



**UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO**  
**POSGRADO EN CIENCIAS BIOLÓGICAS**  
INSTITUTO DE GEOLOGÍA  
**ECOLOGÍA**

**ANÁLISIS DE LA DIVERSIFICACIÓN TAXONÓMICA Y MORFOLÓGICA DE  
CLUPEOMORPHA (ACTINOPTERYGII: TELEOSTEI) DURANTE EL CRETÁCICO**

**TESIS**

**(POR ARTÍCULO CIENTÍFICO)**

**TAXIC AND MORPHOLOGIC DIVERSIFICATION DURING EARLY RADIATION  
OF CLUPEOMORPHA (ACTINOPTERYGII: TELEOSTEI)**

QUE PARA OPTAR POR EL GRADO DE:

**MAESTRA EN CIENCIAS BIOLÓGICAS**

PRESENTA:

**EDNA PATRICIA RODRÍGUEZ SÁNCHEZ**

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**CIUDAD UNIVERSITARIA, CD.MX., 2022**



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ASUNTO: Oficio de Jurado

**M. en C Ivonne Ramírez Wence**  
**Directora General de Administración Escolar, UNAM**  
*Presente*

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **22 de agosto de 2022** se aprobó el siguiente jurado para el examen de grado de **MAESTRA EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **ECOLOGÍA** de la alumna **RODRÍGUEZ SÁNCHEZ EDNA PATRICIA** con número de cuenta **312145439** por la modalidad de graduación de **tesis por artículo científico** titulado: **"TAXIC AND MORPHOLOGIC DIVERSIFICATION DURING EARLY RADIATION OF CLUPEOMORPHA (ACTINOPTERYGII: TELEOSTEI)"**, que es producto del proyecto realizado en la maestría que lleva por título: **"ANÁLISIS DE LA DIVERSIFICACIÓN TAXONÓMICA Y MORFOLÓGICA DE CLUPEOMORPHA (ACTINOPTERYGII: TELEOSTEI) DURANTE EL CRETÁCICO"**, ambos realizados bajo la dirección del **DR. JESÚS ALVARADO ORTEGA**, quedando integrado de la siguiente manera:

Presidente: **DR. ERNESTO VELÁZQUEZ VELÁZQUEZ**  
Vocal: **DR. KLEYTON MAGNO CANTALICE SEVERIANO**  
Vocal: **DR. LUIS FERNANDO DEL MORAL FLORES**  
Vocal: **M. EN C. CHRISTIAN LAMBARRI MARTÍNEZ**  
Secretario: **DRA. CLAUDIA PATRICIA ORNELAS GARCÍA**

Sin otro particular, me es grato enviarle un cordial saludo.

**A T E N T A M E N T E**  
**"POR MI RAZA HABLARÁ EL ESPÍRITU"**  
Ciudad Universitaria, Cd. Mx., a 12 de octubre de 2022

**COORDINADOR DEL PROGRAMA**



**DR. ADOLFO GERARDO NAVARRO SIGÜENZA**



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## Resumen

Los peces constituyen un grupo antiguo cuyas características han permitido su amplia diversificación a lo largo de la historia. Presentan una amplia diversidad en cuanto a especies, formas, fisiología, comportamiento y hábitats, lo cual a su vez dificulta la reconstrucción de su historia evolutiva. De todos los clados de peces que han existido, la subclase Actinopterygii es la que actualmente cuenta con la mayor riqueza y cuya gran diversificación se presentó en el límite del Albiano-Cenomaniano. Para estudiar esta diversificación, se empleó el registro fósil del superorden Clupeomorpha perteneciente al periodo Cretácico, usando enfoques tanto táxicos como morfológicos; posteriormente, se reconocieron los tipos de radiación y sus interacciones. Clupeomorpha es un grupo diverso con una amplia distribución espacial, temporal y ecológica, que además ha sido extensamente estudiado en las últimas décadas. Para analizar la diversificación táxica se propuso un modelo para calcular las tasas de origen, y para analizar la diversificación morfológica se aplicó morfometría geométrica. Los resultados sugieren la ausencia de una radiación táxica debido al incremento constante del origen de taxa. En contraste, sugieren la presencia de una climática-geográfica-disparificación y similar a una amplia diversificación asociada a la expansión de la ocupación de los filomorfoespacios y el incremento de la disparidad, de acuerdo con las clasificaciones actuales. Esto resalta la incompatibilidad de las clasificaciones de radiaciones actuales con el caso de estudio. Asimismo, resalta la necesidad de generar más trabajos en torno al concepto y delimitación de los tipos de radiación, así como de producir más estudios de caso que integren ambos tipos de diversificación.

## **Abstract**

Fish are an ancient group whose characteristics have allowed their wide diversification throughout the history. They present a wide diversity of species, shapes, physiology, behavior, and habitats, which also hinder the reconstruction of their evolutionary history. Of all the existing fish clades, the subclass Actinopterygii is the one that has the greatest current richness and whose great diversification occurred at the Albian-Cenomanian boundary. To study this diversification, we employed the fossil record of the superorder Clupeomorpha from the Cretaceous period, using both taxic and morphological approaches; then, we recognized the radiation types and their interactions. Clupeomorpha is a diverse group with a wide spatial, temporal, and ecological distribution, which has also been extensively studied in recent decades. To analyze the taxic diversification, a model was proposed to calculate the rates of origin, and to analyze the morphological diversification, geometric morphometry was applied. The results suggest the absence of taxic radiation due to the constant increase in the taxa origination. In contrast, they suggest the presence of a climatic-geographical-disparification and broad diversification-like due to the expansion of the phylomorphospaces occupation and the disparity increase, according to the current classifications. This exhibits the incompatibility of the current radiation classifications with the case study. Likewise, it highlights the need to generate more researches related to the concept and delimitation of the radiation types, and to produce more case studies that integrate both types of diversification.

## Introducción general

Los peces constituyen un grupo de más de 500 millones de años (Ma), cuyas características les han permitido diversificarse ampliamente a lo largo de la historia de la vida. Se conocen como peces a aquellos vertebrados que presentan aletas, branquias y usualmente escamas, constituyendo un grupo parafilético debido a la exclusión de los tetrápodos (Helfman *et al.*, 2009; Nelson *et al.*, 2016). Representan más de la mitad de la riqueza de los vertebrados con más de 36,305 especies descritas (Fricke *et al.*, 2022). Además, muestran una amplia diversidad en cuanto a formas, fisiología, comportamiento y hábitats, lo cual hace difícil reconstruir su historia evolutiva. Actualmente los peces (fósiles y recientes) se clasifican en un total de 10 Clases: Myxini (peces bruja), Petromyzontida (lampreas), †Pteraspidoforma, †Anaspida, †Thelodonti, †Cephalaspidoforma, †Placodermi, Chondrichthyes (peces cartilagosos), †Acanthodii (acantodios) y Osteichthyes (peces óseos y tetrápodos). Esta última es la de mayor diversificación y se constituye por dos grupos, las subclases Sarcopterygii (peces con aletas lobuladas y tetrápodos) y Actinopterygii (peces con aletas radiadas) (Nelson *et al.*, 2016).

De todos los clados anteriormente mencionados, el que más destaca por su enorme riqueza (alrededor de 30,500 especies) es la subclase Actinopterygii (Nelson *et al.*, 2016). El origen de este grupo se ha sugerido en el Silúrico-Devónico (Betancur-R. *et al.*, 2013; Near *et al.*, 2012). Sin embargo, tanto el registro fósil como modelos computacionales indican que estos peces se diversificaron hasta la Era Mesozoica, en tres eventos independientes durante el Jurásico tardío, Cretácico temprano, y Cretácico tardío. Esta última de finales del Albiano y principios del Cenomaniano, se considera como la más grande e importante de todas (Betancur-R. *et al.*, 2013; Friedman & Sallan, 2012; Guinot & Cavin, 2016; Near *et al.*, 2012). Se piensa que afectó a una gran cantidad de clados, incluyendo el superorden Clupeomorpha (Nelson *et al.*, 2016).

A nivel mundial, uno de los clados de actinopterigios que destaca por sus características es el superorden Clupeomorpha o Clupei. Este es un grupo aparentemente monofilético conocidos comúnmente como anchoas, arenques y sardinas. Generalmente se caracterizan por presentar i) bullas osificadas en la cápsula del oído formadas a partir de la conexión otofísica, ii) un canal sensorial supratemporal y comisural que pasa por el parietal o supraoccipital, iii) escudos abdominales, y iv) el hipural 2 fusionado al centro ural (Arratia, 2018; Grande, 1985; Nelson *et al.*, 2016). Actualmente se reconocen dos ordenes, uno constituido únicamente por especies fósiles (†Ellimmichthyiformes), y otro por especies recientes y fósiles (Clupeiformes). Estos se distinguen porque los peces Ellimmichthyiformes muestran una línea lateral completa, dientes en el paresfenoides, un foramen grande y parietales que se juntan en la parte media; en contraste, los peces Clupeiformes muestran *recessus lateralis* y los parietales se encuentran separados por el supraoccipital (Grande, 1985; Nelson *et al.*, 2016).

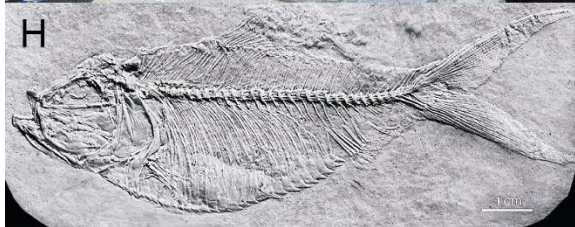
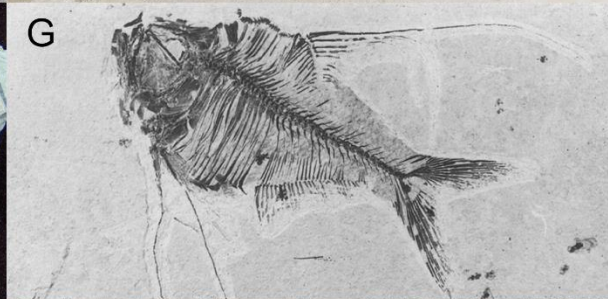
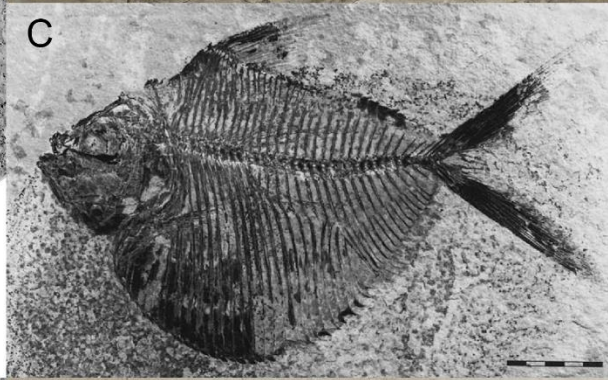
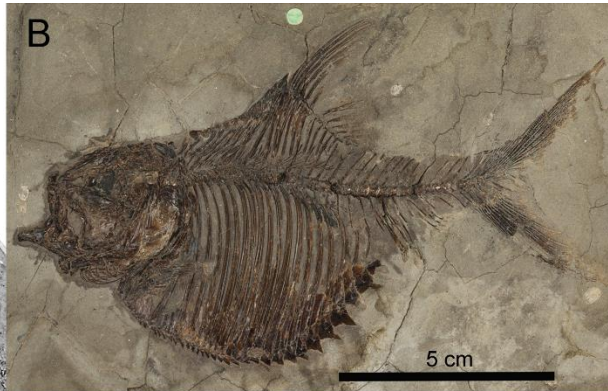
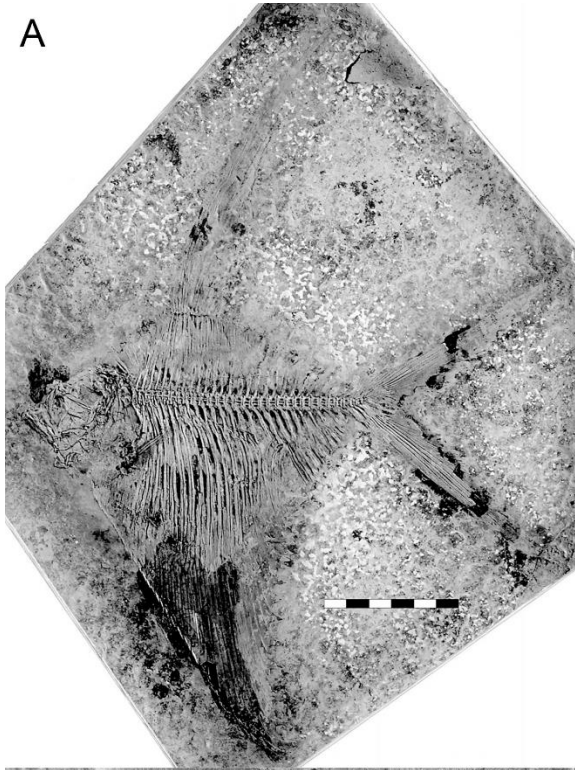
Los clupeomorfos conforman un grupo taxonómica y ecológicamente diverso, con una amplia distribución espacio-temporal. Actualmente se reconocen aproximadamente 434 especies recientes, contenidas en 83 géneros y 10 familias (Fricke *et al.*, 2022). Estos

presentan tallas que varían de los 2 cm (*Amazonsprattus* Roberts, 1984) hasta un metro de longitud (*Chirocentrus* Cuvier, 1816; Helfman *et al.*, 2009). Los clupeiformes se alimentan de plancton y forman cardúmenes de gran tamaño por lo que son presas de otros vertebrados y son clave en las cadenas tróficas (Ganias, 2014). Son de los peces más abundantes de la actualidad (Grande, 1985), mostrando incluso una gran importancia comercial con un tercio del total de la pesca mundial (Ganias, 2014). Además, el grupo muestra una distribución cosmopolita, y aunque se distribuye en todos los tipos de ambientes, se presentan de forma abundante en ambientes marinos (80% de especies actuales; Helfman *et al.*, 2009). Asimismo, muestran un registro desde el Cretácico temprano al presente. Se han descrito 190 especies fósiles contenidas en 74 géneros, de las cuales 62 pertenecen al Cretácico (Mesozoico) y 128 al Cenozoico (SI Apéndice, Tabla S1; Ilustración 1).

En las últimas décadas, la mayor atención se ha centrado en especies fósiles de Clupeomorpha (Ilustración 1). La mayoría de los estudios se han enfocado a la descripción de especies (ej. Alvarado-Ortega *et al.*, 2020; Chang & Maisey, 2003; Forey *et al.*, 2003; Khalloufi *et al.*, 2010) y a las relaciones filogenéticas dentro del grupo (ej. Alvarado-Ortega *et al.*, 2008; Boukhalfa *et al.*, 2018; Chen *et al.*, 2021; Marramà *et al.*, 2019; Vernygora & Murray, 2021). En contraste, se han presentado pocos trabajos sobre la paleodistribución de las especies (Boukhalfa *et al.*, 2018; Chen *et al.*, 2021; Malabarba & Di Dario, 2017; Murray & Wilson, 2013). A pesar de los numerosos estudios que se han realizado, las especies fósiles presentan problemas en cuanto a la taxonomía y filogenias propuestas. Esto se debe a que la descripción de las especies llega a realizarse con un solo ejemplar o material mal preservado. Además, existen inconsistencias en la codificación de caracteres, lo que resulta en notables contradicciones de las filogenias. Por otra parte, es de resaltar que la mayoría de los trabajos mencionados son descriptivos. La excepción son los modelos cladistas para obtener filogenias y un estudio de morfometría tradicional empleado para separar especies fósiles (Melgarejo-Damián, 2011). Por lo tanto, han quedado relegadas y de forma injustificada, ciertas preguntas de paleobiología (estudio de la expresión de la diversidad biológica en el tiempo geológico; com. per. Jesús Alvarado-Ortega). Por ejemplo, sobre la diversificación de taxa y de formas corporales (Ilustración 1) a lo largo del Mesozoico y Cenozoico.

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**Ilustración 1.** Especies fósiles de Clupeomorpha descritas alrededor del mundo. A. *Rhombichthys intoccabilis* (Khalloufi *et al.*, 2010); B. *Ellimmichthys spinosus* (de Figueiredo & Gallo, 2021); C. *Triplomystus noorae* (Forey *et al.*, 2003); D. *Scutatoclupea bacchiae* (Bannikov, 2015); E. *Scombroclupea macrophthalma* Heckel, 1849 (Muséum, National D'Histoire Naturelle); F. *Tunisiaclupea speratus* (Boukhalfa *et al.*, 2018); G. *Sorbinichthys elusivo* (Bannikov & Bacchia, 2000); H. *Ellimma branneri* (Chang & Maisey, 2003); I. *Armigatus brevissimus* Blainville, 1818 (Muséum, National D'Histoire Naturelle).



De estas especies fósiles, seis (10%) han sido descritas a partir de localidades cretácicas de México (Tabla 1; SI Apéndice, Fig. S5), contribuyendo de forma significativa al conocimiento del superorden. Estas especies muestran afinidades morfológicas con aquellas mediterráneas del este del Mar de Tetis (SI Apéndice, Fig. S3). La excepción es *Ranulfoichthys dorsonudum* Alvarado-Ortega, 2014, que presenta caracteres únicos y plesiomórficos que no coinciden con los de los dos ordenes ya mencionados, indicando entonces una divergencia temprana del taxón (SI Apéndice, Fig. S1). En cuanto a la ecología, los clupeomorfos mexicanos se distribuían en ambientes de transición (Cantera Tlayúa y El Espinal; Alvarado-Ortega & Ovalles-Damián, 2008; Alvarado-Ortega *et al.*, 2020) y marinos de poca profundidad (El Chango; Than-Marchese *et al.*, 2020), lo cual señala la diversidad de ambientes en los que se distribuían. Entonces, las especies mexicanas aportan información relevante sobre la morfología, ecología y evolución de la ictiofauna distribuida al oeste del Mar de Tetis (SI Apéndice, Fig. S3) y en el límite temporal del Cretácico temprano-tardío (también llamado Albiano-Cenomaniano).

**Tabla 1.** Especies del superorden Clupeomorpha descritas de localidades mexicanas.

<b>Especie</b>	<b>Autor</b>	<b>Edad</b>	<b>Localidad</b>
<i>Armigatus carrenoae</i>	Alvarado-Ortega, Than-Marchese, Melgarejo-Damián (2020)	Albiano	Cantera Tlayúa (Puebla)
<i>Paraclupea seilacheri</i>	Alvarado-Ortega, Melgarejo-Damián (2017)	Albiano	Cantera Tlayúa (Puebla)
<i>Ranulfoichthys dorsonudum</i>	Alvarado-Ortega (2014)	Albiano	Cantera Tlayúa (Puebla)
<i>Scombroclupea javieri</i>	Than-Marchese, Alvarado-Ortega, Matamoros, Velázquez-Velázquez (2020)	Cenomaniano	El Chango (Chiapas)
<i>Scombroclupea occidentalis</i>	Giersch, Frey, Stinnesbeck, Ifrim, Padilla Gutierrez (2011)	Cenomaniano	Loma la Mula (Coahuila)
<i>Triplomystus applegatei</i>	Alvarado-Ortega, Ovalles-Damián (2008)	Cenomaniano	El Espinal (Chiapas)

México es un país megadiverso que también contó con una gran diversidad biológica en el pasado, de la cual destaca su paleoictiofauna. Actualmente se han descrito y registrado numerosas -y no contabilizadas- especies de peces fósiles mexicanos provenientes de más de 50 localidades (González-Rodríguez *et al.*, 2013). Estos aportes tienen gran relevancia e impacto en el entendimiento de la sistemática, ecología, biogeografía y evolución de los peces. Por ejemplo, varias de estas especies representan el primer registro para el continente (Cantalice *et al.*, 2019), e incluso el más antiguo de ciertos grupos en Norteamérica (Cantalice *et al.*, 2019) y el mundo (Cantalice & Alvarado-Ortega, 2016); asimismo, pueden indicar diversificaciones tempranas de determinados clados (Alvarado-Ortega, 2014; Cantalice *et al.*, 2021).

La predominancia de los peces en el registro fósil mexicano se puede asociar tanto a factores antropogénicos como geológicos. Por un lado, se encuentra el notable aumento de las últimas décadas en el estudio de ejemplares, así como en la descripción de nuevas especies (Cantalice *et al.*, 2019; González-Rodríguez *et al.*, 2013). Por otro lado, gran parte del territorio mexicano estuvo cubierto por mares tropicales a lo largo de la Era Mesozoica, los cuales contenían una gran diversidad de especies marinas. Además, durante la Era Cenozoica se formaron numerosos cuerpos de agua continentales aislados, que pudieron provocar la diversificación y endemismo de peces dulceacuícolas (González-Rodríguez, 2013). Por lo tanto, la mayoría de los registros suelen ser de peces óseos cuyos restos se preservaron en yacimientos generalmente cretácicos y algunos del Cenozoico -varios de excelente preservación o tipo *Lagerstätte* (Alvarado-Ortega *et al.*, 2006; Cantalice *et al.*, 2019; González-Rodríguez *et al.*, 2013).



## Main Manuscript for

Taxic and morphologic diversification during early radiation of Clupeomorpha (Actinopterygii: Teleostei).

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Figures 1 to 3



## **Abstract**

Evolutionary radiation is a problematic concept whose definition and classification have recently changed (Erwin, 1992). Radiations can be defined as the pattern of abrupt increase in diversity of a lineage (Raup, 1984). It is relevant to evaluate the presence and interaction of different types of radiation in extant and fossil organisms to adequately delimitate the radiation types and to know the diversity in the context of Earth's history. Here we employed superorder Clupeomorpha in the Early-Late Cretaceous as a study case to recognize the radiation types and their interactions, using both taxic and morphologic approaches. Clupeomorpha is a diverse and ancient teleostean superorder with a wide geographic and ecological distribution, that has been extensively studied (Grande, 1985). We proposed a model to calculate the origin rates to analyze the taxic diversification and employed geometric morphometrics to analyze the morphologic diversification at the time boundary. The results of the Clupeomorpha study suggest the absence of taxic radiation due to the constant increase in the taxa origination, but the presence of a climatic-geographical-disparification and broad diversification-like due to the expansion of the phylomorphospace occupation and the disparity increase, according to the current classifications. This exhibits the incompatibility of the current radiation classifications with the case study.

## **Significance Statement**

We analyzed the Clupeomorpha fish radiation for the Albian-Cenomanian boundary as a case study to recognize the radiation types and their interactions. We proposed a mathematical model to calculate the origin rates and used geometric morphometrics to determine the phylomorphospaces occupancy. Our results challenge the current classifications and reveal the dynamic and poorly studied interaction between taxic and morphological diversification exhibited by complex radiations.

## **Main Text**

### **Introduction**

Evolutionary radiation is a historically widely employed and problematic concept whose definition and classification have recently changed. For a long time, all radiations were considered adaptive, a term that lacks consensus (1, 2). According to several authors, adaptive radiation is the accelerated diversification resulting from the ecological differentiation of sympatric species associated with various biotic factors (e.g. extinction of lineages, development of adaptive traits) (1, 3, 4). This term referred almost exclusively to taxic diversification, leaving aside the shape variation (disparity) (2). However, several types of radiation are now recognized. Therefore, the radiation definition should be more inclusive, for example, the pattern of abrupt increase in diversity of a lineage (5). The new classifications include taxic and morphologic diversification that can develop in short or long periods. For example, Simões et al. (4) classification focused on radiation causes and separated taxic from morphological (disparification) diversification, where the first occurs due to exaptations (exaptive), vicariance (geographic), climate change (climatic), or reduced rate of extinction (pseudoradiation). On the other hand, the classification proposed by Erwin (2) combined both types of diversification, separating the radiations according to the number of species produced, morphological divergence, and hierarchical level.

The radiations can be complex and little understood processes, determined by numerous factors (2–4). Perhaps, for this reason, the evaluation of the interactions of different types of radiation in both extinct and fossil groups is a topic that until today has been little addressed. In addition, the

taxic and morphological diversifications are not comprehensively studied (2). Even when, these studies may provide valuable information for the interpretation of the radiation processes of the biological communities and be a source of complementary evidence to the integral understanding the evolution (6, 7). The detection of the interaction between different types of radiation would help to elucidate the complexity of radiation. It would also help to clarify the relevance of the classifications or the delimitation of new proposals. Likewise, it would help to understand in an integrated way the evolution of organisms in the context of the Earth's history and thus to explain the great diversity of extant and past organisms and shapes. Addressing this type of study requires different approaches to analyze and integrate taxonomic and shape information over time. Currently, numerous procedures and models have been developed to analyze diversification. For example, speciation (8) and origination (9) rates can be used to compare taxic diversity. Moreover, they quantified disparity through the occupation of the morphospace (mathematical space that shows the distribution of shapes) (10, 11), obtained through the application of geometric morphometrics that uses cartesian coordinates (landmarks) and multivariate statistical analyzes complemented with the phylogeny (12, 13). In addition, a relatively well-studied group of organisms with an abundant fossil record correctly described, of good quality, and with a wide spatial and temporal distribution is required (9, 14).

In this paper, we analyze the taxic and morphological diversification of the superorder Clupeomorpha (Actinopterygii: Teleostei) including an important biological moment, the Early-Late Cretaceous boundary, to recognize the radiation types and their interactions throughout the evolution of this fish group. Clupeomorpha is a diverse and ancient teleostean superorder that dates back to the Early Cretaceous (Valanginian, 139 Ma) and today contains approximately 200 fossil species (SI Appendix, Table S1) plus 400 extant species, commonly known as herrings, anchovies, and sardines. Today, this clade involves two orders, the Ellimmichthyiformes consisting solely of fossil species, and the Clupeiformes that incorporate both extinct and the totality of existing species. Clupeomorphs have a wide geographic and ecological distribution since they occur worldwide in all types of aquatic environments (15–17). The fossil record suggests both taxic and morphological radiation for Clupeomorpha at the Early-Late Cretaceous boundary (15) that matches the so-called “great Cenomanian diversification” event of actinopterygians, which is associated with the increase of epicontinental seas and the water surface temperatures (18). The fossil record of clupeomorphs has become drastically rich in recent decades with the discovery of new outcrops and species (SI Appendix, Table S1, Table S2). Although the phylogenetic hypotheses published about this clade are still somewhat problematic; such discoveries have made it possible to recognize the early taxic and morphological diversification experienced in this clade.

## Results

Taxic diversification metrics obtained suggest a constant diversification of Clupeomorpha along the Early and Late Cretaceous (Fig. 1). The calculation of the number of originated taxa showed a considerable increase in the number of Ellimmichthyiformes and total species originated, but a constant number of Clupeiformes species and total genera originated during the Albian-Cenomanian (Fig. 1A). However, when analyzing these changes in lineage history richness with the proposed origin rates (Fig. 1B), an almost constant growth from the oldest record to the Cenomanian was observed for both genera and species. Likewise, we detected a low and gradual increase in the origin of total genera and Clupeiformes species for the Eocene-Oligocene boundary. It highlights that most of the Clupeomorpha species belonged to the order Ellimmichthyiformes during the Cretaceous, and later this relationship was reversed for the Cenozoic. In the phylogenetic hypothesis obtained in the present research (SI Appendix, Fig. S1) the Clupeomorpha consists of the orders Ellimmichthyiformes and Clupeiformes as previously suggested (16) plus three early diverging species, *Ornategulum sardinoides*, *Ranulfoichthys dorsonudum*, and

*Scutatospinosus itapagipensis*. This taxic pattern of diversification exhibited a conspicuous change in body shapes.

On the other hand, morphologic diversification suggested an increase in Clupeomorpha shape variation in the Early-Late Cretaceous boundary. We applied geometric morphometrics to 75 specimens corresponding to 39 species with a digitization error of 6.5% (SI Appendix, Table S2). From phylogenetically aligned component analysis (PACA; Fig. 2), the PC1 explained 39.55% of the shape variation and was associated with fish height and length, negative values represented deep-body fish and positive values represented fusiform fishes. The PC2 explained 30.41% of the shape variation and was associated with the position of the fins. The negative values represented fish with dorsal and caudal fin insertion higher, on the other hand, positive values represented fish with dorsal and caudal fin insertion lower, pectoral fin higher, and pelvic fin further back. During Early Cretaceous, both Ellimmichthyiformes and Clupeiformes exhibited a reduced phylomorphospace composed of fusiform and slightly deep-body fish (Fig. 2A). Later in the Late Cretaceous, the phylomorphospace of Clupeomorpha experienced a wide expansion because they acquired a variety of body shapes, which included the change of the shape of the trunk and the modification of the fins (Fig. 2B). Some of these Late Cretaceous fish presented similar body shapes; however, in some others, the body became deeper (*Rhombichthys intoccabilis*), elongated (*Scombroclupea occidentalis*), the pelvic fin insertion was far back (*Scutatoclupea bacchiai*), or the dorsal fin insertion turned higher (*Sorbinichthys elusive*). Then, no significant differences were detected in the Early and Late Cretaceous shapes (MANOVA,  $df = 1$ ,  $F = 0.733$ ,  $P = 0.595$ ). Since this wide variation is associated with Cenomanian species (SI Appendix, Fig. S2), the morphospace expansion can be attributed to the Albian-Cenomanian boundary. Moreover, Clupeiformes species exhibited only fusiform shapes in the Late Cretaceous (Fig. 2B). In addition, most Early Cretaceous species belonged to localities in the Western Tethys Sea, and most Late Cretaceous species belonged to the Eastern Tethys Sea (Fig. 2). Therefore, no significant differences were detected in the fish shape attributed to the spatial distribution (MANOVA,  $df = 1$ ,  $F = 0.420$ ,  $P = 0.894$ ) or the interaction of spatial-temporal distribution (MANOVA,  $df = 1$ ,  $F = 0.863$ ,  $P = 0.511$ ). Likewise, no allometry was detected (MANOVA,  $df = 1$ ,  $F = 0.974$ ,  $P = 0.371$ ), i.e. the shape change associated with size change.

To complement the morphospace occupation analyses, the disparity (Fig. 3A) and morphological evolution rates (Fig. 3B) values were calculated. As expected, Late Cretaceous fish had higher disparity than their Early Cretaceous relatives, species from localities at the Eastern Tethys Sea east also had higher disparity than those western species, and the orders showed the same degree of disparity (Fig. 3A). Regarding morphological evolution rates (Fig. 3B), Late Cretaceous species also had a higher rate compared to Early Cretaceous species, but this difference was not significantly different ( $P = 0.276$ ). In contrast, the disparity patterns changed for the other groups, species from eastern and western Tethys Sea localities had similar values ( $P = 0.995$ ), and Ellimmichthyiformes species presented higher but not significant values compared to Clupeiformes and early diverging species ( $P = 0.377$ ).

## Discussion

The calculated metrics for taxic and morphological diversification showed contrasting patterns. The metrics suggest a gradual taxic diversification from the first record of Clupeomorpha (139 Ma) to the Cenomanian (100 Ma) given by Ellimmichthyiformes species, possibly associated with the origin and subsequent diversification of the superorder that was stopped by global environmental changes that raised extinction rates of actinopterygians (18). Further diversification in the Cenozoic (Eocene-Oligocene boundary, 33.9 Ma) given by Clupeiformes species was also revealed (Fig. 1). In contrast, the shape metrics obtained suggest the exploration enlargement of the morphospace occupied by the fish species at the Albian-Cenomanian boundary (100 Ma; Fig. 2-3), defined as

radiation according to the concept given previously. The differences in morphological diversification were not significant because several of the Late Cretaceous species showed the same shapes as those of the Early Cretaceous. This gave way to an ecological replacement of the ichthyofauna and not only taxonomic since there is a strong link between fish morphology and ecology (19). In addition, the question arises whether these fish with new shapes competed with species from other groups with similar shapes or turned out to be empty and available ecological niches. Moreover, some authors agree that changes in shapes and ecological opportunities were greater in the early history of most of the groups, being subsequently demised by genetic, epigenetic, and developmental constraints, and ecological saturation, respectively (7, 20, 21). Then, the shape changed and the ecological consequences of Clupeomorpha represented superficially modifications (20).

Since we found no evidence of allometry and the strong association of the fish body shape with food and habitat (19), a change in either or both factors may have occurred at the Albian-Cenomanian boundary. All current species of Clupeiformes have fusiform bodies shapes (except *Pristigaster*) (16) and feed on plankton forming large schools in the tropical and temperate open ocean and pelagic environments (80% of the species are marine, the rest are freshwater) (22, 23). The clupeiforms have niche lability with several transitions from marine to freshwater environments, therefore they show the ability to adapt to a wide range of salinity and temperature conditions which represent unimportant barriers (23). These skills could explain the diversity of environments, regions, and ages that species inhabited, as well as, Clupeomorpha's complex paleogeographic history (24, 25). Although Clupeomorpha species inhabited marine, lacustrine, brackish water, and freshwater environments, all the Late Cretaceous species used in the morphometric study were marine (SI Appendix, Table S2; SI Appendix Fig. S2). Furthermore, Late Cretaceous species with extreme shapes were distributed worldwide, changing the idea of the Mediterranean region as a Clupeomorpha center of diversification (25, 26). Then this Late Cretaceous morphological diversity can be associated with high sea surface temperatures, the highest sea level ever known in Earth's history, and the rise of numerous epicontinental seas (18, 26). Such changes in environmental conditions, may increase worldwide independently and control differently food inputs for plankton-feeding fish, habitus type, phenotypical changes, and habitat fragmentation (25, 26). For example, the temperature rise can generate faster mutation rates plus the selection of short-lived plankton generations that limits dispersal (18). In addition, epicontinental seas are protected environments that favor the diversification of marine organisms (18) and in which many of the Clupeomorpha species were distributed (SI Appendix, Fig. S3). Regarding habitus, taller bodies and shorter caudal peduncles species such as *Rhombichthys intocabilis* (Fig. 2) usually present omnivorous habits, and longer bodies as *Scombroclupea occidentalis* (Fig. 2) are associated with swimming in the water column (19). The interaction of these factors with changes in development paths and contingency (21, 27) may result in the Late Cretaceous diversity of fish shape and radiation. However, some difficulties and artifacts that should be considered arise in this type of study.

As already mentioned, few works integrate the taxonomic and morphological diversity of fossil taxa, and each one has its scope. For example, both approaches are conditioned by the incomplete fossil record, the ability in the recognition and description of species and other taxonomic hierarchies, and scientific interest (6, 9, 14, 27). Furthermore, taxonomic approaches patterns are determined by mathematical models of diversification rates that slice continuous data (1). We consider that the model proposed in this work adequately exposes these patterns not from a specific number of taxa (1) but from the context of the lineage history of organisms. On the other hand, the patterns in studies of the disparity and morphospace occupation can change according to sample size (14), the completeness and conservation of the fossil (7, 14, 28), and the procedures for obtaining (images taken with different protocols we used) (29), processing (13), and analyzing the data (30). These difficulties together with the learning of new mathematical and bioinformatic tools are possibly the cause of the relatively few morphometric studies with fossils since only two has been published for fish bodies (31,32) and even fewer of those that integrate phylogenetic information e.g. (33–35).

However, generation more studies of this type are relevant to determine the patterns and factors underlying the diversifications and radiations.

To our knowledge, Foote (6) presented the only integrated study that analyzed both taxonomic and morphological diversity for echinoderm and trilobite data of Paleozoic. We found slight similarities with the Proetida analysis for the Devonian with the continuous increase of taxic diversity and the increase in morphological diversity in pulse. Like us, Foote (6) observed several discordances between taxic and morphological diversity over taxa and time, and he concluded that a unique correspondence is non-existent between them and different patterns can emerge according to several factors. Therefore, integrating both perspectives help us to understand and interpret the patterns behind the radiations.

Considering the current radiation classifications, none of them adequately represents the Clupeomorpha case study for the Albian-Cenomanian boundary. According to Simões et al. (4), Clupeomorpha has radiation of type climatic-geographical-disparification. Our results together with others indicate a dynamic interaction with or without concordance between taxic and morphological diversification (27), therefore they should not be deliberately separated (2). Although Erwin´s classification (2) considers this interaction, none of his categories seem to fully encompass the Clupeomorpha radiation. He describes the Cretaceous marine radiation as a broad diversification, i.e. the expansion of global diversity involving different lineages due to new ecologic opportunities with a large increase in the number of species and moderate to high morphological divergence. Although the number of Clupeomorpha taxa does not seem to increase greatly (Fig. 1), it occurred for other actinopterygians (18). Since Clupeomorpha showed a moderate and gradual taxic diversification together with a moderate and abrupt morphological diversification associated with various internal and external factors, we suggest that Clupeomorpha exhibited similar or broader radiation to the broad diversification (SI Appendix, Fig. S4). This case study does not fit with current classifications therefore these need to be changed as more fossil specimens are described and more studies of this type are carried out to determine the patterns and factors that make up complex radiations.

## Materials and Methods

### *Origin rates*

To evaluate the taxic diversification, the origin rate was calculated using all Clupeomorpha fossil species described to date. Of the total 190 species, 62 belonged to the Cretaceous, 40 to Paleogene, 72 to Neogene, and 16 to Paleogene-Neogene (SI Appendix, Table S1). The richness calculated from fossil species usually presents problems of description from limited characters, irregular temporal and spatial sampling associated with fossilization bias and scientific interest. Therefore, origin rates calculated from higher hierarchies (like gender or family) have greater stability and are recommended (6, 9). In this study, both the species and genera origin rates were calculated.

The number of taxa originated and the rates of origin were calculated respectively from

$$Nx_{ti} = \frac{Nx_{min} + Nx_{max}}{2} \quad (1)$$

$$OR = \frac{Nx_{ti}}{\sum_1^{\infty} Nx_t} \quad (2)$$

where  $Nx_{min}$  is the number of taxa belonging to a precise Age (from Cretaceous species) or Epoch (for Paleogene and Neogene species),  $Nx_{max}$  is the sum of  $Nx_{min}$  and the number of imprecisely dated taxa spanning that time interval (e.g. Cenomanian-Turonian). The origin rate  $OR$  is the average number of taxa  $i$  originated in a particular time interval  $Nx_t$ , divided by the sum of all taxa originated up to that time. For  $Nx_{min}$  calculation of genera, the oldest and most accurate record

available was used. Data visualization were performed using R platform (36) and “ggplot2” package (37).

### *Material*

To study the morphologic diversification, the morphospace occupation pattern of fossils from the Early-Late Cretaceous was analyzed. We used 75 almost complete specimens belonging to the two orders Ellimmichthyiformes and Clupeiformes, three families, 20 genera, and 39 species. We employed images from scientific articles and public photographic repositories. In addition, we photographed specimens from scientific collections in Mexico (SI Appendix, Table S2; SI Appendix, Fig. S5).

### *Geometric morphometrics*

We digitalized twice 15 landmarks and 35 semilandmarks (SI Appendix, Fig. S6) using Friedman (31) and Farré et al. (19) configurations that consider well-preserved anatomical features associated with shape, feeding, and locomotion. However, 26 specimens presented some missing landmarks that represent a low percentage of missing data (10.7%) and allow a realistic estimation (28, 38). Missing landmarks were estimated using the Thin-Plate Spline Interpolation (TPS) method. TPS uses deformation grids to determine the missing data from the interpolation and minimization of bending energy of a set of reference specimens (39). Furthermore, this method is effective for semilandmarks, certain fish configurations, and specimens with little to intermediate missing data (38–40). Estimates were obtained from groups of the same family or order (for undetermined families), taking into account the taxonomic variation (28, 39). Then, the configurations were superimposed using the Procrustes Generalized Analysis method to eliminate extra information on location, scale, and orientation (13). Moreover, semilandmark sliding was performed with the Procrustes Distance method (13) and digitization error was calculated following Bailey and Byrnes protocol (41). The material was digitalized with tpsDig2 (42) and processed with R platform (36) and the “geomorph” package (43).

### *Phylogenetic analysis*

According to the phylogenetical comparative method, more phylogenetic related taxa tend to resemble morphologically each other and lose the independence of data (44), therefore phylogeny was considered in the analysis. Clupeomorpha phylogeny (SI Appendix, Fig. S1) was obtained from the character matrix of Than-Marchese et al. (45). A Bayesian inference analysis of 56 taxa and 71 characters was performed with 20 million generations, 2 runs, 4 strings, and 0.2 temperature. Bayesian analysis was performed with MrBayes software (46) and the consensus tree was cut with Mesquite software (47).

### *Morpho-statistics analysis*

To analyze the space-temporal patterns of morphospace occupation, species were classified according to their dating in Early Cretaceous (16 spp.) and Late Cretaceous (23 spp.), and their distribution to the Easter (22 spp.) and Western (17 spp.) Tethys Sea (SI Appendix, Fig. S3). To determine differences in temporal, spatial, and taxonomic shape, a series of statistical analyzes were performed. First, to study morphospace occupation, a phylogenetically aligned component analysis (PACA) was performed using the average shape of the species. PACA is an order method that reduces dimensions, and like other methods, integrates phylogeny information and conserves the distances among data. In contrast to other methods, PACA aligns the residuals of the phylogenetic covariance matrix that maximizes the phylogenetical signal in the first component, then it shows the variation that is more related to phylogeny (48). PACA is the method that best fits since Clupeomorpha data has a considerable phylogeny signal ( $K = 0.52$ ;  $P = 0.027$ ), i.e. the degree to which phylogenetically closest species show similar phenotypes, and it is calculated from the observed and expected shape variation, according to the Brownian motion evolution model (49).

In addition, MANOVA linear analyzes were performed with an iteration of 999 and integrated the phylogeny, to compare changes in shape in the Early-Late Cretaceous, east-west of the Tethys Sea, and the interaction of both factors. Similarly, the allometry presence was evaluated using the average centroid size and average shape of the species. Then, to compare the shape variation between temporal, spatial, and taxonomic groups, we calculated the disparity from the variation of the Procrustes Distances of species average shape (the distances of the specimens to the average shape of the groups to be compared) (50). In this case, groups containing organisms from Early and Late Cretaceous, Easter and Wester Tethys Sea, and Ellimmichthyiformes and Clupeiformes orders. Finally, to determine changes in morphological diversity, the rates of morphological diversification  $\sigma^2_{\text{mult}}$  were calculated from the species' average shape and the phylogeny, which assumes the accumulation of variation under a Brownian movement evolution model (51). Analyses and data visualization were performed using R platform (36) and “abind” (52), “ape” (53), “geomorph” (43), “ggplot2” (37), and “phytools”(54) packages (the code is available at SI Appendix; the analysis files are available at [https://github.com/IGPaleo/Clupeomorpha\\_radiation](https://github.com/IGPaleo/Clupeomorpha_radiation)).

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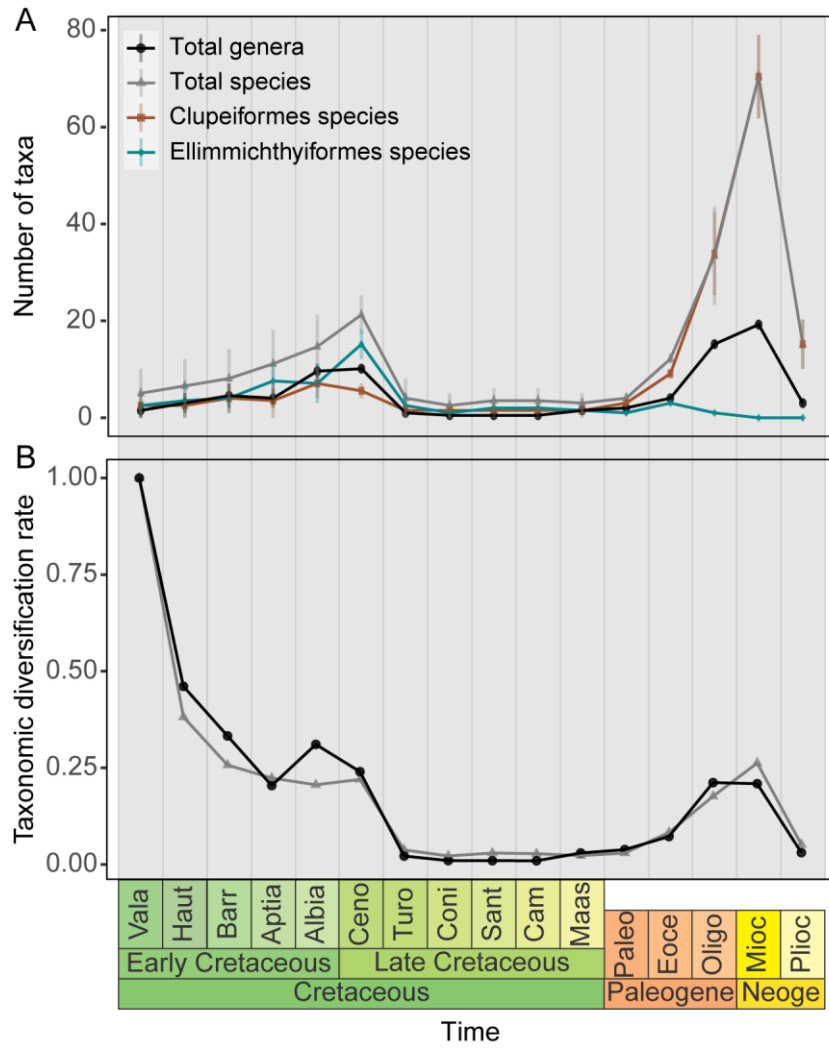


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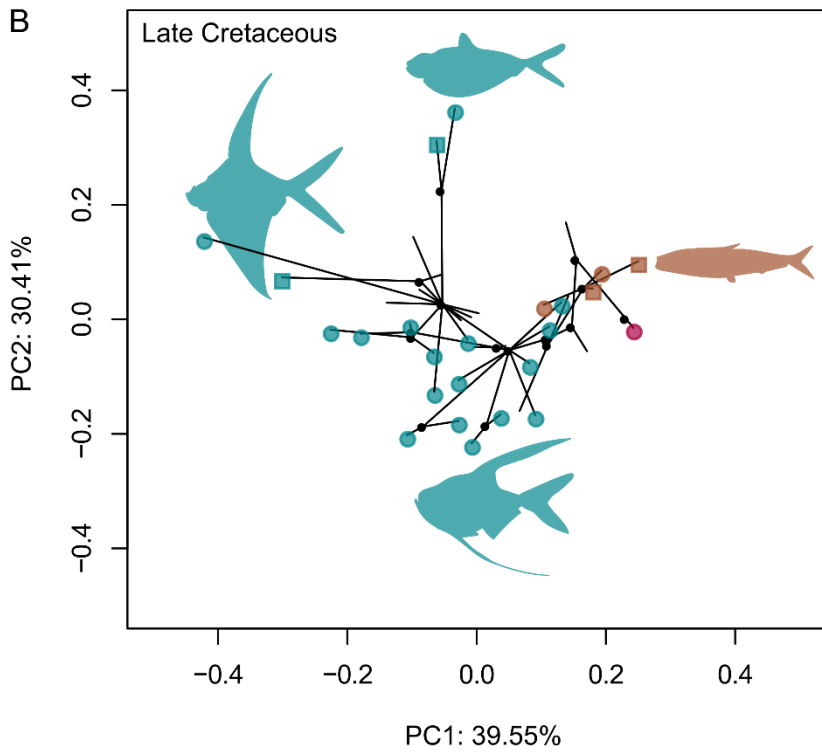
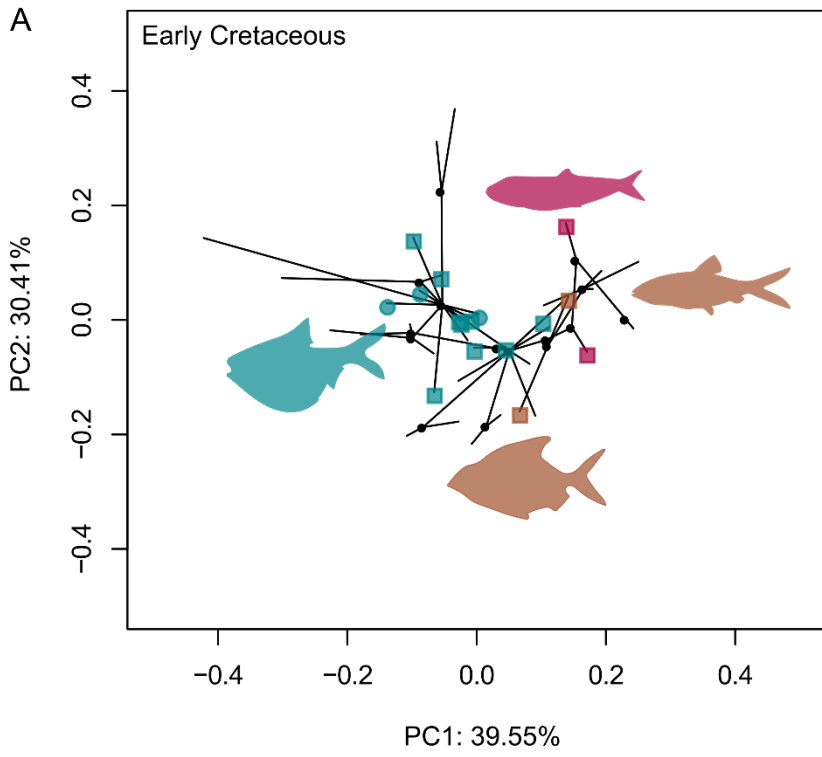
## Figures and Tables

**Figure 1.** Taxic diversification of Clupeomorpha in deep time. A. Number of genera and species originated in time according to equation (1). The vertical lines of each point correspond to the standard deviation. B. Origin rate of genera (black) and species (gray) in time according to equation

(2). On the horizontal axis time is divided into Ages (Cretaceous in green) and Epochs (Paleogene in orange and Neogene in yellow).

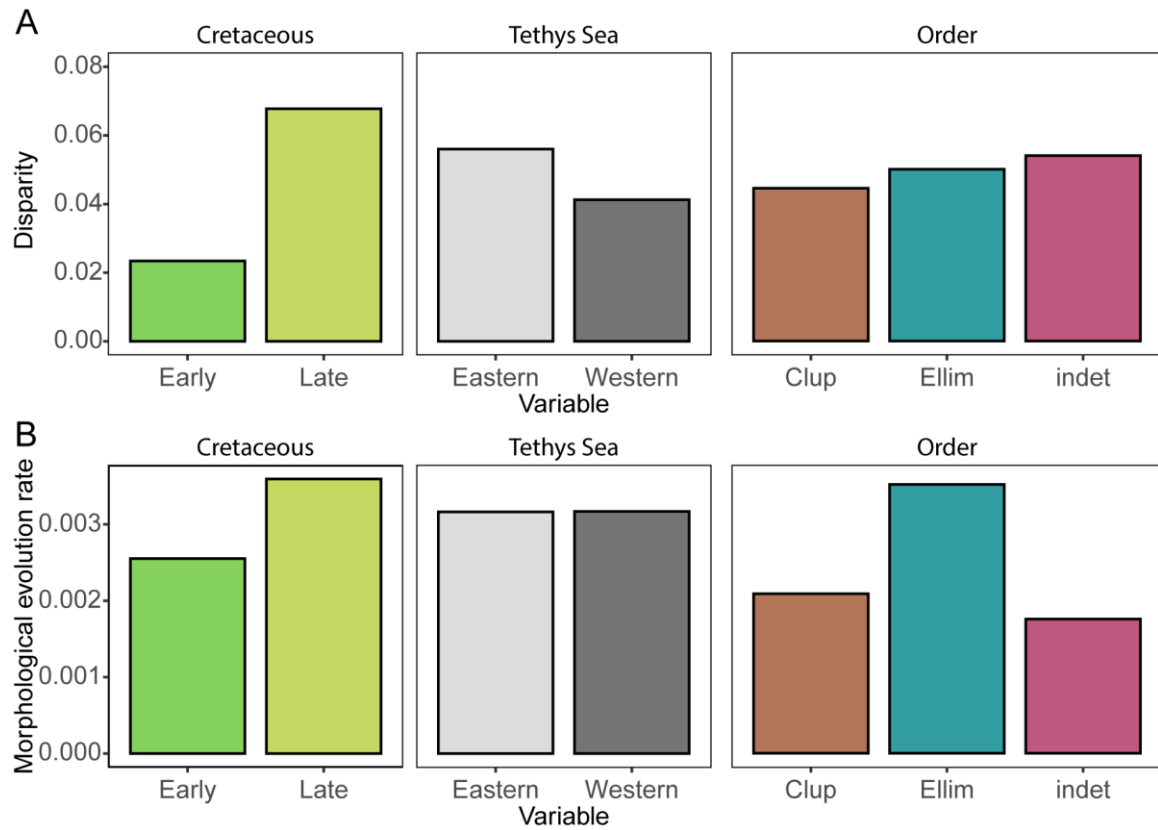


**Figure 2.** Phylomorphospaces occupied by Clupeomorpha Cretaceous species. A. Representation of Early Cretaceous species. B. Representation of Late Cretaceous species. Black lines indicate phylogenetic relationships and black circles nodes; brown figures indicate Clupeiformes species, turquoise figures Ellimmichthyiformes species, and magenta figures early-diverging taxa with indeterminate order (SI Appendix, Fig. S1); colored circles indicate species from localities at the east of Tethys Sea, and colored square species from localities at the west. The representations of the fish shapes clockwise from the top correspond to A. *Ranulfoichthys dorsonudum*; *Santanaclupea silvasantosi*, *Pseudoellimma gallae*, and *Tunisiaclupea speratus*; B. *Scutatoclupea bacchiai*, *Scombroclupea occidentalis*, *Sorbinichthys elusivo*, and *Rhombichthys intoccabilis*.



- Early-diverging taxa
- Clupeiformes
- Ellimmichthyiformes
- Easter Tethys Sea
- Wester Tethys Sea

**Figure 3.** Comparison of the values of A. disparity and B. morphological evolution rate between groups of Early and Late Cretaceous species, eastern and western Tethys Sea, Ellimmichthyiformes (Ellim), Clupeiformes (Clup), and indeterminate (indet; early-diverging species) order (SI Appendix, Fig. S1).



## Discusión general

Uno de los objetivos de este trabajo fue analizar la diversificación tóxica y morfológica de Clupeomorpha en el límite del Cretácico temprano-tardío. Se observó una clara discrepancia entre los patrones de ambos tipos de diversificación. Por una parte, la diversificación tóxica señala un crecimiento casi constante de la riqueza (Fig. 1), y por otra parte, la morfológica indica una notable expansión del morfoespacio ocupado (Fig. 2-3). ¿Qué tan común es la discordancia entre estos dos tipos en los organismos? Desafortunadamente, como ya se mencionó anteriormente, solo conocemos un trabajo que ha analizado los dos tipos de diversificación (Foote, 1993). Sin embargo, tanto el estudio de Foote (1993) como éste, indican que no necesariamente hay una correlación positiva entre los dos tipos, sino que se pueden presentar diferentes patrones asociados a la historia evolutiva del grupo. Por lo tanto, se requieren de más estudios que comparen ambos tipos de diversificación en diferentes grupos de organismos e intervalos de tiempo. Dichos estudios ayudarán a dilucidar los patrones y procesos evolutivos del pasado, como por ejemplo la presencia de radiaciones.

Asimismo, nos preguntamos ¿qué factores y procesos dieron pauta a la radiación descrita? Como ya se mencionó, el límite Albiano-Cenomaniano presenta peculiaridades como: i) temperaturas elevadas con gradientes latitudinales débiles (global: ~30 °C, actual ~17°C; oceánica: 20-35 °C, actual de 0-30 °C), mostrando su máximo en el Cenomaniano-Turoniano (global: ~35 °C; oceánica: 20-43 °C) (Hay & Floegel, 2012; O'Brien *et al.*, 2017); ii) amplio incremento del nivel del mar (190-270 m por encima del actual) (Ziegler *et al.*, 1985) asociado al incremento de la expansión del suelo oceánico (Gale, 2004; Seton *et al.*, 2009); iii) bajos niveles de CO<sub>2</sub> (~250 ppm) en comparación al Albiano (~340) y el presente (~400 ppm) (Barral *et al.*, 2017); iv) su posición entre dos eventos de anoxia oceánica (OAE, por sus siglas en inglés) del final del Albiano (OEA1d) y Cenomaniano-Turoniano (OEA2), con posibles cambios en la productividad y el ciclo del carbono (Barral *et al.*, 2017; Wilson & Norris, 2001); v) cambios en la circulación oceánica asociada al incremento en la salinidad y la formación de mares epicontinentales de alta comunicación al océano (Gale, 2004; Hay, 2008; Hay & Floegel, 2012); vi) eventos de reorganización global de la tectónica de placas asociado a su desaceleración y el cese de ciertas zonas de subducción (Olierook *et al.*, 2020). Sin embargo, existen vacíos y contradicciones en las explicaciones de la presencia e interacción de estas variables ambientales. Entonces, estos factores fisicoquímicos pudieron influir de forma pasiva (ej. selección natural, deriva génica) y/o activa (ej. modificaciones epigenéticas, rearrreglo de redes genética, plasticidad fenotípica) (Noguera-Solano *et al.*, 2021) en la modificación del fenotipo, la diversidad y la dinámica de los peces y de otros organismos -no obstante, se desconocen varios aspectos de los mecanismos evolutivos de interacción ambiente-organismo. Para este límite se han reportado diversificaciones de radiolarios, foraminíferos (Ando *et al.*, 2010; Górný *et al.*, 2022; Kopaevich & Vishnevskaya, 2016), dinosaurios (Cifelli *et al.*, 1997) y angiospermas (McLoughlin *et al.*, 2010).

El segundo objetivo del trabajo fue reconocer los tipos de radiaciones de Clupeomorpha para el límite del Cretácico temprano-tardío, así como las interacciones de estas, de acuerdo con las clasificaciones propuestas (Erwin, 1992; Simões *et al.*, 2016). En general, resalta la incompatibilidad entre las características de este estudio de caso con los tipos de

radiaciones propuestos. En el caso de Simões *et al.* (2016), los clupeomorfos cretácicos muestran una radiación de tipo climática-geográfica-disparificación. Esto debido al aumento de la temperatura, la formación de mares epicontinentales y la expansión del morfoespacio, respectivamente. Sin embargo, como ya se mencionó anteriormente, Simões *et al.* (2016) contemplan mayoritariamente a la diversificación táxica, que en este caso no entra dentro del concepto de radiación establecido. Asimismo, se basa únicamente en la causas de las radiaciones, sin embargo, recientemente se ha evidenciado que la diversificación de los organismos se asocia a numerosos factores internos y externos (Jablonka & Lamb, 2014; Laland *et al.*, 2015; Payne & Wagner, 2019), varios de los cuales se dejaron fuera. En contraste, la clasificación de Erwin (1992) se basa en características de divergencia, reflejando entonces la interacción de la diversificación táxica y morfológica. Asimismo, muestra numerosos ejemplos compatibles con la clasificación, ajustándose con los patrones de la historia evolutiva de ciertos organismos. Sin embargo, los clupeomorfos no se acoplan completamente a la clasificación (SI Apéndice, Fig. S4), mostrando posibles nuevas variantes. Por lo tanto, se quiere de una pronta revisión exhaustiva de los fundamentos, utilidades y efectividad de las escasas clasificaciones, y por supuesto, de la generación de más estudios de caso.

Este trabajo muestra ciertos aportes respecto al material y los procedimientos empleados. Por ejemplo, el estudio resalta la importancia del papel de la biota mexicana en estudios globales, en particular de la evolución de la ictiofauna. En este caso particular, las especies mexicanas fueron esenciales en la representación de la fauna de: i) el oeste del mar de Tetis, ii) ambos lados del límite temporal inmediato (Edades del Albiano y Cenomaniano), resaltando *S. occidentalis* por su forma elongada (Fig. 2B); y iii) los grupos taxonómicos establecidos, destacando *R. dorsonudum* por su diversificación temprana (SI Apéndice, Fig. S1). Además, como ya se mencionó, este trabajo es uno de los dos que ha analizado de forma integrativa la diversificación de un clado en el tiempo geológico, empleando tanto la diversificación táxica como morfológica. Respecto a la diversificación táxica, el modelo matemático propuesto parece representar adecuadamente la dinámica de la riqueza a lo largo de un intervalo de tiempo geológico. Esto debido a que toma en consideración la propia historia del clado (Fig. 1B), es decir la riqueza previa acumulada, en lugar de colocar un umbral arbitrario respecto al número de especies (Fig. 1A; Olson & Arroyo-Santos, 2009). Respecto a la diversificación morfológica, este es uno de los pocos trabajos que genera un filomorfoespacio a partir de ejemplares fósiles (Deline *et al.*, 2018; Hopkins & Smith, 2015; Wang *et al.*, 2019; Wright, 2017), siendo de hecho, el único para peces fósiles. Además, es uno de los tres (Clarke & Friedman, 2018; Friedman, 2010) que ha analizado la forma corporal de peces fósiles.

Asimismo, los resultados de este estudio contribuyen de forma significativa en el conocimiento tanto de Clupeomorpha como de las diversificaciones. Respecto al primer punto, se obtuvo una filogenia relativamente robusta que modifica las relaciones de ciertos taxones previamente establecidas, destacando las especies de divergencia temprana que no se incluyen en ninguno de los dos ordenes (SI Apéndice, Fig. S1). Es de mencionar que, esta es la primera vez que se emplean métodos de Inferencia Bayesiana para obtener una filogenia de especies fósiles de Clupeomorpha. Además, robustece la existencia de una

radiación de Clupeomorpha (a nivel morfológico) y posiblemente de los actinopterigios en límite Albiano-Cenomaniano. Respecto a las diversificaciones, este estudio resalta la dinámica -y no necesariamente positiva- relación entre la diversificación táxica y morfológica de los organismos. Finalmente, evidencia la complejidad de las radiaciones y la falta de su estudio en cuanto a clasificaciones asertivas y estudios de caso.

Debido a esta complejidad y al estudio de eventos históricos, es que el presente estudio presenta ciertas limitaciones. El factor más dominante es el uso de fósiles. Es ampliamente conocida la incompletitud del registro fósil, evidenciando el gran componente estocástico (variación del resultado de un sistema asociada a factores intrínsecos y extrínsecos; Alon, 2019) de los procesos tafonómicos. Siendo que se eliminan ciertos elementos, tamaños y formas, lo cual además complica la descripción los taxa (Foote, 1997; Sepkoski, 1998). Además, se presenta un sesgo espacio-temporal, siendo que no existen localidades que representen todos los intervalos de tiempo y regiones geográficas (Smith, 2001; Vilhena & Smith, 2013), sugiriendo que los patrones detectables pueden ser más bien regionales y no globales (Foote, 1997). Por lo tanto, el descubrimiento de nuevos taxa en el futuro podrían modificar en cierta medida los patrones de estos análisis.

Cada uno de los análisis muestran cierto grado de sensibilidad a determinados factores, los cuales deben ser tomados en cuenta para establecer la robustez de los resultados. Particularmente, el análisis de la diversificación táxica, en comparación de la morfológica, es más sensible a los sesgos temporales y taxonómicos (sobre todo a una jerarquía de especie) debido a que depende completamente de los taxa previamente descritos (Foote, 1993; Sepkoski, 1998; Smith, 2001). En este caso, existen numerosas localidades cenomanianas alrededor del mundo, por lo que el incremento de la riqueza en el límite Albiano-Cenomaniano podría ser un artefacto. En contraste, los análisis morfométricos pueden llegar a ser sensibles a factores como: i) bajo tamaño muestral (Arbour & Brown, 2014; Couette & White, 2010; Neeser, *et al.*, 2009); ii) falta de un procedimiento estándar para obtener las fotografías (Arnqvist & Mårtensson, 1998; Evin, *et al.*, 2020); iii) pérdida de ciertas regiones del cuerpo (sobre todo la curvatura de los escudos ventrales; SI Apéndice, Fig. S6; Arbour & Brown, 2014; Couette & White, 2010; Neeser *et al.*, 2009); iv) el modelo de estimación de marcas perdidas por TPS es dependiente de la cantidad de variación (moderada en este caso; Neeser *et al.*, 2009); v) la topología de la filogenia; y vi) el modelo de evolución usado en el cálculo de las tasas de evolución morfológica (Adams, 2014).

A pesar de las limitaciones, las herramientas empleadas mostraron ser considerablemente robustas y generalizables, por lo que puede ser aplicado a diversos organismos e intervalos de tiempo. Por ejemplo, para estudiar detalladamente “la gran diversificación del Cenomaniano” (Guinot & Cavin, 2016), ya que estas herramientas pueden usarse en otros grupos de Actinopterygii. Asimismo, podría analizarse la diversificación de otros organismos marinos para determinar la influencia en las comunidades, y no únicamente en grupos aislados (Gould, 1980). Además, podrían aplicarse a eventos particulares e importantes como la “explosión del Cámbrico”, la terrestreización de invertebrados y vertebrados o las extinciones masivas del Pérmico y Cretácico/Paleógeno. O bien, aplicarse a altas jerarquías taxonómicas y grandes intervalos de tiempo para determinar los patrones de diversificación de los organismos a lo largo de su historia evolutiva.



## **Conclusión**

El superorden Clupeomorpha es un grupo diverso y extensamente estudiado, que además cuenta con una amplia distribución espacial, temporal y ecológica. Dichas características permitieron detectar una diversificación táxica casi constante y una morfológica abrupta y moderada (radiación) para el límite del Cretácico temprano-tardío. Los patrones de este caso de estudio evidencian la incompatibilidad con las dos clasificaciones actuales de radiaciones. Esto a su vez resalta la importancia de generar más estudios en torno a la definición y clasificación de las radiaciones, así como de más casos de estudio analizados de forma integrativa mediante ambos tipos de diversificación.

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## **Supplementary Information for** Taxic and morphologic diversification during early radiation of Clupeomorpha (Actinopterygii: Teleostei).

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### **This PDF file includes:**

Supplementary text  
Figures S1 to S5  
Tables S1 to S2  
SI References

### **Other supplementary materials for this manuscript include the following:**

Datasets S1



## Supplementary Information Text

### Morphometric Geometric

In this section the code to perform the morphometric analyzes is described in detail.

**A. Process data.** Read and estimate missing landmarks for both digitalizations.

```
# Read TPS file
cup<-readland.tps("Clupeomorpha_3_14ene22.tps",specID = "imageID",
                 negNA = TRUE,readcurves= TRUE)

##
## 35 curve points detected per specimen and are appended to fixed landm
arks.

# Estimate missing Landmarks by taxonomic groups
# Armigatidae
a <-cup[, ,c(4,5,6,7,20,21,22,23,24,26,28,40,41,42,68)] #15
a <-estimate.missing(a, method=c("TPS"))
# Paraclupeidae
b <-cup[, ,c(15,16,17,18,19,29,30,31,33,34,35,36,44,45,46,47,
            48,49,50,51,52,53,54,57,61,84,86,88,89,90,91,92,
            93,95,96)] #35
b <-estimate.missing(b, method=c("TPS"))
# Sorbinichthyidae
c <-cup[, ,c(58,59,60,62,63,64)] #6
c <-estimate.missing(c, method=c("TPS"))
# ScombroLupea
d <- cup[, ,c(1,2,11,13,55,56,70,71,72,73,74,75)] #12
d <-estimate.missing(d, method=c("TPS"))
# Ellimmichthyiformes: Ornategulum and Ranulfoichthys
e <-cup[, ,c(4,5,6,7,15,16,17,20,21,23,24,33,34,35,36,40,41,44,45,
            46,47,48,49,50,53,54,57,58,59,61,62,63,64,67,68,76,77,
            82,83,84,90,8,9,10,37)] # 4
e <-estimate.missing(e, method=c("TPS"))
e <-e[, ,c(42,43,44,45)]
# Clupeiformes: SantaLupea and Pseudoellimma
f <- cup[, ,c(11,55,70,71,72,73,74,75, 65,66,94)] #3
f <-estimate.missing(f, method=c("TPS"))
f <- f[, ,c(9,10,11)]
cup3 <- abind(a,b,c,d,e,f)
```

Generalized Procrustes Analysis

```
# Define semilandmarks
sliders = define.sliders (16:50)
# Perform GPA
ProCup3 <- gpagen(cup3, curves=sliders, print.progress = FALSE)
```

**B. Digitization error**

```

# Join the two sets of digitization
cup23 <- abind(cup2, cup3)
# Perform GPA
ProCup23 <- gpagen(cup23, curves=sliders, print.progress = FALSE)
# Create group names
Digitalization <- rep(c("dos", "tres"), each=75)
gdf_23 <- geomorph.data.frame(shape = ProCup23$coords,
                             Digitalization = Digitalization)
# Perform MANOVA
dig<-procD.lm(shape ~ Digitalization, data = gdf_23, iter = 999,
              print.progress = FALSE)
# Calculate digitization error
CM1 <- dig$aov.table$MS[1]
CM2 <- dig$aov.table$MS[2]
rep <- (((CM1 - CM2)/2) / (CM2 + ((CM1 - CM2)/2)))*100
ME <- (100 + rep)
ME
## [1] 6.459387

```

### C. Phylomorphospaces

Obtain the mean shape and change the names

```

# Obtain species mean shape
A_a <- mshape(ProCup3$coords[, , c(6,10,11)])
A_b <- mshape(ProCup3$coords[, , c(12,13,14)])
A_c <- mshape(ProCup3$coords[, , c(1,2,3,4)])
A_d <- mshape(ProCup3$coords[, , c(8)])
A_n <- mshape(ProCup3$coords[, , c(5)])
A_o <- mshape(ProCup3$coords[, , c(7)])
A_s <- mshape(ProCup3$coords[, , c(15)])
C_c <- mshape(ProCup3$coords[, , c(9)])
D_b <- mshape(ProCup3$coords[, , c(21,24,25,26,27)])
D_d <- mshape(ProCup3$coords[, , c(23)])
D_s <- mshape(ProCup3$coords[, , c(50)])
E_b <- mshape(ProCup3$coords[, , c(28,29,30,31,32)])
E_l <- mshape(ProCup3$coords[, , c(41)])
Ey_g <- mshape(ProCup3$coords[, , c(43)])
Ey_l <- mshape(ProCup3$coords[, , c(22,44)])
Ey_m <- mshape(ProCup3$coords[, , c(49)])
Ey_s <- mshape(ProCup3$coords[, , c(45)])
O_s <- mshape(ProCup3$coords[, , c(72)])
P_c <- mshape(ProCup3$coords[, , c(42)])
P_s <- mshape(ProCup3$coords[, , c(16,17,18,19)])
P_g <- mshape(ProCup3$coords[, , c(75)])
R_d <- mshape(ProCup3$coords[, , c(69,70,71)])
R_i <- mshape(ProCup3$coords[, , c(39)])
Sa_s <- mshape(ProCup3$coords[, , c(73,74)])
Sc_d <- mshape(ProCup3$coords[, , c(62)])
Sc_j <- mshape(ProCup3$coords[, , c(59,60)])
Sc_m <- mshape(ProCup3$coords[, , c(61,64,65,66,67,68)])
Sc_o <- mshape(ProCup3$coords[, , c(57,58,63)])
Su_b <- mshape(ProCup3$coords[, , c(40)])
Su_i <- mshape(ProCup3$coords[, , c(46,47)])

```

```

So_a <- mshape(ProCup3$coords[, ,c(55,55,56)])
So_e <- mshape(ProCup3$coords[, ,c(51,52,53)])
T_m <- mshape(ProCup3$coords[, ,c(34)])
T_r <- mshape(ProCup3$coords[, ,c(35,36)])
T_a <- mshape(ProCup3$coords[, ,c(20)])
T_n <- mshape(ProCup3$coords[, ,c(37)])
T_o <- mshape(ProCup3$coords[, ,c(38)])
T_s <- mshape(ProCup3$coords[, ,c(48)])
T_d <- mshape(ProCup3$coords[, ,c(33)])
# Join the data sets
phy2 <- abind::abind(A_a,A_b,A_c,A_d,A_n,A_o,A_s,C_c,D_b,
                    D_d,D_s,E_b,E_l,Ey_g,Ey_l,Ey_m,Ey_s,O_s,
                    P_c,P_s,P_g,R_d,R_i,Sa_s,Sc_d,Sc_j,Sc_m,
                    Sc_o,Su_b,Su_i,So_a,So_e,T_m,T_r,T_a,T_n,
                    T_o,T_s,T_d,along = 3)
# Change the names to match the phylogeny file
dimnames(phy2)[[3]] <- c("Armigatus_alticorpus", "Armigatus_brevissimus",
  "Armigatus_carrenoae", "Armigatus_dalmaticus",
  "Armigatus_namourensis", "Armigatus_oligodentatus",
  "Armigatus_felixi", "Codoichthys_carnavali",
  "Diplomystus_birdi", "Diplomystus_dubertreti",
  "Diplomystus_solignaci", "Ellimma_branneri",
  "Ellimma_longipectoralis", "Ellimmichthys_goodi",
  "Ellimmichthys_longicostatus", "Ellimmichthys_maceioensis",
  "Ellimmichthys_spinosus", "Ornategulum_sardinoides",
  "Paraclupea_chetungensis", "Paraclupea_seilacheri",
  "Pseudoellimma_gallae", "Ranulfoichthys_dorsonudum",
  "Rhombichthys_intoccabilis", "Santanaclupea_silvasantosi",
  "Scombroclupea_diminuta", "Scombroclupea_javieri",
  "Scombroclupea_macrophtalma", "Scombroclupea_occidentalis",
  "Scutatoclupea_bacchiai", "Scutatospinosus_itapagipensis",
  "Sorbinichthys_africanus", "Sorbinichthys_elusivo",
  "Thorectichthys_marocensis", "Thorectichthys_rhadinus",
  "Triplomystus_applegatei", "Triplomystus_noorae",
  "Triplomystus_oligoscutatus", "Tunisiaclupea_speratus",
  "Tycheoichthys_dunveganensis")

```

Obtain phylomorphospace

```

# Read the phylogeny
bayes <- read.nexus("Matriz_11ene22_Bayes_JAO_tax_fil.con.tre")
# Performe PACA
PHY <- gm.prcomp(phy2, phy= bayes, align.to.phy= TRUE)
# Plot Phylomorphospace
phylomorphospace(bayes, PHY$x, pch=19,cex=5, xlim=c(-.5,.5), ylim=c(-.5,.5))

## Warning in phylomorphospace(bayes, PHY$x, pch = 19, cex = 5, xlim = c(-0.5, :
X
## has more than 2 columns. Using only the first 2 columns.

```

## D. Tests

Prepare the data and groups

```

# Mean Centroid Size
A_a <- mean(ProCup3$Csize[c(6,10,11)])
A_b <- mean(ProCup3$Csize[c(12,13,14)])
A_c <- mean(ProCup3$Csize[c(1,2,3,4)])
A_d <- mean(ProCup3$Csize[c(8)])
A_n <- mean(ProCup3$Csize[c(5)])
A_o <- mean(ProCup3$Csize[c(7)])
A_s <- mean(ProCup3$Csize[c(15)])
C_c <- mean(ProCup3$Csize[c(9)])
D_b <- mean(ProCup3$Csize[c(21,24,25,26,27)])
D_d <- mean(ProCup3$Csize[c(23)])
D_s <- mean(ProCup3$Csize[c(50)])
E_b <- mean(ProCup3$Csize[c(28,29,30,31,32)])
E_l <- mean(ProCup3$Csize[c(41)])
Ey_g <- mean(ProCup3$Csize[c(43)])
Ey_l <- mean(ProCup3$Csize[c(22,44)])
Ey_m <- mean(ProCup3$Csize[c(49)])
Ey_s <- mean(ProCup3$Csize[c(45)])
O_s <- mean(ProCup3$Csize[c(72)])
P_c <- mean(ProCup3$Csize[c(42)])
P_s <- mean(ProCup3$Csize[c(16,17,18,19)])
P_g <- mean(ProCup3$Csize[c(75)])
R_d <- mean(ProCup3$Csize[c(69,70,71)])
R_i <- mean(ProCup3$Csize[c(39)])
Sa_s <- mean(ProCup3$Csize[c(73,74)])
Sc_d <- mean(ProCup3$Csize[c(62)])
Sc_j <- mean(ProCup3$Csize[c(59,60)])
Sc_m <- mean(ProCup3$Csize[c(61,64,65,66,67,68)])
Sc_o <- mean(ProCup3$Csize[c(57,58,63)])
Su_b <- mean(ProCup3$Csize[c(40)])
Su_i <- mean(ProCup3$Csize[c(46,47)])
So_a <- mean(ProCup3$Csize[c(55,55,56)])
So_e <- mean(ProCup3$Csize[c(51,52,53)])
T_m <- mean(ProCup3$Csize[c(34)])
T_r <- mean(ProCup3$Csize[c(35,36)])
T_a <- mean(ProCup3$Csize[c(20)])
T_n <- mean(ProCup3$Csize[c(37)])
T_o <- mean(ProCup3$Csize[c(38)])
T_s <- mean(ProCup3$Csize[c(48)])
T_d <- mean(ProCup3$Csize[c(33)])

# Join data sets
CS <- abind(A_a,A_b,A_c,A_d,A_n,A_o,A_s,C_c,D_b,
           D_d,D_s,E_b,E_l,Ey_g,Ey_l,Ey_m,Ey_s,O_s,
           P_c,P_s,P_g,R_d,R_i,Sa_s,Sc_d,Sc_j,Sc_m,
           Sc_o,Su_b,Su_i,So_a,So_e,T_m,T_r,T_a,T_n,
           T_o,T_s,T_d)
Cretaceous <- c("Late", "Late", "Early", "Late", "Late", "Late", "Late", "Early",
               "Early", "Late", "Late", "Late", "Early", "Early",
               "Early", "Early", "Early", "Early", "Late", "Early",
               "Early", "Early", "Early", "Late", "Early", "Late",
               "Late", "Late", "Late", "Late", "Early", "Late", "Late",
               "Late", "Late", "Late", "Late", "Late", "Late", "Early", "Late")
World <- c("East", "East", "West", "East", "East", "East", "East", "West", "West",
          "East", "East", "East", "West", "West", "East", "West", "West")

```

```

"West", "East", "East", "West", "West", "West", "East", "West",
"East", "West", "East", "West", "East", "West", "East", "East",
"East", "East", "West", "East", "East", "East", "West")
Order <- c("Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "indeterminate",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Clupeiformes", "indeterminate", "Ellimmichthyiformes",
"Clupeiformes", "Clupeiformes", "Clupeiformes",
"Clupeiformes", "Clupeiformes", "Ellimmichthyiformes",
"indeterminate", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes",
"Ellimmichthyiformes", "Ellimmichthyiformes")
# Add the names of the phylogeny
names(Cretaceous)<-bayes$tip.label
names(World)<-bayes$tip.label
names(Order)<-bayes$tip.label

```

Obtain phylogenetic signal

```

ps <- physignal(phy2, bayes, iter = 999, seed = NULL,
               print.progress = FALSE)
summary(ps)

##
## Call:
## physignal(A = phy2, phy = bayes, iter = 999, seed = NULL, print.progress = FA
LSE)
##
##
##
## Observed Phylogenetic Signal (K): 0.5178
##
## P-value: 0.027
##
## Effect Size: 2.0316
##
## Based on 1000 random permutations

```

Obtain MANOVA test

```

# Cretaceous - World test
gdf <- geomorph.data.frame(shape = phy2, bayes = bayes, CS = CS,
                          World = World, Cretaceous = Cretaceous)
CW<-procD.pgls(shape ~ Cretaceous*World, phy = bayes, data = gdf,

```

```

iter = 999,print.progress = FALSE)
summary(CW)

##
## Analysis of Variance, using Residual Randomization
## Permutation procedure: Randomization of null model residuals
## Number of permutations: 1000
## Estimation method: Generalized Least-Squares (via OLS projection)
## Sums of Squares and Cross-products: Type I
## Effect sizes (Z) based on F distributions
##
##           Df      SS      MS      Rsq      F      Z Pr(>F)
## Cretaceous    1  0.2445 0.24454 0.01981 0.7331 -0.25058 0.595
## World         1  0.1399 0.13994 0.01133 0.4195 -1.21586 0.894
## Cretaceous:World 1  0.2880 0.28798 0.02332 0.8633 -0.04216 0.511
## Residuals    35 11.6749 0.33357 0.94554
## Total        38 12.3474
##
## Call: procD.lm(f1 = shape ~ Cretaceous * World, iter = iter, seed = seed,
##   RRPP = TRUE, SS.type = SS.type, effect.type = effect.type,
##   int.first = int.first, Cov = Cov, data = data, print.progress = print.pro
##   gress)

# Allometry test
CS<- procD.lm (shape ~ CS, phy = bayes, data = gdf, iter= 999,
              turbo = TRUE,print.progress = FALSE)
summary(CS)

##
## Analysis of Variance, using Residual Randomization
## Permutation procedure: Randomization of null model residuals
## Number of permutations: 1000
## Estimation method: Ordinary Least Squares
## Sums of Squares and Cross-products: Type I
## Effect sizes (Z) based on F distributions
##
##           Df      SS      MS      Rsq      F      Z Pr(>F)
## CS         1 0.04959 0.049593 0.02565 0.9741 0.33019 0.371
## Residuals 37 1.88372 0.050911 0.97435
## Total     38 1.93331
##
## Call: procD.lm(f1 = shape ~ CS, iter = 999, turbo = TRUE, data = gdf,
##   phy = bayes, print.progress = FALSE)

```

Obtain disparity values

```

# Early-Late Cretaceous
MD1<-morphol.disparity(phy2 ~ 1, groups= Cretaceous, iter= 999,
                      print.progress = FALSE)
a <-MD1$Procrustes.var
# East-West of Tethys Sea
MD3<-morphol.disparity(phy2 ~ 1, groups= World, iter= 999,
                      print.progress = FALSE)
b <-MD3$Procrustes.var
# Taxonomic orders

```

```

MD2<-morphol.disparity(phy2 ~ 1, groups= Order, iter= 999,
                        print.progress = FALSE)
c <-MD2$Procrustes.var
# Create Plot
clup <- data.frame(Name = c("Early Cretaceous", "Late Cretaceous",
                            "Tethys East", "Tethys West",
                            "Clupeiformes", "Ellimmichthyiformes",
                            "indeterminate"),
                  Name2 = c("a", "b", "a", "b", "a", "b", "c"),
                  Variable = c("Cretaceous", "Cretaceous",
                               "World", "World",
                               "Order", "Order", "Order"),
                  Value = c(a,b,c))
clup$Variable <- factor(clup$Variable, levels = c("Cretaceous", "World", "Order"))
ggplot(clup, aes(x= Name2, y= Value)) +
  geom_bar(aes(fill=Name2), stat = "identity", color="black", alpha=0.8) +
  facet_wrap(~ Variable) +
  ylab("Disparity") + xlab ("Variable") + ylim(0,0.08) +
  scale_fill_manual(values=c("sienna", "turquoise4", "maroon")) +
  theme(panel.background = element_blank(),
        panel.border=element_rect(fill=NA, size=.5),
        strip.background = element_rect(fill = NA),
        axis.title.x = element_text(size=12),
        axis.title.y = element_text(size=12),
        axis.text.y = element_text(size=10),
        axis.text.x = element_text(size=10),
        legend.position="none")

```

Obtain morphological evolution rates

```

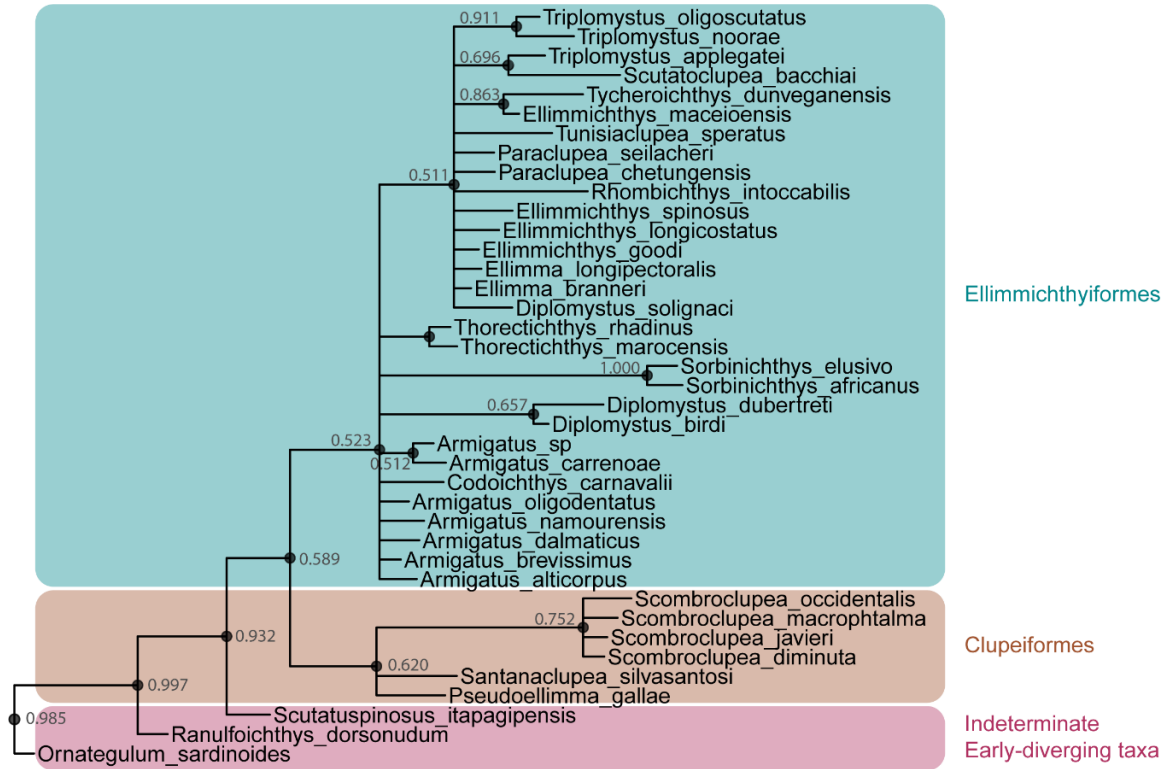
# Early-Late Cretaceous
MD1 <- compare.evol.rates(phy2, phy=bayes, gp=Cretaceous,
                          iter=999, print.progress = FALSE)
a<-MD1$sigma.d.gp
# East-West of Tethys Sea
MD2 <- compare.evol.rates(phy2, phy=bayes, gp=World,
                          iter=999, print.progress = FALSE)
b<-MD2$sigma.d.gp
# Taxonomic orders
MD3 <- compare.evol.rates(phy2, phy=bayes, gp=Order,
                          iter=999, print.progress = FALSE)
c<-MD3$sigma.d.gp
#Create plot
clup <- data.frame(Name = c("Early Cretaceous", "Late Cretaceous",
                            "Tethys East", "Tethys West",
                            "Clupeiformes", "Ellimmichthyiformes",
                            "indeterminate"),
                  Name2 = c("a", "b", "a", "b", "a", "b", "c"),
                  Variable = c("Cretaceous", "Cretaceous", "World",
                               "World", "Order", "Order", "Order"),
                  Value = c(a,b,c))
clup$Variable <- factor(clup$Variable, levels = c("Cretaceous", "World", "Order"))
ggplot(clup, aes(x= Name2, y= Value)) +
  geom_bar(aes(fill=Name2), stat = "identity", color="black", alpha=0.8) +
  facet_wrap(~ Variable) +

```

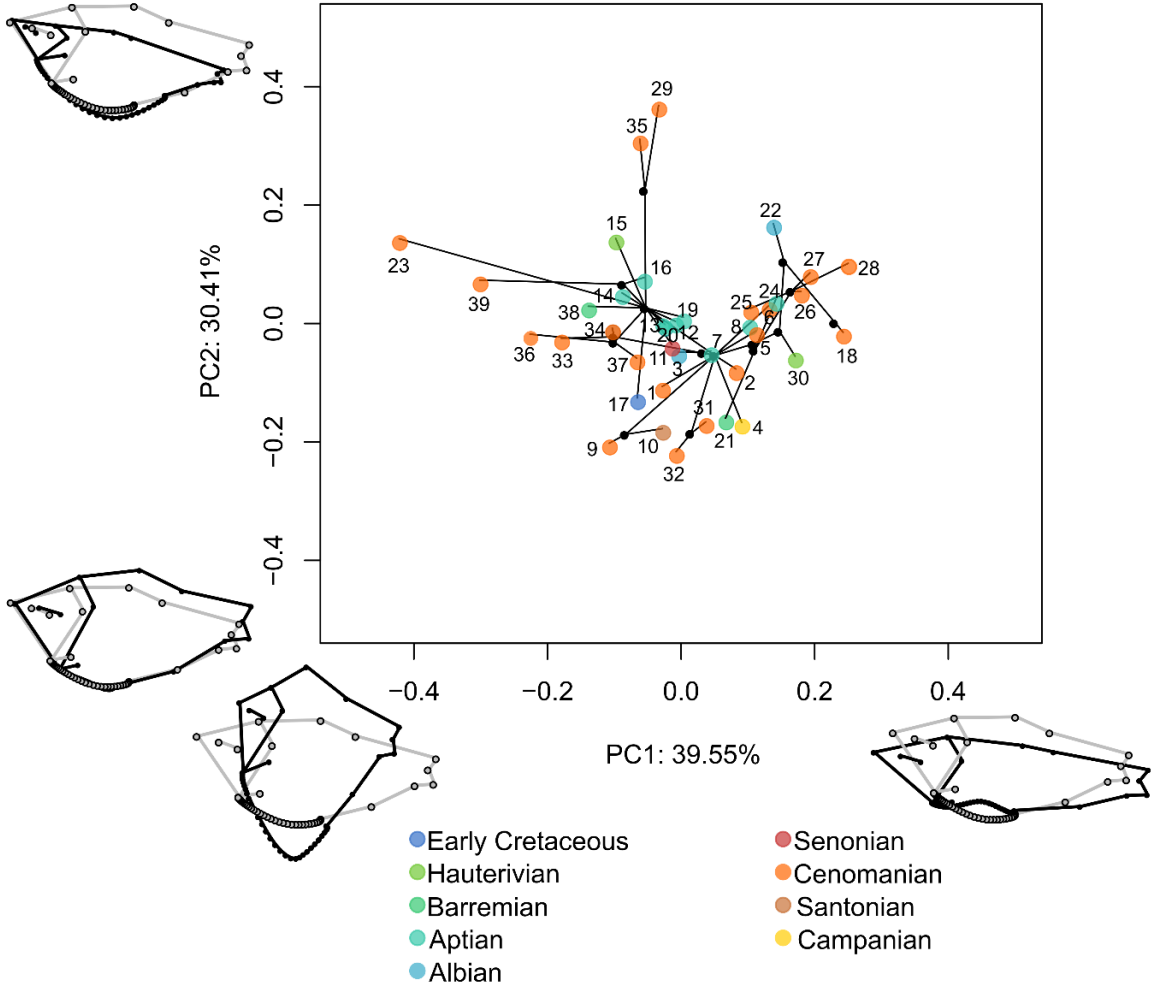
```
ylab("Morphological evolution rate") + xlab ("Variable") +
scale_fill_manual(values=c("sienna","turquoise4","maroon")) +
theme(panel.background = element_blank(),
       panel.border=element_rect(fill=NA,size=.5),
       strip.background = element_rect(fill = NA),
       axis.title.x = element_text(size=12),
       axis.title.y = element_text(size=12),
       axis.text.y = element_text(size=10),
       axis.text.x = element_text(size=10),
       legend.position="none")
```



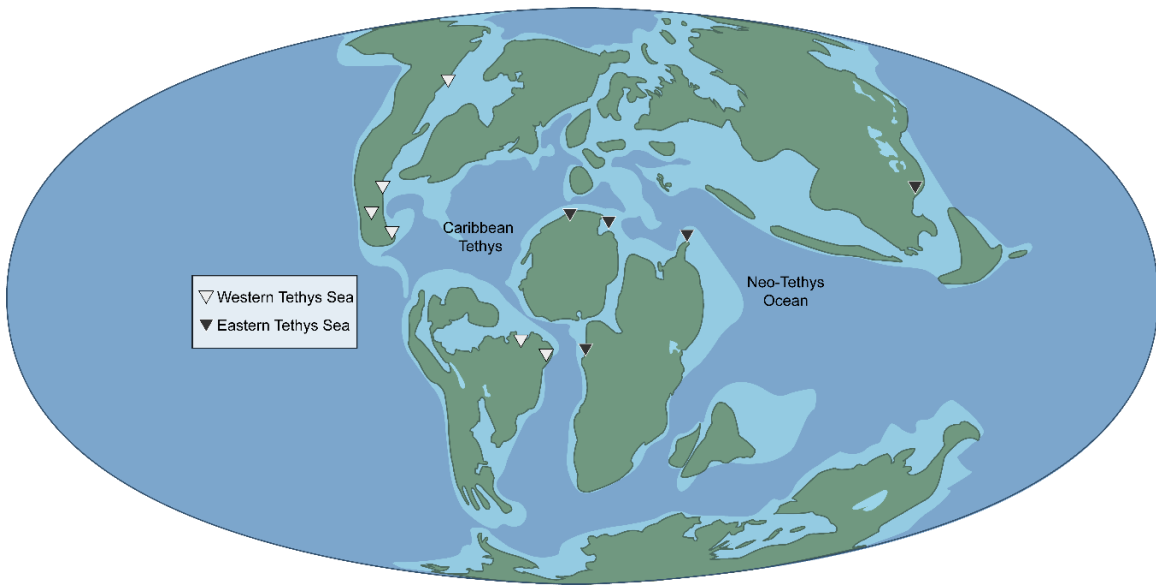
**Fig. S1.** Clupeomorpha phylogeny from Than Marchese et al. (work in press). Values at nodes indicate the clade probability. We indicated the orders in different colors according to phylogeny: Clupeiformes (brown), Ellimmichthyiformes (turquoise), and the indeterminate species that diverged early (magenta).



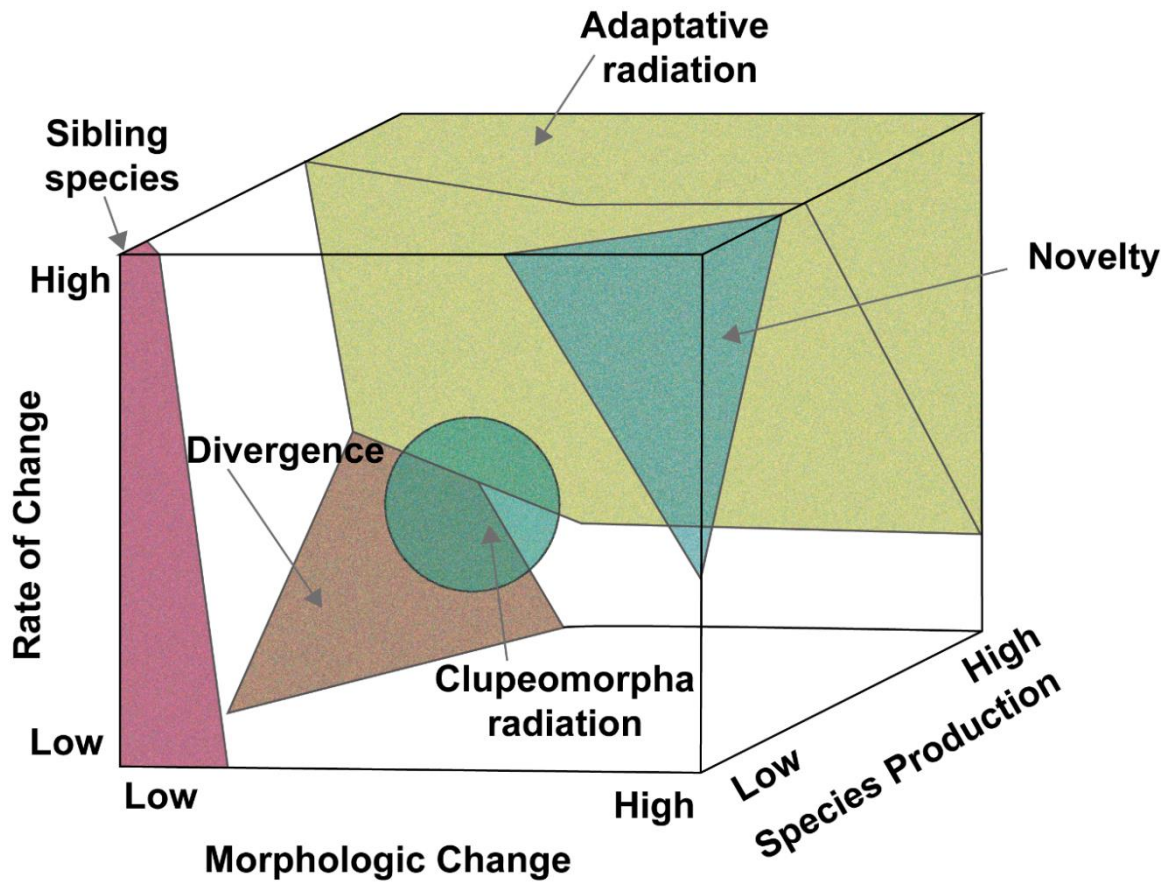
**Fig. S2.** PC1 and PC2 of PACA, numbered according to the species in Table S2 and colored according to the time interval dated. Diagrams of the shape change (black) with respect to the average shape (light gray) are shown.



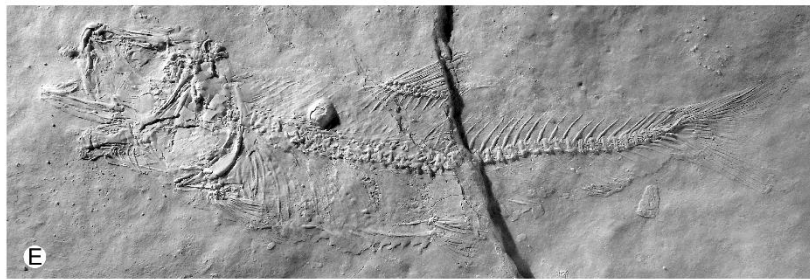
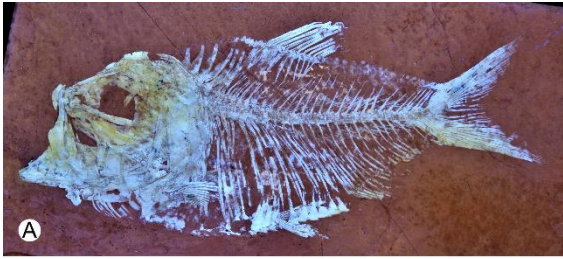
**Fig. S3.** Regions containing the fossiliferous localities of the specimens used in the morphometric analysis, and their classification according to their position east (black) or west (white) of the Tethys Sea. Scotese's Cenomanian (96.6 Ma) projection (1).



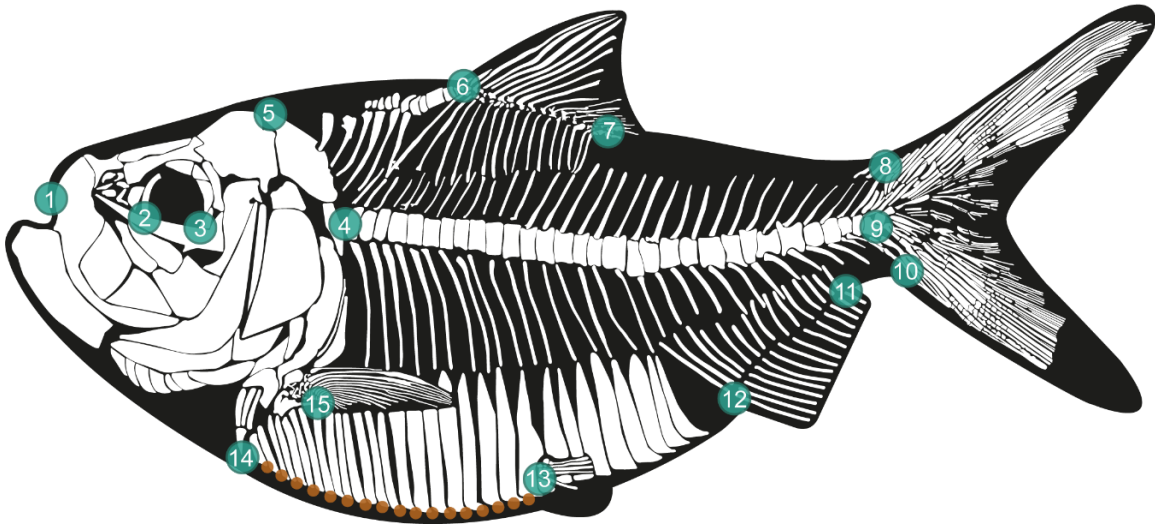
**Fig. S4.** Clupeomorpha radiation position in relation to Erwin (2) classification and diagram. Clupeomorpha exhibits a gradual taxonomic diversification and a moderate and abrupt morphological diversification that we visualized like a sphere (green) in the middle of the space composed by taxonomic and morphological change. See Erwin's work for more details of radiation and diversification types.



**Fig. S5.** Images of Clupeomorpha species obtained from biological collections of Mexico. A. *Armigatus carrenoa*; B. *Armigatus* sp.; C. *Paraclupea seilacheri*; D. *Triplomystus applegatei*; E. *Ranulfoichthys dorsonudum*; F. *Sombroclupea javieri*; G. *Sombroclupea occidentalis*.



**Fig. S6.** Configuration used in the morphometric analysis of Clupeomorpha fossil fish. Turquoise shows the landmarks that indicate: 1) antero-ventral end of the upper jaw (maxilla); 2) anterior end of the eye (parasphenoid); 3) posterior end of the eye (paresphenoid); 4) union of the skull and spinal column; 5) postero-dorsal end of the skull (supraoccipital crest); 6) dorsal fin anterior insertion; 7) dorsal fin posterior insertion; 8) dorsal insertion of caudal fin; 9) posterior margin of caudal peduncle; 10) fin ventral insertion flow; 11) posterior insertion of anal fin; 12) anterior insertion of anal fin; 13) antero-ventral insertion of the pelvic fin; 14) antero-ventral insertion of the pectoral girdle; 15) antero-ventral insertion of the pectoral fin. Semilandmarks are shown in brown, representing the curvature between the insertion of the pelvic fin (13) and pectoral girdle (14).



**Table S1.** List of the species used in the calculation of the origin rates of Clupeomorpha genera and species (3-16). Dating is incorporated, in the case of empty spaces a precise dating is not available or incorporated.

<b>Era</b>	<b>Period</b>	<b>Epoch</b>	<b>Age</b>	<b>Order</b>	<b>Genus</b>	<b>Species</b>
Mesozoic	Cretaceous	Early	Hauterivian	indeterminate	<i>Scutatuspinosus</i>	<i>itapagipensis</i>
Mesozoic	Cretaceous	Early	Hauterivian- Barremian	Ellimmichthyiformes	<i>Ellimmichthys</i>	<i>longicostatus</i>
Mesozoic	Cretaceous	Early	Barremian	Clupeiformes	<i>Pseudoellimma</i>	<i>gallae</i>
Mesozoic	Cretaceous	Early	Barremian	Ellimmichthyiformes	<i>Tunisiaclupea</i>	<i>speratus</i>
Mesozoic	Cretaceous	Early	Barremian- Aptian	Clupeiformes	<i>Cynoclupea</i>	<i>nelsoni</i>
Mesozoic	Cretaceous	Early	Aptian	Ellimmichthyiformes	<i>Codoichthys</i>	<i>carnavallii</i>
Mesozoic	Cretaceous	Early	Aptian	Ellimmichthyiformes	<i>Ellimma</i>	<i>branneri</i>
Mesozoic	Cretaceous	Early	Aptian	Ellimmichthyiformes	<i>Ellimma</i>	<i>cruzi</i>
Mesozoic	Cretaceous	Early	Aptian	Ellimmichthyiformes	<i>Ellimma</i>	<i>longipectoralis</i>
Mesozoic	Cretaceous	Early	Aptian-Albian	Ellimmichthyiformes	<i>Ellimmichthys</i>	<i>goodi</i>
Mesozoic	Cretaceous	Early	Aptian-Albian	Ellimmichthyiformes	<i>Ellimmichthys</i>	<i>maceioensis</i>
Mesozoic	Cretaceous	Early	Aptian-Albian	Clupeiformes	<i>Histiurus</i>	<i>elatus</i>
Mesozoic	Cretaceous	Early	Aptian-Albian	Clupeiformes	<i>Histiurus</i>	<i>serioloides</i>
Mesozoic	Cretaceous	Early	Aptian-Albian	Clupeiformes	<i>Histiurus</i>	<i>ventricosus</i>
Mesozoic	Cretaceous	Early	Aptian-Albian	Ellimmichthyiformes	<i>Paraclupea</i>	<i>chetungensis</i>
Mesozoic	Cretaceous	Early	Albian	Ellimmichthyiformes	<i>Armigatus</i>	<i>carrennae</i>
Mesozoic	Cretaceous	Early	Albian	Clupeiformes	<i>Erichalcis</i>	<i>arcta</i>
Mesozoic	Cretaceous	Early	Albian	Ellimmichthyiformes	<i>Foreyclupea</i>	<i>loonensis</i>
Mesozoic	Cretaceous	Early	Albian	Clupeiformes	<i>Nolfia</i>	<i>riachuelensis</i>
Mesozoic	Cretaceous	Early	Albian	Ellimmichthyiformes	<i>Paraclupea</i>	<i>seilacheri</i>
Mesozoic	Cretaceous	Early	Albian	indeterminate	<i>Ranulfoichthys</i>	<i>dorsonudum</i>
Mesozoic	Cretaceous	Early	Albian	Clupeiformes	<i>Santanaclupea</i>	<i>silvasantosi</i>
Mesozoic	Cretaceous	Early	Albian	Clupeiformes	<i>Spratticeps</i>	<i>gaultinus</i>
Mesozoic	Cretaceous	Early	Neocomian	Clupeiformes	" <i>Clupea</i> "	<i>antiqua</i>
Mesozoic	Cretaceous	Early	Neocomian	Clupeiformes	" <i>Clupea</i> "	<i>voironensis</i>
Mesozoic	Cretaceous	Early	Valanginian- Barremian	Ellimmichthyiformes	<i>Ezkutuberezi</i>	<i>carmeni</i>
Mesozoic	Cretaceous	Early		Ellimmichthyiformes	<i>Diplomystus</i>	<i>altisomus</i>
Mesozoic	Cretaceous	Early		Ellimmichthyiformes	<i>Diplomystus</i>	<i>kokuraensis</i>
Mesozoic	Cretaceous	Early		Ellimmichthyiformes	<i>Diplomystus</i>	<i>primotinus</i>
Mesozoic	Cretaceous	Early		Ellimmichthyiformes	<i>Ellimmichthys</i>	<i>spinosus</i>
Mesozoic	Cretaceous	Early		Clupeiformes	<i>Eoknightia</i>	<i>caheni</i>
Mesozoic	Cretaceous	Early		Clupeiformes	<i>Haplospondylus</i>	<i>clupeoides</i>
Mesozoic	Cretaceous	Early		Clupeiformes	<i>Nolfia</i>	<i>kwangoensis</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Armigatus</i>	<i>alticorpus</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Armigatus</i>	<i>brevissimus</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Armigatus</i>	<i>namourensensis</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Diplomystus</i>	<i>birdi</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Kwangoclupea</i>	<i>dartevellei</i>

Mesozoic	Cretaceous	Late	Cenomanian	indeterminate	<i>Ornategulum</i>	<i>sardinoides</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Rhombichthys</i>	<i>intoccabilis</i>
Mesozoic	Cretaceous	Late	Cenomanian	Clupeiformes	<i>Scombroclupea</i>	<i>diminuta</i>
Mesozoic	Cretaceous	Late	Cenomanian	Clupeiformes	<i>Scombroclupea</i>	<i>javieri</i>
Mesozoic	Cretaceous	Late	Cenomanian	Clupeiformes	<i>Scombroclupea</i>	<i>macrophthalma</i>
Mesozoic	Cretaceous	Late	Cenomanian	Clupeiformes	<i>Scombroclupea</i>	<i>occidentalis</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Scutatoclupea</i>	<i>bacchiai</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Sorbinichthys</i>	<i>elusivo</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Triplomystus</i>	<i>aplegatei</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Triplomystus</i>	<i>noorae</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Triplomystus</i>	<i>oligoscutatus</i>
Mesozoic	Cretaceous	Late	Cenomanian	Ellimmichthyiformes	<i>Tychoichthys</i>	<i>dunveganensis</i>
Mesozoic	Cretaceous	Late	Santonian	Ellimmichthyiformes	<i>Diplomystus</i>	<i>dubertreti</i>
Mesozoic	Cretaceous	Late	Cenomanian-Turonian	Ellimmichthyiformes	<i>Armigatus</i>	<i>oligodentatus</i>
Mesozoic	Cretaceous	Late	Cenomanian-Turonian	Ellimmichthyiformes	<i>Sorbinichthys</i>	<i>africanus</i>
Mesozoic	Cretaceous	Late	Cenomanian-Turonian	Ellimmichthyiformes	<i>Thorectichthys</i>	<i>macroensis</i>
Mesozoic	Cretaceous	Late	Cenomanian-Turonian	Ellimmichthyiformes	<i>Thorectichthys</i>	<i>rhadinus</i>
Mesozoic	Cretaceous	Late	Campanian	Ellimmichthyiformes	<i>Armigatus</i>	<i>dalmaticus</i>
Mesozoic	Cretaceous	Late	Maastrichtian	Ellimmichthyiformes	<i>Horseshoeichthys</i>	<i>armaserratus</i>
Mesozoic	Cretaceous	Late		Clupeiformes	" <i>Diplomystus</i> "	<i>coverhamensis</i>
Mesozoic	Cretaceous	Late		Clupeiformes	" <i>Diplomystus</i> "	<i>kasachstanicus</i>
Mesozoic	Cretaceous	Late		Clupeiformes	" <i>Diplomystus</i> "	<i>miutus</i>
Mesozoic	Cretaceous	Late		Ellimmichthyiformes	<i>Gasteroclupea</i>	<i>branisai</i>
Mesozoic	Cretaceous	Late	Senonian	Ellimmichthyiformes	" <i>Diplomystus</i> "	<i>solignaci</i>
Cenozoic	Paleogene	Paleocene		Ellimmichthyiformes	" <i>Diplomystus</i> "	<i>trebicianensis</i>
Cenozoic	Paleogene	Paleocene		Clupeiformes	<i>Knightia</i>	<i>vetusta</i>
Cenozoic	Paleogene	Paleocene		Clupeiformes	<i>Primisardinella</i>	<i>gentrix</i>
Cenozoic	Paleogene	Eocene		Clupeiformes	" <i>Clupea</i> "	<i>catopygoptera</i>
Cenozoic	Paleogene	Eocene		Clupeiformes	" <i>Horaclupea</i> "	<i>geei</i>
Cenozoic	Paleogene	Eocene		Ellimmichthyiformes	<i>Diplomystus</i>	<i>dentatus</i>
Cenozoic	Paleogene	Eocene		Ellimmichthyiformes	<i>Diplomystus</i>	<i>shengliensis</i>
Cenozoic	Paleogene	Early Eocene		Ellimmichthyiformes	<i>Eoellimmichthys</i>	<i>superstes</i>
Cenozoic	Paleogene	Eocene		Clupeiformes	<i>Gosiutichthys</i>	<i>parvus</i>
Cenozoic	Paleogene	Eocene		Clupeiformes	<i>Horaclupea</i>	<i>intertrappea</i>
Cenozoic	Paleogene	Eocene		Clupeiformes	<i>Knightia</i>	<i>alta</i>
Cenozoic	Paleogene	Eocene		Clupeiformes	<i>Knightia</i>	<i>eocaena</i>
Cenozoic	Paleogene	Eocene		Clupeiformes	<i>Knightia</i>	<i>yuyanga</i>
Cenozoic	Paleogene	Eocene		Clupeiformes	<i>Scombroclupea?</i>	<i>murlii</i>
Cenozoic	Paleogene	Oligocene		Clupeiformes	" <i>Clupea</i> "	<i>bassanii</i>
Cenozoic	Paleogene	Oligocene		Clupeiformes	" <i>Clupea</i> "	<i>breviceps</i>



Cenozoic	Paleogene	Oligocene	Clupeiformes	"Clupea"	<i>gracillima</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	"Clupea"	<i>grandonii</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	"Clupea"	<i>latissima</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	"Clupea"	<i>ombonii</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	"Clupea"	<i>scheuchzeri</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	"Clupea"	<i>vectensis</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	"Pellonula"	<i>grasionescui</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Alosa</i>	<i>aralensis</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Alosina</i>	<i>salmonea</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Chasmoclupea</i>	<i>aegyptica</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Etrumeus</i>	<i>hafizi</i>
Cenozoic	Paleogene	Oligocene	Ellimmichthyiformes	<i>Guiclupea</i>	<i>superstes</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Maicopiella</i>	<i>longimana</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Opisthonema</i>	<i>antethrissa</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Opisthonema</i>	<i>persicum</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Palaeodenticeps</i>	<i>tanganikae</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Paretrumeus</i>	<i>avitus</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Pomolobus</i>	<i>antiquus</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Pomolobus</i>	<i>curtus</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Pomolobus</i>	<i>facilis</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Pseudohilsa</i>	<i>nikosi</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Rupelia</i>	<i>rata</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Sardina</i>	<i>necteodosciobanensis</i>
Cenozoic	Paleogene	Oligocene	Clupeiformes	<i>Sardinella</i>	<i>denticulata</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>arcuata</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>dentex</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>doljeana</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>elongata</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>fontannesii</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>gorjensis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>haidingeri</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>heterocerca</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>hungarica</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>intermedia</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>maceki</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>melettaeformis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>mucronata</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>spinosa</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>styriaca</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>tenuissima</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>tiejei</i>
Cenozoic	Neogene	Miocene	Clupeiformes	"Clupea"	<i>ventricosa</i>

Cenozoic	Neogene	Miocene	Clupeiformes	<i>"Diplomystus"</i>	<i>marmorensis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alisea</i>	<i>grandis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>baykali</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>crassa</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>elongata</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>fortipinnata</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>numidica</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>ovalis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>pinarthusarensis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>renoui</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>sculptata</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Alosa</i>	<i>weileri</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Chatoessus</i>	<i>brevis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Chatoessus</i>	<i>humilis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Chatoessus</i>	<i>tenuis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Clupeonella</i>	<i>binagadensis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Clupeonella</i>	<i>humilis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Clupeonella</i>	<i>pliocenica</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Clupeops</i>	<i>insignis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Entringus</i>	<i>scintillans</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Eosardinella</i>	<i>hoshinaiensis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Epelichthys</i>	<i>michaelis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Etrumeus</i>	<i>boulei</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Ganoessus</i>	<i>clepsydra</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Ganolytes</i>	<i>cameo</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Lembicus</i>	<i>meiklejohni</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Maicopiella</i>	<i>brevicauda</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Opisthonema</i>	<i>palosverdensis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Pseudohilsa</i>	<i>brevicauda</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Quisque</i>	<i>gilberti</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Sahelinia</i>	<i>gregaria</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Sardina</i>	<i>prisca</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Sardinella</i>	<i>beogradensis</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Sardinella</i>	<i>brouweri</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Sardinella</i>	<i>perrata</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Sarmatella</i>	<i>vucotinovici</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Spratelloides</i>	<i>lemoinei</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Xenothrissa</i>	<i>aphrasta</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Xyne</i>	<i>grex</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Xyrinius</i>	<i>barbarae</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Xyrinius</i>	<i>elmodenae</i>
Cenozoic	Neogene	Miocene	Clupeiformes	<i>Xyrinius</i>	<i>houshi</i>

Cenozoic	Neogene	Miocene- Pliocene	Clupeiformes	<i>Austroclupea</i>	<i>zuninoi</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	" <i>Clupea</i> "	<i>gervaisi</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	" <i>Clupea</i> "	<i>linderi</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	" <i>Clupea</i> "	<i>lorcae</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	<i>Hilsa</i>	<i>elegans</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	<i>Hilsa</i>	<i>lata</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	<i>Hilsa</i>	<i>oblonga</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	<i>Hilsa</i>	<i>torosa</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	<i>Knightia</i>	<i>brasiliensis</i>
Cenozoic	Neogene	Pliocene	Clupeiformes	<i>Sardinella</i>	<i>milanovskii</i>
Cenozoic	Neogene	Plio- Pleistocene	Clupeiformes	<i>Engraulis</i>	<i>macrocephalus</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	" <i>Clupea</i> "	<i>heckeli</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	" <i>Clupea</i> "	<i>inflata</i>
Cenozoic	Paleogene- Neogene	Oligocene- Miocene	Clupeiformes	" <i>Clupea</i> "	<i>crenata</i>
Cenozoic	Paleogene- Neogene	Oligocene- Miocene	Clupeiformes	" <i>Clupea</i> "	<i>parisoti</i>
Cenozoic	Paleogene- Neogene	Oligocene- Miocene	Clupeiformes	" <i>Clupea</i> "	<i>sahleri</i>
Cenozoic	Paleogene- Neogene	Oligocene- Miocene	Clupeiformes	" <i>Clupea</i> "	<i>voinovi</i>
Cenozoic	Paleogene- Neogene	Oligocene- Miocene	Clupeiformes	<i>Alosa</i>	<i>ganuina</i>
Cenozoic	Paleogene- Neogene	Oligocene- Miocene	Clupeiformes	<i>Sardinella</i>	<i>engrauliformis</i>
Cenozoic	Paleogene- Neogene	Oligocene- Miocene	Clupeiformes	<i>Sardinella</i>	<i>sardinites</i>
Cenozoic	Neogene	Miocene	Clupeiformes	" <i>Clupea</i> "	<i>lanceolata</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	" <i>Clupea</i> "	<i>sagorensis</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	" <i>Clupea</i> "	<i>sarmatica</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	<i>Caspialosa</i>	<i>praecursor</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	<i>Clupanodon</i>	<i>tanegashimaensis</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	<i>Clupeonella</i>	<i>mediocris</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	<i>Clupeonella</i>	<i>pliocena</i>
Cenozoic	Paleogene- Neogene		Clupeiformes	<i>Clupeonella</i>	<i>vexata</i>

**Table S2.** List of Clupeomorpha images used in the morphometric analysis, as well as their classification, dating, distribution, environment, reference, and identification number. The Mexican collections from which photographs were obtained are indicated: \* = Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México; ^ = Museo Eliseo Palacios Aguilera, Secretaría de Medio Ambiente e Historia Natural de Chiapas; + = Museo de Paleontología de Múzquiz

Order	Species	Collection number	Country	Age	Environment	Ref.	No.
Ellimmichthyiformes	<i>Armigatus alticorpus</i>	BMNH P.63134	Lebanon	Cenomanian	Marine	(13)	1
Ellimmichthyiformes	<i>Armigatus alticorpus</i>	TMP 1998-65.11 A	Lebanon	Cenomanian	Marine	(17)	1
Ellimmichthyiformes	<i>Armigatus alticorpus</i>	TMP 1998-65.11 D	Lebanon	Cenomanian	Marine	(17)	1
Ellimmichthyiformes	<i>Armigatus brevissimus</i>	MNHN.F.HAK1691 A	Lebanon	Cenomanian	Marine	(18)	2
Ellimmichthyiformes	<i>Armigatus brevissimus</i>	MNHN.F.HAK1691 B	Lebanon	Cenomanian	Marine	(18)	2
Ellimmichthyiformes	<i>Armigatus brevissimus</i>	MNHN.F.HAK1695	Lebanon	Cenomanian	Marine	(18)	2
Ellimmichthyiformes	<i>Armigatus carrenoae</i>	IGM 11536	Mexico	Albian	Marine	(3)*	3
Ellimmichthyiformes	<i>Armigatus carrenoae</i>	IGM 11537	Mexico	Albian	Marine	(3)*	3
Ellimmichthyiformes	<i>Armigatus carrenoae</i>	IGM 11538	Mexico	Albian	Marine	(3)*	3
Ellimmichthyiformes	<i>Armigatus carrenoae</i>	IGM 11540	Mexico	Albian	Marine	(3)*	3
Ellimmichthyiformes	<i>Armigatus dalmaticus</i>	CNHM 9423	Croatia	Campanian	Marine	(19)	4
Ellimmichthyiformes	<i>Armigatus namourensis</i>	BMNH P.59808	Lebanon	Cenomanian	Marine	(13)	5
Ellimmichthyiformes	<i>Armigatus oligodentatus</i>	UALVP 51622	Morocco	Cenomanian-Turonian	Marine	(20)	6
Ellimmichthyiformes	<i>Armigatus</i> sp.	CT 8837	Mexico	Albian	Marine	*	7
Ellimmichthyiformes	<i>Codoichthys carnavaalii</i>	DGM 435-P	Brazil	Aptian	Marine	(21)	8
Ellimmichthyiformes	<i>Diplomystus birdi</i>	AMNH 10188	Lebanon	Cenomanian	Marine	(22)	9
Ellimmichthyiformes	<i>Diplomystus birdi</i>	MNHN.F.HAK1724	Lebanon	Cenomanian	Marine	(18)	9
Ellimmichthyiformes	<i>Diplomystus birdi</i>	MNHN.F.HAK1849	Lebanon	Cenomanian	Marine	(18)	9
Ellimmichthyiformes	<i>Diplomystus birdi</i>	MNHN.F.HAK833	Lebanon	Cenomanian	Marine	(18)	9
Ellimmichthyiformes	<i>Diplomystus birdi</i>	MNHN.F.HAK835	Lebanon	Cenomanian	Marine	(18)	9
Ellimmichthyiformes	<i>Diplomystus dubertreti</i>	MNHN.F.SHA2052	Lebanon	Santonian	Marine	(18)	10
Ellimmichthyiformes	<i>"Diplomystus" solignaci</i>		Tunisia	Senonian	Marine	(23)	11
Ellimmichthyiformes	<i>Ellimma branneri</i>	CM 5258/4	Brazil	Aptian	Marine	(24)	12
Ellimmichthyiformes	<i>Ellimma branneri</i>	CM 5249/2	Brazil	Aptian	Marine	(24)	12
Ellimmichthyiformes	<i>Ellimma branneri</i>	AMNH 10048	Brazil	Aptian	Marine	(24)	12
Ellimmichthyiformes	<i>Ellimma branneri</i>	AMNH 10057	Brazil	Aptian	Marine	(24)	12
Ellimmichthyiformes	<i>Ellimma branneri</i>	AMNH 10060	Brazil	Aptian	Marine	(24)	12
Ellimmichthyiformes	<i>Ellimma longipectoralis</i>	MCT 1471-P	Brazil	Aptian	Lacustrine	(25)	13
Ellimmichthyiformes	<i>Ellimmichthys goodi</i>	FMNH UC2163	Rep. Equ. Guine	Aptian-Albian	Freeshwater	(26)	14
Ellimmichthyiformes	<i>Ellimmichthys longicostatus</i>	AMNH 734	Brazil	Early Cretaceous	Marine	(22)	15
Ellimmichthyiformes	<i>Ellimmichthys longicostatus</i>	NHM P. 10350	Brazil	Hauterivian-Barremian	Lacustrine	(27)	15
Ellimmichthyiformes	<i>Ellimmichthys maceioensis</i>	MCP 4039PV	Brazil	Aptian-Albian	Marine	(28)	16

Ellimmichthyiformes	<i>Ellimmichthys spinosus</i>	NHM P. 7109	Brazil	Early Cretaceous	Lacustrine	(27)	17
indeterminate	<i>Ornategulum sardinioides</i>	MNHN.F.HAK1996	Lebanon	Cenomanian	Marine	(18)	18
Ellimmichthyiformes	<i>Paraclupea chetungensis</i>	IVPP V3002.7	China	Aptian-Albian	Freeshwater	(26)	19
Ellimmichthyiformes	<i>Paraclupea seilacheri</i>	IGM 4720	Mexico	Albian	Marine	(29)*	20
Ellimmichthyiformes	<i>Paraclupea seilacheri</i>		Mexico	Albian	Marine	*	20
Ellimmichthyiformes	<i>Paraclupea seilacheri</i>	IGM 4717	Mexico	Albian	Marine	(29)*	20
Ellimmichthyiformes	<i>Paraclupea seilacheri</i>	IGM 4719	Mexico	Albian	Marine	(29)*	20
Clupeiformes	<i>Pseudoellimma gallae</i>	Pz.UERJ 497	Brazil	Barremian	Brackish waters	(11)	21
indeterminate	<i>Ranulfoichthys dorsonudum</i>	IGM 9034	Mexico	Albian	Marine	(30)*	22
indeterminate	<i>Ranulfoichthys dorsonudum</i>	IGM 9035	Mexico	Albian	Marine	(30)*	22
indeterminate	<i>Ranulfoichthys dorsonudum</i>	IGM 9036	Mexico	Albian	Marine	(30)*	22
Ellimmichthyiformes	<i>Rhombichthys intocabilis</i>	HUJ EY603F	Palestine	Cenomanian	Marine	(31)	23
Clupeiformes	<i>Santanaclupea silvasantosi</i>	AMNH 12790	Brazil	Albian	Marine	(14)	24
Clupeiformes	<i>Santanaclupea silvasantosi</i>	AMNH 12789	Brazil	Albian	Marine	(14)	24
Clupeiformes	<i>Scombroclupea diminuta</i>	BMNH P.63136	Lebanon	Cenomanian	Marine	(13)	25
Clupeiformes	<i>Scombroclupea javieri</i>	IHNFG 5297	Mexico	Cenomanian	Marine	(10)^	26
Clupeiformes	<i>Scombroclupea javieri</i>	IHNFG 5298	Mexico	Cenomanian	Marine	(10)^	26
Clupeiformes	<i>Scombroclupea macrophthalma</i>	BMNH P.63143	Lebanon	Cenomanian	Marine	(18)	27
Clupeiformes	<i>Scombroclupea macrophthalma</i>	MNHN.F.HAK1252	Lebanon	Cenomanian	Marine	(18)	27
Clupeiformes	<i>Scombroclupea macrophthalma</i>	MNHN.F.HAK1413	Lebanon	Cenomanian	Marine	(18)	27
Clupeiformes	<i>Scombroclupea macrophthalma</i>	MNHN.F.HAK1474G	Lebanon	Cenomanian	Marine	(18)	27
Clupeiformes	<i>Scombroclupea macrophthalma</i>	MNHN.F.HAK1100	Lebanon	Cenomanian	Marine	(18)	27
Clupeiformes	<i>Scombroclupea macrophthalma</i>	MNHN.F.HAK437	Lebanon	Cenomanian	Marine	(18)	27
Clupeiformes	<i>Scombroclupea occidentalis</i>	CPC-433	Mexico	Cenomanian	Marine	(12)	28
Clupeiformes	<i>Scombroclupea occidentalis</i>	CPC-434	Mexico	Cenomanian	Marine	(12)	28
Clupeiformes	<i>Scombroclupea occidentalis</i>	MUZ 480	Mexico	Cenomanian	Marine	+	28
Ellimmichthyiformes	<i>Scutatoclupea bacchiae</i>	PIN 5089/4	Lebanon	Cenomanian	Marine	(32)	29
indeterminate	<i>Scutatuspinosus itapagipensis</i>	DGM 1164-P	Brazil	Neocomian Hauterivian	Lacustrine	(33)	30
indeterminate	<i>Scutatuspinosus itapagipensis</i>	DGM DNPM 1252-P	Brazil	Neocomian Hauterivian	Lacustrine	(34)	30
Ellimmichthyiformes	<i>Sorbinichthys africanus</i>	UALVP 51640	Morocco	Cenomanian-Turonian	Marine	(35)	31
Ellimmichthyiformes	<i>Sorbinichthys africanus</i>	UALVP 51641	Morocco	Cenomanian-Turonian	Marine	(35)	31
Ellimmichthyiformes	<i>Sorbinichthys africanus</i>	UALVP 47186	Morocco	Cenomanian-Turonian	Marine	(35)	31

Ellimmichthyiformes	<i>Sorbinichthys elusivo</i>	CLC 431	Lebanon	Cenomanian	Marine	(36)	32
Ellimmichthyiformes	<i>Sorbinichthys elusivo</i>	AGMV VP1	Lebanon	Cenomanian	Marine	(36)	32
Ellimmichthyiformes	<i>Sorbinichthys elusivo</i>	MCSNT 12238	Lebanon	Cenomanian	Marine	(36)	32
Ellimmichthyiformes	<i>Thorectichthys macrocensis</i>	UALVP 47178	Morocco	Cenomanian-Turonian	Marine	(37)	33
Ellimmichthyiformes	<i>Thorectichthys rhadinus</i>	UALVP 51653	Morocco	Cenomanian-Turonian	Marine	(37)	34
Ellimmichthyiformes	<i>Thorectichthys rhadinus</i>	UALVP 51664	Morocco	Cenomanian-Turonian	Marine	(37)	34
Ellimmichthyiformes	<i>Triplomystus applegatei</i>	INAH 1941	Mexico	Cenomanian	Marine	(34)*	35
Ellimmichthyiformes	<i>Triplomystus noorae</i>	BMNH P.62517	Lebanon	Cenomanian	Marine	(13)	36
Ellimmichthyiformes	<i>Triplomystus oligoscutatus</i>	BMNH P.63155	Lebanon	Cenomanian	Marine	(13)	37
Ellimmichthyiformes	<i>Tunisiaclupea speratus</i>	KABSF01a	Tunisia	Barremian	Marine	(38)	38
Ellimmichthyiformes	<i>Tycheoichthys dunveganensis</i>	CMN 52730	Canada	Cenomanian	Marine	(39)	39

**Dataset S1 (separate file).** The files to perform the geometric morphometric analysis are available at [https://github.com/IGPaleo/Clupeomorpha\\_radiation](https://github.com/IGPaleo/Clupeomorpha_radiation)

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