'Dea A. 2025. Historical ecology of the Southern Central American Pacific coast. *Philosophical Transactions of Royal Society B* 380:20240042. https://doi.org/10.1098/rstb.2024.0042
De Gracia C, Correa-Metrio A, Carvalho M, Velez-Juarbe J, Přikryl T, Jaramillo C, Kriwet J. 2022. Towards a unifying systematic scheme of fossil and living billfishes (Teleostei, Istiophoridae). *Journal of systematic palaeontology* 20:1–36.
Domingo L, Tomassini RL, Montalvo CI, Sanz-Pérez D, Alberdi MT. 2020. The Great American Biotic Interchange revisited: a new perspective from the stable isotope record of Argentine Pampas fossil mammals. *Scientific Reports* 10:1608.
Farris DW, Jaramillo C, Bayona G, Restrepo-Moreno SA, Montes C, Cardona A, Mora A, Speakman RJ, Glascock MD, Valencia V. 2011. Fracturing of the Panamanian Isthmus during initial collision with South America. *Geology* 39:1007–1010.
Fierstine HL. 1978. A New Marlin, *Makaira panamensis*, from the Late Miocene of Panama. *Copeia* 1978:1.
Fitch JE. 1984. Osteichthyan otoliths. In DD Gillette. A marine ichthyofauna from the Miocene of Panama and the Tertiary Caribbean Faunal Province. *Journal of Vertebrate Paleontology* 4(2):172–186.
Fitch JE, Brownell RL Jr. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. *Journal of the Fisheries Research Board of Canada* 25:2561–2575.

Girone A, Nolf D, Cavallo O. 2010. Fish otoliths from the pre-evaporitic (Early Messinian) sediments of northern Italy: their stratigraphic and palaeobiogeographic significance. *Facies* 56:399–432.

GjØsaeter J. 1984. Mesopelagic fish, a large potential resource in the Arabian Sea. *Deep-sea research. Part A, Oceanographic research papers* 31:1019–1035.

Grossman EL, Robbins JA, Rachello-Dolmen PG, Tao K, Saxena D, O'Dea A. 2019. Freshwater input, upwelling, and the evolution of Caribbean coastal ecosystems during formation of the Isthmus of Panama. *Geology* 47:857–861.

Haimovici M, Dos S. Rodrigues L, Lucato SHB, De A. Freire M, Fischer LG, Cardoso LG. 2024. Otolith atlas for marine fishes of the southwestern Atlantic occurring along southern Brazil (28° S-34° S). *Marine and fishery sciences* 37. DOI: 10.47193/mafis.3712024010101.

Hanna CD, Church CC. 1928. Freezing and thawing to disintegrate shales. *Journal Paleontology* 2:131.

Haug GH, Tiedemann R. 1998. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. *Nature* 393:673–676.

Hendy AJW. 2013. Spatial and stratigraphic variation of marine paleoenvironments in the middle-upper Miocene Gatun formation, isthmus of panama. *Palaios* 28:210–227.

Herrig E. 1966. Ostracoden aus der Weißen Schreibkreide (Unter-Maastricht) der Insel Rügen. *Paläontologische Abhandlungen* 2:693–1024.

Hill MO. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54:427–432.

Hsieh TC, Ma KH, Chao A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in ecology and evolution* 7:1451–1456.

Jackson JBC, O'Dea A. 2023. Evolution and environment of Caribbean coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 120:e2307520120.

Jackson JBC, Todd JA, Fortunato H, Jung P. 1999. Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. *Bulletins of American paleontology* 357:193–230.

Jones DS, Allmon WD. 1995. Records of upwelling, seasonality and growth in stable isotope profiles of Pliocene mollusk shells from Florida. *Lethaia* 28:61–74.

Kordas RL, Pawar S, Kontopoulos D-G, Woodward G, O'Gorman EJ. 2022. Metabolic plasticity can amplify ecosystem responses to global warming. *Nature communications* 13:2161.

Kotlyar AN. 1996. Beryciform Fishes of the World Ocean. VNIRO Publishing, Moscow, 368 pp. [In Russian]

Leonhard I, Agiadi K. 2023. Addressing challenges in marine conservation with fish otoliths and their death assemblages. *Geological Society, London, Special Publications* 529:243–262.

Lin C-H, Brzobohatý R, Nolf D, Girone A. 2017. Tortonian teleost otoliths from northern Italy: taxonomic synthesis and stratigraphic significance. *European journal of taxonomy* 322:1–44. DOI: 10.5852/ejt.2017.322.

user 10.7.2025 10:53
Gelöscht: .

Lin C-H, Chang C-W. 2012. *Otolith Atlas of Taiwan Fishes*. National Museum of Marine Biology & Aquarium.

Lin C-H, Chiang Y-P, Tuset VM, Lombarte A, Girone A. 2018. Late Quaternary to Recent diversity of fish otoliths from the Red Sea, central Mediterranean, and NE Atlantic sea bottoms. *Geobios* 51:335–358. DOI: 10.1016/j.geobios.2018.06.002

Lin C-H, De Gracia B, Pierotti MER, Andrews AH, Griswold K, O'Dea A. 2019. Reconstructing reef fish communities using fish otoliths in coral reef sediments. *PloS one* 14:e0218413.

Lin C-H, Girone A, Nolf D. 2015. Tortonian fish otoliths from turbiditic deposits in northern Italy: taxonomic and stratigraphic significance. *Geobios* 48:249–261. DOI: 10.1016/j.geobios.2015.03.003

Lin C-H, Girone A, Nolf D. 2016. Fish otolith assemblages from Recent NE Atlantic sea bottoms: A comparative study of palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 446:98–107. DOI: 10.1016/j.palaeo.2016.01.022

Lin C-H, Lin J-S, Chen K-S, Chen M-H, Chen C-Y, Chang C-W. 2020. Feeding habits of bigeye tuna (*Thunnus obesus*) in the western Indian ocean reveal a size-related shift in its fine-scale piscivorous diet. *Frontiers in marine science* 7:582571. DOI: 10.3389/fmars.2020.582571.

Lin C-H, Taviani M, Angeletti L, Girone A, Nolf D. 2017. Fish otoliths in superficial sediments of the Mediterranean Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 471:134–143. DOI: 10.1016/j.palaeo.2016.12.050

Lin C-H, Wei C-L, Ho SL, Lo L. 2023a. Ocean temperature drove changes in the mesopelagic fish community at the edge of the Pacific Warm Pool over the past 460,000 years. *Science advances* 9:eadf0656. DOI: 10.1126/sciadv.adf0656

Lin C-H, Wu S-M, Lin C-Y, Chien C-W. 2023b. Early Pliocene otolith assemblages from the outer-shelf environment reveal the establishment of mesopelagic fish fauna over 3 million years ago in southwestern Taiwan. *Swiss Journal of Palaeontology* 142:23.

Martin R, Dunn D. 2000. Otoliths of the Late Miocene Gatun Formation of Panama. *Gulf Coast Association of Geological Societies Transactions* 50:687–696.

Martin RP, Olson EE, Girard MG, Smith WL, Davis MP. 2018. Light in the darkness: New perspective on lanternfish relationships and classification using genomic and morphological data. *Molecular phylogenetics and evolution* 121:71–85.

Nelson JS, Grande TC, Wilson MVH. 2016. *Fishes of the world*. John Wiley & Sons.

Ng S-L, Lin C-H, Liu K-M, Joung S-J. 2024a. New records of three mesopelagic fish species from southwestern Taiwan. *Thalassas: An International Journal of Marine Sciences* 40:81–90.

Ng S-L, Liu K-M, Joung S-J. 2023. *Malakichthys formosus*, a new species of small seabass (Acropomatiformes: Malakichthyidae) from southwestern Taiwan. *Zootaxa* 5380:380–386.

Ng S-L, Liu H-W, Mediodia DP, Lin Y-T, Lee C-H, Lin C-F, Huang S-P, Wu S-M, Tung C-R, Ho H-C, Lin C-H. 2024b. An updated checklist of fishes of Dongsha Island, Taiwan, northern South China Sea. *ZooKeys* 1220:175–242.

Nolf D. 1976. Les otoliths des Téléostéens néogènes de Trinidad. *Eclogae Geologicae Helvetiae* 69:703–742.

Nolf D. 1985. *Otolithi piscium*. Fischer, Stuttgart, New York.

Nolf D. 2013. *The diversity of fish otoliths, past and present*. Royal Belgian Institute of Natural Sciences, Brussels

Nolf D, Aguilera O. 1998. Fish otoliths from the Cantaure Formation (Early Miocene of Venezuela). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 68:237–262.

Nolf D, Brzobohatý R. 1992. Fish otoliths as paleobathymetric indicators. *Paleontologia i Evolucio* 24–25:255–264.

Nolf D, Steurbaut E. 1983. Révision des otolithes de téléostéens du Tortonien stratotypique et de Montegibbio (Miocène Supérieur d'Italie septentrionale). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 20:143–197.

Nolf D, Stringer GL. 1992. Neogene paleontology in the northern Dominican Republic. *Bulletins of American paleontology* 102:41–81.

O'Dea A, Jackson J, Fortunato H, Smith T, Croz D, Kg Todd J. 2007. Environmental change preceded Caribbean mass extinction by 2 million years. *Proceedings of the National Academy of Sciences* 104:5501–5506.

O'Dea A, Lessios HA, Coates AG, Eytan RI, Restrepo-Moreno SA, Cione AL, Collins LS, de Queiroz A, Farris DW, Norris RD, Stallard RF, Woodburne MO, Aguilera O, Aubry M-P, Berggren WA, Budd AF, Cozzuol MA, Coppard SE, Duque-Caro H, Finnegan S, Gasparini GM, Grossman EL, Johnson KG, Keigwin LD, Knowlton N, Leigh EG, Leonard-Pingel JS, Marko PB, Pyenson ND, Rachello-Dolmen PG, Soibelzon E, Soibelzon L, Todd JA, Vermeij GJ, Jackson JBC. 2016. Formation of the isthmus of Panama. *Science advances* 2:e1600883.

Papastamatiou YP, Wetherbee BM, O'Sullivan J, Goodmanlowe GD, Lowe CG. 2010. Foraging ecology of Cookiecutter Sharks (*Isistius brasiliensis*) on pelagic fishes in Hawaii, inferred from prey bite wounds. *Environmental biology of fishes* 88:361–368.

Pyenson ND, Vélez-Juarbe J, Gutstein CS, Little H, Vigil D, O'Dea A. 2015. *Isthminia panamensis*, a new fossil inioid (Mammalia, Cetacea) from the Chagres Formation of Panama and the evolution of "river dolphins" in the Americas. *PeerJ* 3:e1227.

Rivaton J, Bourret P. 1999. *Les otolithes des poissons de l'Indo-Pacifique*. Institut de recherche pour le développement.

Schäfer W. 1972. *Ecology and palaeoecology of marine environments*. University of Chicago Press, Chicago.

Schubert RJ. 1908. Fischreste. In: Toula F ed. *Eine jungtertiäre Faunavon Gatun am Panama-Kanal*. Jb. k.k. Geol. Reichsanst., 687–691.

Schwarzhans W. 2013. A comparative morphological study of the Recent otoliths of the genera *Diaphus*, *Idiolychnus* and *Lobianchia* (Myctophidae). *Palaeo Ichthyologica* 13:41–82.

Schwarzhans W. 2019. A comparative morphological study of Recent otoliths of the Congridae, Muraenesocidae, Nettastomatidae and Colocongridae (Anguilliformes). *Memorie della società Italiana di scienze naturali e del museo di storia naturale di Milano* 46:327–354.

Schwarzhans W, Aguilera O. 2013. Otoliths of the Myctophidae from the Neogene of tropical America. *Palaeo Ichthyologica* 13:83–150.

Schwarzhans W, Aguilera O. 2016. Otoliths of the Ophidiiformes from the Neogene of tropical America. *Palaeo Ichthyologica* 14:91–124.

Schwarzhans WW, Aguilera OA. 2024. Otoliths of the Gobiidae from the Neogene of tropical America. *Swiss Journal of Palaeontology* 143:13.

Schwarzhans W, Nielsen S. 2021. Fish otoliths from the early Miocene of Chile: a window into the evolution of marine bony fishes in the Southeast Pacific. *Swiss journal of palaeontology* 140. DOI: 10.1186/s13358-021-00228-w.

Schwarzhans W, Ohe F, Tsuchiya Y, Ujihara A. 2022. Lanternfish otoliths (Myctophidae, Teleostei) from the Miocene of Japan. *Zitteliana* 96:103–134.

Schwarzhans WW, Prokofiev AM. 2017. Reappraisal of *Synagrops* Günther, 1887 with rehabilitation and revision of *Parascombrops* Alcock, 1889 including description of seven new species and two new genera (Perciformes: Acropomatidae). *Zootaxa* 4260:1–74.

Stigall AL, Bauer JE, Lam AR, Wright DF. 2017. Biotic immigration events, speciation, and the accumulation of biodiversity in the fossil record. *Global and Planetary Change* 148:242–257.

Stiles E, Montes C, Jaramillo C, Gingras MK. 2022. A shallow-water depositional interpretation for the upper Miocene Chagres Formation (Caribbean coast of Panama). *Geological Society of America bulletin*. DOI: 10.1130/b36291.1.

Stringer G. 1998. Otolith-based fishes from the Bowden shell bed (Pliocene) of Jamaica: systematics and palaeoecology. *Contributions to Tertiary and Quaternary Geology* 35:147–160.

Stringer G, Starnes J, Leard J, Puckett M. 2020. Taphonomic and paleoecologic considerations of a phenomenal abundance of teleostean otoliths in the Glendon Limestone (Oligocene, Rupelian), Brandon, Mississippi. *Journal of the Mississippi Academy of Sciences* 65(1):101.

Titus BM, Gibbs HL, Simões N, Daly M. 2024. Topology testing and demographic modeling illuminate a novel speciation pathway in the Greater Caribbean sea following the formation of the Isthmus of Panama. *Systematic biology* 73:758–768.

Velez-Juarbe J, Wood AR, De Gracia C, Hendy AJW. 2015. Evolutionary patterns among living and fossil kogiid sperm whales: Evidence from the Neogene of central America. *PloS one* 10:e0123909.

Vigil DI, Laurito CA. 2014. Nuevos restos de un Odontoceti fósil (Mammalia: Cetacea, Physeteroidea) para el Mioceno Tardío de Panamá, América Central. *Revista geológica de América central*. DOI: 10.15517/rgac.v0i50.15123.

Welton BJ. 2015. The marine fish fauna of the Middle Pleistocene Port Orford Formation and Elk River Beds, Cape Blanco, Oregon. *New Mexico Museum of Natural History and Science Bulletin* 66:1–45.

user 30.6.2025 20:30

Gelöscht: Schwarzhans W, Milàn J., Carnevale G. 2021. A tale from the middle Paleocene of Denmark: A tube-dwelling predator documented by the ichnofossil *Lepidenteron mortenseni* n. isp. and its predominant prey, *Bobbitichthys* n. gen. *rosenkrantzi* (Macrouridae, Teleostei). *Bulletin of the Geological Society of Denmark* 69:35–52.

Woodring WP. 1957. Geology and paleontology of Canal Zone and adjoining parts of Panama. *U.S. Geological Survey Professional Paper* 306A:145.

Yamanoue Y, Matsuura K. 2004. A review of the genus *Malakichthys* Döderlein (Perciformes: Acropomatidae) with the description of a new species. *Journal of fish biology* 65:511–529.

Figures

Figure 1. Sampling site and geological map. Figure modified after Collins et al. (1996) and Carrillo-Briceño et al. (2015).

Figure 2. Stratigraphic section and observed fossils (A, modified after Carrillo-Briceño et al. 2015; Stiles et al. 2022) and photographs of the site (B–D). (C and D) Abundant fish otoliths and associated ichnofossil *Ophiomorpha* are visible on the surface of the outcrop. Red arrow = sampling layer.

kurosa 25.6.2025 15:27
Gelöscht: Lithostratigraphy

Figure 3. Otoliths of Congridae and Argentinidae from the Upper Miocene Chagres Formation, Caribbean Panama. (A and B) *Chiloconger aflorens* sp. nov., (A) holotype, ASIZF 0100943, (B) paratype, ASIZF 0100944. (C) *Rhynchoconger* sp., ASIZF 0100945. (D) *Argentina* sp., ASIZF 0100946. Images are inner views unless otherwise indicated. 1, ventral view; 2, inner view. Scale bar = 1 mm.

user 25.6.2025 21:09
Gelöscht: late

Figure 4. Otoliths of Sternoptychidae and Myctophidae from the Upper Miocene Chagres Formation, Caribbean Panama. (A and B) *Polyipnus* sp., ASIZF 0100947–0948. (C) *Benthosema pluridens* Schwarzhans & Aguliera, 2013, ASIZF 0100949. (D) *Bolinichthys* sp., ASIZF 0100950. Images are inner views. Scale bar = 1 mm.

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Gelöscht: late

Figure 5. Otoliths of *Dasyscopelus* (Myctophidae) from the Upper Miocene Chagres Formation, Caribbean Panama. (A–F) *Dasyscopelus degraciai* (Schwarzhans & Aguliera, 2013), ASIZF 0100951–0956. (G–L) *Dasyscopelus inopinatus* sp. nov., (G, H, J–L) paratypes, ASIZF 0100957–0961, (I) holotype, ASIZF 0100962. Images are inner views unless otherwise indicated. 1, ventral view; 2, inner view. Scale bar = 1 mm.

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Gelöscht: late

Figure 6. Otoliths of *Diaphus* (Myctophidae) from the Upper Miocene Chagres Formation, Caribbean Panama. (A–C) *Diaphus aequalis* Schwarzhans & Aguliera, 2013, ASIZF 0100963–0965. (D–F) *Diaphus apalus* Schwarzhans & Aguliera, 2013, ASIZF 0100966–0968. (G–K) *Diaphus barrigonensis* Schwarzhans & Aguliera, 2013, ASIZF 0100969–0973. (L–O) *Diaphus dumerilii* (Bleeker, 1856), ASIZF 0100974–0977. Images are inner views. Scale bar = 1 mm.

user 25.6.2025 21:09
Gelöscht: late

Figure 7. Otoliths of *Diaphus* and *Diogenichthys* (Myctophidae) from the Upper Miocene Chagres Formation, Caribbean Panama. (A and B) *Diaphus multiserratus* Schwarzhans & Aguliera, 2013, ASIZF 0100978–0979. (C–F) *Diaphus pedemontanus* (Robba, 1970), ASIZF

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Gelöscht: late

0100980–0983. (G–J) *Diaphus rodriguezi* Schwarzhans & Aguliera, 2013, ASIZF 0100984–0987. (K) *Diogenichthys* sp., ASIZF 0100988. Images are inner views unless otherwise indicated. 1, ventral view; 2, inner view. Scale bar = 1 mm.

Figure 8. Otoliths of *Lepidophanes*, *Lobianchiaand*, and *Myctophum* (Myctophidae) from the Upper Miocene Chagres Formation, Caribbean Panama. (A–C) *Lobianchia johnfitchi* Schwarzhans & Aguliera, 2013, ASIZF 0100992–0994. (D–F) *Myctophum arcanum* Schwarzhans & Aguliera, 2013, ASIZF 0100995–0997. (G and H) *Myctophum affine* (Lütken, 1892), 2013, ASIZF 0100998–0999. (I) *Lepidophanes inflectus* Schwarzhans & Aguliera, 2013, ASIZF 0101000. Images are inner views unless otherwise indicated. 1, ventral view; 2, inner view. Scale bar = 1 mm.

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Gelöscht: late

Figure 9. Otoliths of Macrouridae and Bregmacerotidae from the Upper Miocene Chagres Formation, Caribbean Panama. (A and B) *Coelorinchus* sp., ASIZF 0101001–1002. (C–E) *Bregmaceros* sp., ASIZF 0101003–1005. Images are inner views. Scale bar = 1 mm.

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Gelöscht: late

Figure 10. Otoliths of Trachichthyidae, Carapidae, and Ophidiidae from the Upper Miocene Chagres Formation, Caribbean Panama. (A–D) *Hoplostethus boyae* sp. nov., (A) holotype, ASIZF 0101006, (B–D) paratypes, ASIZF 0101007–1009. (E and F) *Carapus* sp., ASIZF 0101010–1011. (G) *Lepophidium limulum* Schwarzhans & Aguliera, 2013, ASIZF 0101012. Images are inner views unless otherwise indicated. 1, ventral view; 2, inner view. Scale bar = 1 mm.

user 25.6.2025 21:09
Gelöscht: late

Figure 11. Otoliths of Opistognathidae and Carangidae from the Upper Miocene Chagres Formation, Caribbean Panama. (A) *Opistognathus* sp., ASIZF 0101013. (B) Carangidae indet., ASIZF 0101014. 1, ventral view; 2, inner view. Scale bar = 1 mm.

user 25.6.2025 21:09
Gelöscht: late

Figure 12. Otoliths of *Malakichthys* (Malakichthyidae) from the Upper Miocene Chagres Formation, Caribbean Panama. (A–F) *Malakichthys schwarzhansi* sp. nov., (A) holotype, ASIZF 0101015, (B–F) paratypes, ASIZF 0101016–1020. Images are inner views unless otherwise indicated. 1, ventral view; 2, inner view. Scale bar = 1 mm.

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Gelöscht: late

Figure 13. Extant *Malakichthys* (Malakichthyidae) otoliths. (A and B) *Malakichthys wakiyae* Jordan & Hubbs, 1925, (A) 86.1 mm SL, CHLOL 10514, (B) 61.4 mm SL, CHLOL 10493. (C and D) *Malakichthys griseus* Döderlein, 1883, (C) 93.7 mm SL, CHLOL 14678, (D) 102.5 mm SL, CHLOL 34344. (E–G) *Malakichthys elegans* Matsubara & Yamaguti, 1943, (E) 131.9 mm SL, CHLOL 8241, (F) 62.9 mm SL, CHLOL 8800, (G) 77.8 mm SL, CHLOL 2605. (H and I) *Malakichthys formosus* Ng, Liu & Joung, 2023, (H) 72.1 mm SL, CHLOL 27488, (I) 64.9 mm SL, CHLOL 31419. (J–L) *Malakichthys barbatus* Yamanoue & Yoseda, 2001, (J) 161.0 mm SL,

CHLOL 27489, (K) 83.51 mm SL, CHLOL 35072, (L) 223.5 mm SL, CHLOL 33087. Images are inner views unless otherwise indicated. 1, ventral view; 2, inner view. Scale bar = 1 mm.

Figure 14. Extant *Ambassis* (Ambassidae) otoliths. (A) *Ambassis kopsii* Bleeker, 1858, 69.8 mm SL, CHLOL 28447. (B and C) *Ambassis miops* Günther, 1872, (B) 22.7 mm SL, CHLOL 31077, (C) 22.3 mm SL, CHLOL 31078. (D and E) *Ambassis urotaenia* Bleeker 1852, 1943, (D) 46.8 mm SL, CHLOL 27116, (E) 34.1 mm SL, CHLOL 27115. (F and G) *Ambassis interrupta* Bleeker, 1853, (F) 34.6 mm SL, CHLOL 27119, (G) 47.8 mm SL, CHLOL 27120. Images are inner views unless otherwise indicated. 1, ventral view; 2, inner view. Scale bar = 1 mm.

Figure 15. Rank abundance of otolith families in the Upper Miocene Chagres Formation, Caribbean Panama. Assemblages are compared with (blue) and without (coral) unweighted sample CH18-1-1. Families are ranked by total abundance across all samples, and plotted on a log scale. Numbers within bars indicate total specimen counts (n). Binomial 95% confidence intervals (error lines) were calculated using Wilson's method and represent uncertainty in abundance estimates relative to total sample size.

user 25.6.2025 21:50
Gelöscht: Late

kurosa 23.6.2025 15:05
Gelöscht: Note that y-axis is log-scaled, and the otolith counts are indicated in parentheses.

Figure 16. Rarefaction curves of otolith-based taxa (Hill numbers) represented by species richness (^{0}D), Shannon diversity (^{1}D), and Simpson (^{2}D) diversity. Assemblages are compared with (left) and without (right) unweighted sample CH18-1-1. Shaded areas represent 95% confidence intervals based on 1000 bootstrap replicates.

Figure 17. Proportion of myctophid otoliths by depth in Caribbean dredge samples. Mesopelagic planktivorous (principally myctophids) otoliths relative to all other otoliths in 187 modern Caribbean shelf sediment dredge samples are plotted (data source: O'Dea et al., 2007; Jackson & O'Dea, 2023).

Figure 18. Reconstruction of Late Miocene middle neritic, mesopelagic fish-dominated ecosystem in Caribbean Panama. The illustration highlights key taxa, including lanternfish, hatchetfish, billfish, *Isistius* sharks, *Otodus megalodon*, *Isthminia panamensis*, and *Lepidochelys* sea turtle. Artwork by Yun-Kae Kiang.

Table

Table 1. List of otolith-based fish taxa from the Upper Miocene Chagres Formation, Caribbean Panama.

kurosa 23.6.2025 15:02
Gelöscht: late

Supplemental files

Table S1. Densities of fish otoliths and *Isistius* teeth from the Upper Miocene Chagres Formation, Caribbean Panama.

kurosa 23.6.2025 15:02
Gelöscht: late

Table S2. Raw data of the composition of otolith-based fish taxa of all samples from the Upper Miocene Chagres Formation, Caribbean Panama.

Editor comments (Kenneth De Baets)

You provide crucial abundant new data and analysis on otoliths from the Chagres Formation and an alternative hypothesis to explain their environmental/ depositional context, which I would love to see published. However, I feel there are some crucial points which need to be addressed before publication:

Highest otolith density: as noted by reviewer 3 you state in some instances that the otolith concentration or density (otoliths/kg of bulk sample) is the highest ever documented which is not entirely correct. Please rephrase those statement to one or among the highest ever documented (as you did already in the conclusion) and cite relevant references for the highest density (compare reviewer 3).
Response: We have rephrased the statement to "among the highest ever documented" otolith concentration and cited relevant references as suggested. - OK

Stratigraphic terminology: Please use capitals when you are referring official Early/Middle/Late Miocene (compare reviewer 3)
Response: Revised as suggested. - OK

Sampling and stratigraphy of samples: The arrow in Figure 2 suggest your samples derive from the same relative position in a sandstone unit which were laterally collected. Is this correct? The stratigraphic provenance of your samples should be more clearly described in text. Also, you mention lithostratigraphy in this figure but you do not list members or formations in Figure 2. Please explicitly mention the lithostratigraphic units (formations, members) for clarity (compare reviewer 3).
Response: Thank you for this comment. We have revised Fig. 2 and its caption to address these concerns. We now label the stratigraphic unit as the Chagres Sandstone Member and explicitly note that the samples were taken laterally from the same stratigraphic horizon. - OK

Missing references: reviewer 3 suggested additional highly relevant references on Carribean otoliths as well as otolith density and taphonomy.
Response: Added. - OK

Range of measurements of morphological traits: you provide measurements for new taxa but given you really provide a large sampling of various species, it would be appropriate to also provide a range of measurements of all species you found (compare reviewer 1). I also feel providing not just the extremes, but the average/median and sample size of measured specimens (compare reviewer 3) would be appropriate for at minimum the new species and the holotypes (compare reviewer 1)

Response: Measurements are added as suggested. - OK

Sensitivity analysis: Given the one sample is unweighted and contains the largest numbers of otoliths (compare reviewer 3), it would be crucial to show how removing or adding it alters the proportion of taxa in your sample. This could be done in multiple ways (showing the proportion of unweighted versus weighted samples in Fig. 15 and/or performing/comparing rarefaction curves including and excluding the unweighted sample. In addition, it would be good to discuss how sample preparation may have contributed to the preservation and assignment of taxa (compare reviewer 3).

Response: We have reanalyzed the samples with and without the unweighted sample (CH18-1-1), and presented separately in our revised Fig. 15. Our sampling and specimen preparation are consistent across all samples; sample CH18-1-1 is simply without an exact weight. - OK and thanks for the extra work.

Confidence intervals: To understand the significance and potential impact of sampling, it would be helpful to understand the binomial error bars or confidence intervals for the relative proportion of collected specimens attributable to each family listed in Fig. 15 compared to the total. Compare Raup (1991) and see for example De Baets et al. (2012; Fig. 5) or Takeda & Tanabe (2014; Fig. 9) for examples when using proportions. Alternatively or additionally, you could show the proportions of specimens attributable to families in the unweighted versus the weighted sample.

Response: We have added Binomial 95% confidence intervals in our Fig. 15. - OK

Upwelling interpretation: The upwelling interpretation is interesting but there may be other ways to explain your observations (compare reviewer 1). It is heavily based on a single study suggesting a shallow water setting while various other studies suggest an alternative interpretation. Also, other studies in similar context of gateways have alternative interpretations for the distribution of ichnofacies (e.g., Miguez-Salas et al. 2021). I feel more extensive and careful discussion on this

Werner Schwarzhans 17.7.2025 19:38
Kommentar [1]: This article is not cited in the new version even though it has a lot to offer.

hypothesis is needed (compare reviewer 1 and 3). Depending on strength of support for coastal upwelling, you may want to consider revising your title accordingly (e.g., remove coastal upwelling from your title or add a question mark). Just to be clear, I feel this hypothesis merits to discussed in detail, but it does not seem to be the only viable hypothesis (compare reviewer 1 and 3). Reviewer 3 also mentioned that Ariid lapilli are common in many Neogene Carribean shallow-marine otolith assemblages and if the lack thereof in your samples could also be consistent with the proposed coastal upwelling paleoenvironment. Also I feel the phrasing of lines 707-716 could be revised for clarity (switch for predator-avoiding to predator-driven feels confusing).

Response: We have elaborated the discussion on the paleoecological interpretation. To explore this question further, we analyzed the proportion of mesopelagic otoliths relative to all other otoliths in 187 modern Caribbean shelf sediment dredge samples (O'Dea et al., 2007; Jackson & O'Dea, 2023). - Shelf samples are not adequate to analyze the abundance of oceanic/mesopelagic biota. This analysis is grossly misleading and contradicts all experiences made by the senior author and myself. I will address that aspect separately and at more length below. - When plotted against depth (Figure 17), these data reveal that modern myctophid otolith assemblages increase from nearshore environments, peaking at around 120-150 m, before declining towards the shelf edge at 200 m.

In short, the extremely shallow, near-shore depths proposed by Stiles et al. (2022) are therefore unlikely. A middle neritic depositional setting can be reconciled with moderate post-depositional tectonic uplift, which is consistent with the tectonically active setting during isthmus formation (O'Dea et al., 2007; Jackson & O'Dea, 2023).

The title of the manuscript is shortened as suggested. Please also see our specific reply on the "predator-avoiding to predator-driven" below.

Werner Schwarzhans 17.7.2025 19:37
Kommentar [2]: Don't agree. See below.

Werner Schwarzhans 17.7.2025 19:36
Gelöscht: as

Werner Schwarzhans 17.7.2025 19:36
Gelöscht: as bathyal depths

Please address these as well as all other points raised including those in annotated pdfs.

Although the reviewers suggested minor revisions, I feel the raised points are more substantial than minor revisions including some possible revisions in species assignments (e.g., Diaphus) and need for additional (sensitivity) analyses. I feel these points can be reasonably and feasible be addressed within a reasonable timeframe.

I look forward to receiving the revised manuscript.

Response: Dear Editor, thank you very much for the effort during the review process. We have revised the manuscript following this guidance whenever necessary throughout our manuscript. Detail responses to reviewers' comments are provided below.

Comments from the annotated pdf

Line 37. This reference would also be highly appropriate in this context: Bacon, C. D., Silvestro, D., Jaramillo, C., Smith, B. T., Chakrabarty, P., & Antonelli, A. (2015). Biological evidence supports an early and complex emergence of the Isthmus of Panama. Proceedings of the National Academy of Sciences, 112(19), 6110-6115.

Response: Thank you for the suggestion. We are aware of the study by Bacon et al. (2015); however, its conclusions regarding the timing and nature of the Isthmus of Panama's emergence are inconsistent with a broad range of geological and paleontological evidence, as supported by a large body of literature (particularly the syntheses presented in O'Dea et al. (2016) and Jackson & O'Dea (2023)). Instead, we have chosen to cite Stigall et al. (2017) and Domingo et al. (2020) in this context.

Line 75. it would be worth explaining this term "transisthmian" for those not so familiar with it

Response: Added (i.e. deposits spanning across the Isthmus of Panama).

Line 214. should be in italics as it concerns a genus

Response: Revised.

Line 246. Please provide measurements for all described species, also those not newly described particularly when they are abundant for the sake of reproducibility. It is unique opportunity to provide measurements of larger samples which would your article be of even broader relevance.

Response: Thank you for this suggestion. We have provided measurements for all newly described species. However, obtaining measurements for all specimens (our collection contains over 6,000 otoliths) would require an enormous investment of time and effort. For the primary group described here (Myctophidae), detailed measurements and descriptions are already published in Schwarzhans & Aguilera (2013), which readers can consult for reference. For minor taxa and other species, we have illustrated representative specimens in

sufficient number to allow readers to appreciate their size and proportions. Given this existing literature and the figures provided, we believe this approach is sufficient for the purposes of this study. - Agreed.

Line 255. "…were assigned to B. pluridens; other, less definitive specimens were conservatively classified under Myctophidae indet. Therefore, the true abundance of B. pluridens may be underestimated." This statement would be more robust if you could explicitly mention which Myctophidae indet. would be candidates to be (re-)assigned to B. pluridens.

Response: Thank you for this comment; we appreciate that further resolution is often desirable. However, in this case, any more specific assignments (to any candidates) would be arbitrary. As stated above, most of the Myctophidae indet. specimens are juvenile otoliths that show intermediate shapes between rounded and sub-rectangular forms. Due to this morphological ambiguity, assigning them to particular species would be too speculative and falls outside the purpose here. - Agreed.

Line 599. Please provide the average/median and sample size of measured specimens in addition to the range of the new species.

Response: Added.

Line 642. of low-abundance

Response: Revised.

Line 689. It does not seem a consensus has been reach on this point so please be more specific to which study this interpretation pertains and discuss pro and contra arguments more extensively.

Response: Please see our specific reply on the paleoecological interpretation below.

Line 710. predator-avoiding is a bit confusing/contra-intuitive as you subsequently (line 714-716) state an important contribution to their presence at this site may be predation? Avoid predators but subsequently are more abundant?

Response: Thank you for this observation. Our intent is to highlight the dynamic nature of the predator–prey interactions in this upwelling-driven ecosystem. Myctophids are indeed well-adapted to predator avoidance (via diel vertical migrations), which allows them to thrive under high predatory

pressure. However, the system's exceptional productivity supports such large prey populations that a substantial proportion of myctophids still fall victim to predators. This intense trophic turnover taht driven by both predator–prey interactions and rapid prey replenishment is ultimately reflected in the sedimentary record.

We have added the following lines for clarity: "Despite these adaptations, a substantial proportion of myctophids still fell prey to predators. However, the extraordinary productivity sustained such a large prey biomass that only a small fraction was consumed at any one time. This rapid turnover resulted in high absolute abundances of myctophid otoliths preserved in the sedimentary record."

Line 728. "The combination of strong coastal upwelling, extremely high planktivore abundance, and intense predation pressure thus explains the ecological observations at Piña."
support or may explain would be more appropriate and cautious given there is no consensus on the ecological observations (compare reviews)

Response: Thank you for pointing this out, please see our reply below (specifically our replies on the paleoecological interpretation to Reviewers #1 and 3 below) - agreed

Fig. 2. Caption. This description is confusing/deceiving (compare also reviews). Please rephrase and also list the actual formation/members for clarity. The arrow suggests your samples derive from the same position within the sandstone bed and were collected laterally. Is this correct? Please modify or explicitly mention this in the text (compare also reviews).

Response: Thank you for this comment. We have revised Fig. 2 and its caption to address these concerns. We now label the stratigraphic unit as the Chagres Sandstone Member and explicitly note that the samples were taken laterally from the same stratigraphic horizon. - good.

Figure 7. The morphology differs significantly between A and B suggesting the former may be another species (compare reviewer). Please correct this issue. It is unclear if this issue just concerns this plate/specimens or if there is a more widespread issue in assigning these specimens. In this context, measurements of the spacing of ridges would to support their re-assignment.

Response: We have revised this species, as also suggested by the Reviewer

#1. Indeed, this is an error during our initial assignment between these two species and we have gone through our collection again. Revised tables and supplementary datasets are revised accordingly. - good

Figure 15. I feel it would be helpful to have actual binomial confidence intervals would help to support your claims (dominance of Myctophidae and some other families compared to most others).
In addition, i feel separating/designating the unweighted from other samples would be helpful to further underline the dominance of Myctophidae beyond the large unweighted sample.
Response: Thank you for the comment. We have reanalyzed the data and revised the figure accordingly.

Figure 16. I feel a sensitivity analyses (e.g., once with and once without the unweighted sample) would help to further underline the dominance of Myctophidae beyond the large unweighted sample.
Response: Thank you for the comment. We have reanalyzed the data and revised the figure accordingly.

Figure 17 is not necessary and in fact misleading.

Figure 18 is nice and captures the situation well. How about including a whale?

Reviewer 1 (Werner Schwarzhans)

Basic reporting

This is a well written and interesting article that is well worth being published in peerj and that will trigger much interest in the ichthyology and palichthyology community.

Response: Thank you very much for providing the review.

The taxonomy is state of the art and the documentation to it is excellent. I found only one little instant of error (see comment to Fig. 7A). I recommend to add more information about sizes of the object, particularly the sizes of holotypes and the ranges of sizes in new species. Also there are mentionings of comparison of extant and fossil otoliths apparently of different sizes but without giving size details.

Response: Thanks f or pointing this error, we have revised the taxonomy of *D. multiserratus*. Measurements are added as suggested. - good

The conclusions are interesting and sound, particular to the explanation how this uniquely enriched otolith clusters may have entered sedimentation. The paleocology is mostly fine, but I doubt the shallow water setting. This is based entirely on sedimentary and trace fossil assemblages while all other fossils indicate deepwater origin. There are alternative explanations available for the trace fossil and sedimentological setting and I have made references to that (Miguez-Salas et al., 2021). At least I would srongly recommend some careful discussion about this interpretation.

Response: As also noted by the editor, we have elaborated the discussion on our paleoecological interpretation.

To explore this question further, we further analyzed the proportion of mesopelagic otoliths relative to all other otoliths in 187 modern Caribbean shelf sediment dredge samples (O'Dea et al., 2007; Jackson & O'Dea, 2023). When plotted against depth (Figure 17), these data reveal that modern myctophid otolith assemblages increase from nearshore environments, peaking at around 120-150 m, before declining towards the shelf edge at 200 m. In short, the extremely shallow, near-shore depths proposed by Stiles et al. (2022) are therefore as unlikely as bathyal depths. A middle neritic depositional setting can be reconciled with moderate post-depositional tectonic uplift, which is consistent with the tectonically active setting during isthmus

formation (O'Dea et al., 2007; Jackson & O'Dea, 2023). - Don't agree. See separate comment at the end.

I made a few further comments in the text but they are all minor in nature.
The authors are to be congratulated for their work and I am looking forward to see the article published soon.
Response: Thank you very much for providing the review.

Experimental design

no comment

Validity of the findings

Excellent study but see discussion on paleo-water depth as mentioned under 1. Basic Reporting and annotated in the pdf.

Additional comments

none

Comments from the annotated pdf
Line 23. "The otolith density in the sediments is the richest known globally" Please quantify.
Response: Revised and added (278.80 ± 135.59 otoliths/kg) - good

Line 57. "This is offensive language. Reword. In fact only myctophid otoliths had so far been studied. Thus one could say: "has not been studied in its entirety...".
Response: Revised to "…has not been investigated in its entirety with respect to its otolith assemblage at the community level." - good

Line 63. This is debatable, see reference Miguez-Salas et al. 2021. The weight of the evidence is more to the other biota, which all indicate deep marine environment.
Response: We have elaborated this in our discussion (see below).

Line 68. "We provide detailed taxonomic remarks, assess taphonomic conditions, reconstruct paleoenvironmental contexts, and discuss trophic dynamics from a paleoecological perspective." This is better to be placed in the abstract.

Response: We agree that a summary of the study's aims and scope is important in the abstract as well. However, we prefer to retain this concluding sentence at the end of the introduction because it provides a logical bridge between the background context and the results, which clearly outlines the structure of the paper for the reader. - OK

Line 86. "The Chagres Formation, deposited between approximately 6.4 and 5.8 Ma (Collins et al., 1996), …" Probably more like 6-5.3 Ma, i.e. Messinian.
Response: The age provided here is based on Collins et al. (1996). - OK, but may need revision at a later stage

Line 179. The detail of measuremens and ratios to the second decimal is debatable. Detail to 0.05 may be enough, i.e. 1.25–1.35 and 1.55–1.8 in this case.
Response: Revised as suggested.

Line 179. Here and later: please give size of holotype and size range of all specimens.
Response: Added.

Line 186. Please give angle. what does poorly divided into ostium and cauda mean? Please be more precise.
Response: Added and revised.

Line 199. give size range in comparison to extant specimens in order to explain the subadult statement. Also it is better to say "small and not fully morphologically mature" rather than "subadult", which is a status that cannot be identified in fossils.
Response: Size range is added and the term "subadult" is revised to "small and not fully morphologically mature specimen" as suggested.

Line 204. this is a tautology. PLease reword or find other characters to mention.
Response: Deleted "with a less elongated form."

Line 223. orthogonal.
Response: Revised.

Line 236. Also very distinctive is the thin, slender rostrum bearing most of the ostium and sticking out perpenticular from the half-moon shaped thick posterior part of the otolith. The rostrum is very fragile and usually broken off in the fossil record, seriously hampering species definitions and recognition.

Response: Thank you for adding these characters, we have added these in our description.

Line 266. "Therefore, the true abundance of B. pluridens may be underestimated." Good point!

Response: Thank you.

Line 293. …, narrower ostium, and the more delicate crenulation of the otolith rims.

Response: Revised.

Line 397. "Nevertheless, distinguishing such variations based solely on the available figures remains difficult." very reasonable comment. In case of good photographs it may be possible but for drawings usually not.

Response: Thank you.

Line 523. "(Boya in Ngäbere, the language of the Ngäbe-Buglé people)" Interesting association. Could the rational be explained just a little bit more?

Response: Yes, we have added a full section to elaborate this: Named in honor of Brígida De Gracia (Boya in Ngäbere, the language of the Ngäbe-Buglé people) for her outstanding contributions to scientific research, public communication, and outreach activities in Panamá. The Ngäbe and their ancestors have inhabited the Isthmus of Panama for millennia, developing traditional ecological knowledge deeply connected to marine productivity cycles. Historical records demonstrate the Ngäbe's reliance on seasonal fish abundance driven by upwelling systems along Panama's Caribbean coast (Cybulski et al. 2025), creating a meaningful temporal bridge between the ancient upwelling ecosystem preserved in the Chagres Formation and the traditional knowledge systems that have recognized and depended upon these productive marine environments through time. - very interesting aspect and thank you for filling this in.

Line 531. How big is the largest specimen you have of this species and how does that compare to large and similar siued specimens of the compared extant species?

Response: We have provided dimensions of the specimens for the type series (see above). This helps us understand the size range of the fossil species as well as comparative material of comparable dimensions.

Line 654. or whales

Response: Added.

Line 658. "Therefore, the clustered distribution of otoliths in the sediments is consistent with deposition from predator excretions rather than from background mortality or mass mortality events." Very valid observation! Given the size of the clusters it is probably whales that are the culprits. They are known to feed on large quantities of myctophids.

Response: Agree, thank you for the positive comments.

Line 676. "Moreover, otoliths appear closely associated with ichnofossils attributed to Ophiomorpha (Stiles et al., 2022; Figs. 2C–2D). This suggests that burrowing organisms likely have contributed to otolith concentrations, either by feeding on fish or fecal material and subsequently incorporating otoliths into their burrows, as reported in other fossil contexts (Schwarzhans & Carnevale, 2021)."

Not in this case I don't think. The association with ichnofossils is highly speculative and has no similarity with the unique occurrence described by Schwarzhans & Carnevale (2021). This explanation should be deleted!

Response: Thank you for the comment. We have revised this line by toning down the statement, as well as removing the citation as suggested. It now reads: "Moreover, otoliths appear closely associated with ichnofossils attributed to *Ophiomorpha* (Stiles et al., 2022; Figs. 2C–2D). This suggests that burrowing organisms contributed to the local redistribution and concentration of otoliths within their burrow systems, either by incorporating otoliths during their activities or perhaps by selectively concentrating organic-rich material containing otoliths (Fig. 2D). While this burrowing activity does not increase the overall abundance of otoliths in the sediment, it creates localised zones of higher otolith density within and around burrow structures." - acceptable

Line 704. "…were the top three most abundant families (Fig. 15) at the site, demonstrating the importance of mesopelagic fauna in what we now understand to be relatively shallow-water deposits."

this I don't believe. All other fish remains too are from bathyal fishes (Hoplostethus, Coelorinchus and even Malakichthys). In addition, benthic foraminifera are also associated with deep marine environment and I believe the same may be due for molluscs, but for the latter I do not recall where I read this. Finally, shark remains also indicate deep marine environment and they will not have resulted from predation. - In a nutshell, even though tempting as true in situ indicators, the trace fossils could still be misleading. For that reference is made to Miguez-Salas et al. (2021) from a comparable setting.

Response: Thank you for the comment. We have elaborated on the discussion on the paleoecological interpretation.

We have added an additional analysis to explore this question further; we analyzed the proportion of mesopelagic otoliths relative to all other otoliths in 187 modern Caribbean shelf sediment dredge samples (O'Dea et al., 2007; Jackson & O'Dea, 2023). When plotted against depth (Figure 17), these data reveal that modern myctophid otolith assemblages increase from nearshore environments, peaking at around 120-150 m, before declining towards the shelf edge at 200 m.

In short, the extremely shallow, near-shore depths proposed by Stiles et al. (2022) are therefore as unlikely as bathyal depths. A middle neritic depositional setting can be reconciled with moderate post-depositional tectonic uplift, which is consistent with the tectonically active setting during isthmus formation (O'Dea et al., 2007; Jackson & O'Dea, 2023). We have revised the interpretation in the discussion and thoroughly modified the text. - Don't agree. See special comment at the end.

Line 734. "As Isistius preferentially parasitizes large marine mammals, fishes, and sharks…"

Not really the main ecology, Isistius is a facultative ectoparasite. See Fishbase and comment below. The extant Isistius brasiliensis (type-species of two in the genus, see Fishbase) is bathypelagic, oceanodrom, i.e. not exactly shallow water. It makes diurnal vertical migrations just like myctophids, and indeed is also known as occasional ectoparasite.

Response: Revised for clarification, the line now reads: "As *Isistius* is a facultative ectoparasite that often feeds on large marine mammals,…" - OK

Line 757. The association with ichnofossils is highly speculative and has no similarity with the unique occurrence described by Schwarzhans & Carnevale (2021). This explanation should be deleted!

Response: Please see our reply above (Line 676).

Line 760. "…the co-occurrence of shallow-water taxa and sedimentological evidence

(Stiles et al., 2022) indicate deposition in a highly dynamic, shallow-marine environment influenced by coastal upwelling"
This assessment is solely based on trace fossils while all other fossils indicate deep water. See mentioned article of Miguez-Salas (2021) in respect to trace fossils.

Response: Please see our reply above (Line 704).

Line 760. "The Piña assemblage, therefore, represents a rare fossil record of a shallow, mesopelagic fish-dominated ecosystem linked to coastal upwelling during the late Miocene."
Very doubtful conclusion with the weight of the evidence speaking against shallow water. Exclude or reword.

Response: Thank you for the comment. We agree and have reworded the conclusion. Please also see our reply above (Line 704).

Figure 7A is Diaphus rodriguezi because of the fewer denticles on the ventral rim and the narrow ostium. 7B is a typical Diaphus multiserratus.

Response: Thank you for your careful correction. We agree and have revised the figure. The material labelled as *D. multiserratus* are also revised thoroughly. - fine

Reviewer 2 (Konstantina Agiadi)

Basic reporting

The study "Remarkable dominance of myctophid otoliths indicates Caribbean coastal upwelling in late Miocene Panama" by Lin and O'Dea is clearly written and structured, and the references are all necessary and pertinent.
Response: Thank you very much for providing the review.

Experimental design

This study presents new findings on the Late Miocene fish fauna of the Caribbean Sea before it was disconnected from the Pacific Ocean, which are important both for our understanding of Miocene marine fish faunas, but also in terms of the provided reconstruction of the paleoceanographic regime in the area, which was the result of tropical climate and oceanic connectivity that is different from the present day. The Introduction provides a thorough overview of this paleoenvironmental setting and how this research fills in an important knowledge gap. The authors use standard methods of investigation and these are described appropriately.
Response: Thank you very much for the positive comments.

Validity of the findings

Although, as the authors mention, the tropical marine fish fauna of the Chagres Formation has been part of previous broader studies, these failed to capture several new species that the authors now identified. In addition, the authors interpret the dominance of mesopelagic fishes in a shallow-water domain as a result of regional upwelling, which is something new. The results are robust and the conclusions well stated.
Response: Thank you very much for the positive comments.

Additional comments

I have noted only some minor comments for the authors to address in the attached pdf.

Comments from the annotated pdf

Abstract. Very minor comment: there is a bit of time until the Isthmus formed so I would suggest to omit the "just" here

Response: Removed.

Abstract. Could you write the value of otolith density here in the abstract as well?

Response: Thank you for pointing this out, as also noted by Reviewer #1, we have added the value.

Abstract. Very minor comment: there is a bit of time until the Isthmus formed so I would suggest to omit the "just" here

Response: Removed.

Line 81. Middle and Late Miocene, as well as Early and Late Pliocene should start with capital letters because the Miocene and the Pliocene are official periods of relative time

Response: Yes, we have revised this thoroughly (also commented by Reviewer #3).

Line 94. please give the description also of the Rio Indio Siltstone

Response: Added.

Line 650. Are there estimates of the sedimentation rates for this section? How much time do these clusters correspond to?

Response: Thank you for this comment. Unfortunately, there are no direct sedimentation rate estimates for this section, so we cannot quantitatively estimate the duration represented by these clusters. However, based on the sedimentological evidence and the broad, irregular vertical and lateral spread of otoliths (rather than their restriction to a single condensed horizon), we interpret that otolith burial was episodic and discontinuous rather than the result of a single event.

Line 650. I suggest to remove this phrase here, because it contradicts what you are saying two paragraphs down about otoliths being incorporated into burrows.

Response: Removed.

Line 668. Although I agree theoretically with this reasonable conclusion, if you did not measure the distance from the surface, to provide here a correlation to support the statement, I would suggest to rephrase or just remove this phrase.

Response: Yes, agree. This line is removed.

Line 710. Is there a modern equivalent for this phenomenon? All species have mechanisms to avoid being eaten, not just Myctophidae. I'm not very convinced that this would be the reason why myctophids, rather than small pelagic fishes dominated this assemblage.

Response: Thank you for this thoughtful comment. We appreciate that all fishes possess predator-avoidance strategies. At present, we cannot fully resolve why myctophids, rather than small pelagic fishes, dominated the assemblage at this locality, and we are not aware of a clear modern analogue for this exact pattern. However, our primary focus is not on explaining taxonomic dominance per se, but on highlighting the exceptional productivity and rapid trophic turnover that characterize this system. This abundant prey biomass efficiently channels primary production up the food web, and is observed both in the Piña fossil assemblage and in specific modern upwelling ecosystems. - Good point by the reviewer. However, myctophids and bristlemouths of the genus Cyclothone are the dominant mesopelagic fishes today and probably also in the Miocene and Pliocene. Cyclothone otoliths are very small and fragile and may be readily resolved in the intestines of a predator while myctophid otoliths are large enough to withstand. At least that could be an explanation why we have so many fossil myctophid otoliths and practically none of Cyclothone.

Line 724. "… tropical upwelling systems in the modern Arabian Sea, where primary production predominantly channels relatively directly into mesopelagic fish communities." Could you elaborate on this please?

Response: By "primary production predominantly channels relatively directly into mesopelagic fish communities," we mean that in these tropical upwelling systems, high planktonic productivity supports dense aggregations of midwater planktivores (myctophids), with less of the energy being routed first through diverse, complex benthic food webs. because a large proportion of primary production is consumed by mesopelagic fishes, this acts as the principal trophic conduit to larger predators. This efficient, shorter food chain results in substantial biomass at the mesopelagic level and supports a predator-rich ecosystem. - good

We have added a line here for clarification: "In these systems, high planktonic

productivity supports dense aggregations of myctophids, bypassing some of the longer and more complex food chains." **- good**

Reviewer 3 (Gary Stringer)

Basic reporting

A. For the majority of the manuscript, the English is understandable and comprehensible.

Response: Thank you very much for providing the review.

There are some places where terminology, punctuation, or word usage could be improved or revised to better match professional English. This also includes stratigraphic usage. Specific examples are provided below and denoted by line numbers:

Lines 1–3. Should be “Late Miocene” in the title as Neogene epochs have been ratified (see reference for line 17). Late is used because it is referring to geologic time. Also, strongly suggest including formational name in title for greater specificity.

Response: Revised as suggested.

Lines 17, 29, 42, 55, 67. On Line 17, it is referring to a rock unit, the Chagres Formation, and it should be Upper Miocene. Early and Late Neogene subseries and subepochs have been ratified, and the initial letter should be uppercase, i.e., Late Miocene (if referring to geologic time) or Upper Miocene (if referring to rocks or rock units). See Aubry et al. (2022) in Episodes. The use is inconsistent in the publication. For example, line 175 has “Late Miocene,” but it should be “Upper Miocene” since it refers to a rock unit. The same applies to Lines 298 and 593. Usage must be corrected and consistent. Line 29 should be “Late Miocene” (referring to time), and Line 42 is “Late Pliocene” since it refers to geologic time. Line 55 should be “Upper Miocene” since it refers to a formation (rock unit). Line 67 should be Late Miocene since it is referring to geologic time.

Response: Thank you for pointing out this mistake, we have revised as suggested.

Line 28 and 699. According to Merriam-Webster, “nearshore” without hyphen is preferred in English.

Response: Revised.

Line 40. Comma not needed after “develop.”

Response: Deleted.

Line 51. There is an extraneous “&” between “Aguilera & Rodrigues” that needs to be deleted.

Response: Deleted.

Line 65. I am not sure if the use of a large bulk sample that was not weighed qualifies as “quantitative.” Part of the study is certainly quantitative with precise weights.

Response: We have separated this sample from the rest of the weighed samples in the subsequent analyses.

Line 81. Middle to Late Miocene since it is referring to geologic time (see line 17).

Response: Revised.

Line 86. The date given, 6.4 –5.8 Ma, for the Chagres Formation would place the formation in the Late Miocene (geologic time). This should certainly be denoted in the text when discussing the geological setting.

Response: Added.

Lines 88 to 89. Suggest: “. . . and is primarily comprised of.” As written, it is not clear as to meaning.

Response: Revised.

Lines 90–91. If these are formal members, then it should be the Lower Toro Limestone Member, the Middle Rio Indio Siltstone Member, and the Upper Chagres Limestone Member. An alternative is to have the Lower Toro Limestone, the Middle Rio Indio Siltstone, and the Upper Chagres Limestone members. In this case, “members” would be lowercase since it is not part of the specific formal name.

Response: Revised.

Lines 197, 330, and 535. Specific name and location of type locality should be included for all new species rather than just “type locality.”

Response:

Line 250. Recommend stating the number of specimens, and this would quantify “relatively common.”

Response: Added.

Line 316. A brief statement on any morphological features of the outer face would be helpful.

Response: Thank you for the comment. Distinctive characters such as an umbo or protrusions of the outer face are described if present. In cases where such traits are absent (which is true for the majority of otoliths), we have instead described the general convexity/concavity or flatness of the outer face. - OK

Line 405. Comma after D. rodriguezi does not appear necessary.

Response: Deleted.

Line 455. Middle Pliocene (uppercase "M").

Response: Revised.

Line 485. The term "pince-nez" is not commonly used in otolith morphology. Recommend that "homosulcoid-type" be used, and if not, add in parentheses after "pince-nez."

Response: Added.

Line 494. Bregmaceros otoliths are not a family as stated in the sentence. Recommend that it read, "Bregmaceros otoliths are representatives of the third most common family . . ."

Response: Thank you for the correction, we have revised the line accordingly.

Lines 731, 737, 750. Should be Late Miocene (uppercase "L"). Use "Late" as it refers to geologic time.

Response: Revised.

Line 742. Comma after "interactions" is not needed.

Response: Deleted.

Line 748. Comma after "conditions" is not needed.

Response: deleted.

Lines 997, 1003, 1008, 1014, 1020, 1027, 1035, 1039, 1046, and 1050. As a rule, lower/middle/upper should be used when referring to rock units, i.e., formations. So, all of these should be Upper Miocene Chagres Formation (shows stratigraphic

position).
Response: Revised.

B. Literature references appear to be mainly complete. However, there are some omissions that need to be inserted. These are given below according to line numbers. In the introduction, the paleontology of otoliths background (taxonomy, morphology, etc.) is not especially exhaustive, but this would vary with the expertise of the reader. It seems sufficient for most readers.
Response: Thank you for carefully checking the completeness of the literature and for your helpful suggestions.

Lines 22–23. The statement, "The otolith density in the sediments is the richest known globally" is not accurate as a higher concentration or density of otoliths has been reported by Stringer, Starnes, Leard, and Puckett (2020). They noted a 1.17 kg sample from a clay interbed of the Oligocene (Rupelian) Glendon Limestone in Mississippi, USA, that yielded 811.1 otoliths/kg. See Line 680 comments for discussion and reference that needs to be added. The present statement in the manuscript must be modified.
Response: Thank you very much for drawing our attention to this important study. We apologize for the oversight. We have modified this line (as also commented by the editor) and added this reference in the discussion (see below).

Line 51. Study by Stringer (1998) in Jamaica needs to be added.
Stringer, G. (1998). Otolith-based fishes from the Bowden shell bed (Pliocene) of Jamaica: Systematics and Palaeoecology. Contributions to Tertiary and Quaternary Geology, Volume 35(1–4):147–160.
Response: Added.

Also, a study by Stringer, Ebersole, and Ebersole (2020) included Neogene otoliths from Panama, Columbia, Ecuador, Trinidad, Venezuela, and Brazil.
Stringer, G., J. Ebersole, and S. Ebersole. 2020. First description of the fossil otolith-based sciaenid Equetulus silverdalensis n. comb., in the Gulf Coastal Plain, USA, with comments on the enigmatic distribution of the species. PaleoBios, 37.ucmp_paleobios_49670.
Response: Thank you for pointing out this additional reference. However, our description here is focused on otolith-based community or assemblage-level

studies rather than single-species case studies.

John E. Fitch also did a preliminary study of the otoliths of the Gatun Formation in Panama and was published in the Journal of Paleontology in 1984. This reference should be included

Fitch, J.E. 1984. Osteichthyan otoliths. In D.D. Gillette. A marine ichthyofauna from the Miocene of Panama and the Tertiary Caribbean Faunal Province. Journal of Vertebrate Paleontology 4(2):172–186.

Response: Added.

Line 64. If the Stiles et al. (2022) paleoenvironment based on ichnofossils and sedimentation is accepted for the Chagres Formation, then the reasoning for accepting it rather than the numerous previous studies should be elucidated and justified. Several of the studies that are not accepted are quoted repeatedly in the text. This is especially important if the paleoenvironment is going to be interpreted as shallow marine with a coastal upwelling.

Response: Thank you for the comment. Please see our revised interpretation in the discussion below (see also our response to the editor and Reviewer #1).

Line 651. Schafer (1972) has a thorough discussion of the death, disintegration, and burial of fishes, including otoliths. Ecology and Palaeoecology of Marine Environments, University of Chicago Press. This reference should be included.

A detailed discussion of the potential for fish species enrichment by otoliths is found in Welton (2015) and should be included and addressed.

"The Marine Fish Fauna of the Middle Pleistocene Port Orford Formation and Elk River Beds, Cape Blanco, Oregon"

Response: Thank you for providing these relevant papers.

Line 680. A higher concentration or density of otoliths has been reported. Stringer, Starnes, Leard, and Puckett (2020) reported that a 1.17 kg sample from a clay interbed of the Oligocene (Rupelian) Glendon Limestone in Mississippi, USA, yielded 811.1 otoliths/kg. Horizontally adjacent samples yielded lower concentrations. The extremely high concentration, after other considerations and possibilities, was postulated to be related to enrichment by Oligocene piscivorous predators, such as toothed whales and other marine mammals.

Stringer, G., J. Starnes, J. Leard, and M. Puckett. 2020. Taphonomic and Paleoecologic Considerations of a Phenomenal Abundance of Teleostean Otoliths in the Glendon Limestone (Oligocene, Rupelian), Brandon, Mississippi. Journal of the Mississippi Academy of Sciences 65(1):101.

Response: Thank you very much for drawing our attention to this important study. We apologize for the oversight. We have added and addressed this reference in the discussion.

C. The structure of the manuscript follows the format of professional article with a title, authors (affiliations), abstract, introduction, geological setting, materials and methods, results (including detailed systematics for new species), discussion (includes taphonomy, preservation, paleoenvironment, paleoecology, conclusions, acknowledgements, and references

There are 16 figures that appear necessary and relevant. Photographs of otoliths are clear with good resolution and clearly labeled. Some photographs do not show diagnostic morphologic features, but this is a result of poor preservation and not the photography. There is one table that is certainly important (list of taxa of the Upper Miocene Chagres Formation). The supplemental files clearly indicate the raw date for each of the 33 samples collected and analyzed by the researchers. A few comments regarding figures and tables and shown by line numbers are provided below.

Response: Thank you for your thorough review and comments.

Figure 2A. Is labeled as "Lithostratigraphy," but the formation and members are not designated, and it is unclear as to what it represents. The stratigraphy should be included, clearly noted, and explained.

Response: Thank you for pointing this out, we have revised the figure accordingly.

Table 1. Title should be Upper Miocene (uppercase "U") since it refers to a rock unit, the Chagres Formation.

Response: Revised.

It would be very informative to have a total weight of the bulk samples as well as a total of the otolith specimens (labeled as "counts") and Isistius teeth specimens on the table.

Response: Yes, these data are provided in our Supplemental files Table S1.

Need to explain why the average number of otoliths per kg has a ± number?

Response: The “±” value represents the standard deviation, which quantifies the variation in otolith densities among individual sediment samples around the mean. This is a standard statistical convention that requires no further explanation.

Explain why the Isistius teeth were listed on Table 1 and other sharks were not.
Response: We included *Isistius* teeth in Table 1 because they are specifically discussed in the text and are the most abundant shark teeth in our collection. Providing a complete inventory of all elasmobranch taxa is beyond the scope of this study.

An extremely important question is the stratigraphic relationship of the 33 samples. Do they represent different vertical stratigraphic positions within the formation, or do they represent horizontal stratigraphic positions (i.e., all samples from the same stratigraphic level in the formation but apart from one another)? This needs to be clearly explained in the text and is very important in the interpretation of the samples.
Response: Thank you for the comment. Our samples are from the same stratigraphic level in the formation but apart from one another. This is now explicitly described in our material and methods section.

Experimental design

2. Experimental design
The manuscript defines the objective of the research and how this is accomplished (Lines 65–69). The importance of the research is explained, and its implications for otolith paleontology in the Neogene of the Caribbean are provided.
For the most part, the methodology is explained so that the research could be duplicated if samples were collected. Researchers applied for the proper permit for collecting, which was approved. All figured specimens and other otoliths are stored at the Biodiversity Research Museum, Academia Sinica, Taiwan. The nomenclature for the new species appears to conform to the International Commission on Zoological Nomenclature and has been registered in ZooBank. A few comments on the methodology are given below with line numbers for identification.
Response: Thank you for your thorough review and comments.

Lines 111–112. If 33 samples weighting approximately 0.6 kg each were collected, then the total weight of the samples was approximately 19.8 kg. This is important information that should be stated. Another alternative is to give the exact weight of the 33 samples based on Table 1. It is very important that the stratigraphic relationship of the samples be detailed and explained. To me, this is essential to this research.

Response: As replied above, our samples are from the same stratigraphic level in the formation but apart from one another (described in our materials and methods section). Weights of each bulk sample are also listed in our Supplemental files Table S1.

Why was a sample collected, but not weighed, and utilized? It seems that it should have been weighed as with the other samples. It can introduce bias into the study, especially with the weight unknown. The sample that was not weighed provided the largest number of specimens. This should be explained.

Response: This single sample was collected from a separate field trip. As suggested by the editor, we have conducted further analyses (sensitivity analysis and confidence intervals) to avoid a biased interpretation.

Lines 118–119. It should be explained why these techniques were utilized. It should also be addressed if the sodium sulfate solution could possibly affect the preservation of the aragonitic otoliths. As noted in the manuscript, an extremely large proportion of the otoliths were poorly preserved.

Response: No, there is no evidence showing that the sodium sulfate solution affects the preservation of otoliths. We use this method simply because it is a standard and widely applied method that accelerates the disaggregation of slightly consolidated sediments, making otolith extraction faster and more efficient.

Line 174. Would be very helpful to have the total number of specimens for all new species, i.e., holotype, paratype(s), and other examined material. This is done on Line 301 for a new myctophid species as "Additional material," but it is not done for new species on Line 174

Response: The total number of specimens is explicitly presented in our Table 1. There is no additional material for three (out of four) new species because all available specimens are included in the type series.

Line 183. Since it is a new species, the convexity of the inner face and outer would be very helpful and diagnostic. A brief description of the outer face is also commonly included in otolith descriptions, especially for new species. This is highly recommended.

Response: Distinctive characters such as an umbo or protrusions of the outer face are described if present. In cases where such traits are absent (which is true for the majority of otoliths), we have instead described the general convexity/concavity or flatness of the outer face.

Validity of the findings

Validity of the Findings

The raw data for the otoliths, the systematic description of the otoliths, and the statistical analysis performed are all provided. Therefore, it appears that the findings should be valid,

Conclusions are well stated and are related to research's objectives.

Response: Thank you for your thorough review and comments.

Line 722. Could there be other factors other than high predator density causing the abundance of Isistius? What is the abundance of other sharks in the samples?

Response: Thank you for this question. Based on the available evidence, we have provided the most probable interpretation in the discussion. *Isistius* teeth strongly dominate the shark tooth assemblage at Piña, as also documented by Carrillo-Briceño et al. (2015). If alternative explanations exist that we may have overlooked, we would be glad to consider them.

Line 739. You state in the Abstract and in other places that the otolith concentration or density (otoliths/kg of bulk sample) is the highest ever documented. Now, in the conclusions, you state that the otolith density is among the highest. The later statement is correct, but the others stating unequivocally that it is the highest concentration globally are not and should be revised.

Response: Thank you and we have revised this statement accordingly (see also our response above).

Additional comments

Overall, the manuscript is well-written, highly informative. The fossil otoliths are well described, and the taxonomy of the otoliths appears to be very accurate. It is an important contribution to the understanding of the Neogene otoliths of the Caribbean.

Response: Thank you for your thorough review and positive comments

Line 122. It is to be presumed that there are no lapilli (utricular otoliths) in the large assemblage. A sentence as to why no lapilli occur in the Chagres Formation would be informative. Ariid lapilli are common in many Neogene Caribbean shallow-marine otolith assemblages as indicated by several references. Could this total lack of ariids be related to the proposed coastal upwelling paleoenvironment?

Response: Thank you very much for this thoughtful comment. We did not find any ariid lapilli in our collection, and we agree that this absence likely have paleoecological significance. It supports our interpretation of a middle neritic depositional environment influenced by coastal upwelling, rather than a more nearshore setting where ariids are typically more common. We have incorporated this point into the discussion.

Some specific comments to the evaluation of the paleowater-depth:

Fig. 17 included in this article shows the distribution of myctophids from samples of the captioned two articles (O'Dea et al., 2007; Jackson & O'Dea, 2023). Myctophid otoliths in Fig. 17 do not exceed 20% of all otoliths at any depth, while in the studied sediments of the Chagres FM they are about 96%. The depths range given in Fig. 17 from 0 to 210 m, i.e., is entirely on the shelf. The vast majority of myctophids are oceanic mesopelagic fishes undertaking dial migration between the surface at night and about 1000 m and more during the day (e.g., Robison et al., 2020). So this interval is hardly relevant to estimate myctophid abundances in sediments.

There are two studies of otoliths from ocean bottom dredges relevant for this.

1.- Schwarzhans (2013) from multiple transects from 30 to over 3000 m in the gulf of Guinea and deepwater of the Azores and,

2. Lin et al. (2017) from the Mediterranean Sea.

Both studies show that myctophid otoliths can occur indeed in relatively shallow water starting at about 50 m over the shelf, but are relatively rare at that depth (<20%) and composed of relatively few species that tolerate shelf conditions. The majority of myctophids kick in below 200 m, reach a maximum at about 500 to 1000m, which is consistent with their mode of live, and then show an abundance of >70% of all otoliths and a much higher diversity of species.

Therefore the underlying conclusion of a mid-shelf setting cannot be maintained. All biota speak for a bathyal environment, perhaps upper bathyal between 300 and 500 m. The argumentation presented here is entirely based on a data-set based on an article evaluating bioturbation and sedimentology. This is of course very valid, but it overlooks that all other biotic aspects speak against such an interpretation. In addition, the article by Miguez-Salas et al. (2021), which was recommended in the previous review, is not even cited. This article shows that similar sedimentary features can occur in deep-marine contourites and the trace fossils as well. The setting of the Chagres FM would be in a comparable position and should not be overlooked in my opinion. I see the interpretation of the paleoenvironment, particularly as to the paleo-depth requiring additional scrutiny and it should not be left as is.

I would further suggest to exclude Fig. 17 from the article since it is not relevant, i.e., even misleading since it does not show bathyal communities.