UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS

REGIONALIZACIÓN BIOGEOGRÁFICA MARINA CON BASE EN LA DISTRIBUCIÓN GLOBAL DE LAS FAMILIAS DE VETIGASTROPODA (MOLLUSCA: GASTROPODA)

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS
(SISTEMÁTICA)

PRESENTA:

M. EN C. LUIS GABRIEL AGUILAR ESTRADA

TUTOR PRINCIPAL DE TESIS: DR. JUAN JOSÉ MORRONE LUPI
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CIUDAD UNIVERSITARIA, CD. MX. MAYO, 2023

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UNAM POSGRADO

POSGRADO CIENCIAS BIOLÓGICAS

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
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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 de Posgrado en Ciencias Biológicas, celebrada el día **30 de enero de 2023** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **AGUILAR ESTRADA LUIS GABRIEL** con número de cuenta **304147638** con la tesis titulada: **"Regionalización biogeográfica marina con base en la distribución global de las familias de Vetigastropoda (Mollusca: Gastropoda)",** realizada bajo la dirección del **DR. JUAN JOSÉ MORRONE**

Presidente:	**DR. FERNANDO ÁLVAREZ NOGUERA**
Vocal:	**DR. PÍNDARO DÍAZ JAIMES**
Vocal:	**DRA. EDNA NARANJO GARCÍA**
Vocal:	**DRA. MARÍA MARTHA REGUERO REZA**
Secretario:	**DR. DAVID NAHUM ESPINOSA ORGANISTA**

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

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 24 de abril de 2023

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

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María de Lourdes y Juan Manuel Estrada

“No todo lo que parece es, no todo lo que es parece. Pero entre el ser y el parecer hay siempre un punto de entendimiento, como si ser y parecer fuesen dos planos inclinados que convergen y se unen. Hay un declive, la posibilidad de escurrir por él, y, si así sucede, se llega al punto en el que al mismo tiempo, se contacta con el ser y el parecer”

JS

“… existe el deber de ofrecer una respuesta a quien la espera día tras día, mes a mes, con impaciencia y hasta con desasosiego porque el libro entregado, ese manuscrito, es algo más que una montaña de letras, lleva un ser humano dentro, con su inteligencia y su sensibilidad”

PDR

“…Nadie dijo que sería fácil,
solo dijeron que sería divertido
y ahora ni divertido es”
IRB

Ad altiora et meliora semper

MDC

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RESUMEN

Se analizaron los patrones de distribución de 937 especies de moluscos (Mollusca: Vetigastropoda) de 251 géneros y 34 familias con base en las metodologías del análisis de trazos y la biogeografía cladística. Se obtuvieron cerca de 8,700 registros. Para el análisis panbiogeográfico se generaron 505 trazos individuales, 26 trazos generalizados y 5 nodos panbiogeográficos. Estos resultados son congruentes con lo encontrado en estudios similares con grupos como peces bruja, tiburones, poliquetos y crustáceos, lo que está relacionado con que dichos grupos de gasterópodos pertenecieron a biotas ancestrales que ahora se encuentran fragmentadas. Para el análisis biogeográfico cladístico se utilizó el Análisis de Parsimonia de Brooks llevado a cabo mediante la propuesta de Glasby (2006) con poliquetos. Se encontraron 40 cladogramas taxonómicos de áreas y se generó un único cladograma general de áreas que muestra una separación en dos grandes reinos Pantropical y Frío-Templado, del primero surgen dos regiones: Océano Indico Occidental e Pacífico Indo Occidental, del segundo reino surgen dos regiones: Magallánica-Antártica y Boreal. Los resultados obtenidos mediante el análisis de parsimonia de Brooks muestran congruencia con lo encontrado a través del método panbiogeográfico que se aplicó, así como con otros estudios que utilizan invertebrados marinos para proponer otras áreas de endemismo u otras propuestas de regionalización en el océano.

Palabras clave: Biogeografía, Biogeografía marina, Cladística, Inventario, Mapas de distribución, Moluscos marinos, Registros de ocurrencia, Panbiogeografía.

ABSTRACT

Distribution patterns of 937 species of molluscs (Mollusca: Vetigastropoda) of 251 genera and 34 families were analyzed based on the methodologies of track analysis and cladistic biogeography. About 8,700 records were obtained. For panbiogeographic analysis, 505 individual tracks, 26 generalized tracks and 5 panbiogeographic nodes were generated. These results are consistent with what was found in similar studies with groups such as witch fish, sharks, polychaetes and crustaceans, which is related to the fact that these groups of gastropods belonged to ancestral biotas that are now fragmented. For the cladistic biogeographic analysis, the Brooks parsimony analysis carried out through the proposal of Glasby (2006) with polychaetes was used. We found 40 taxonomic cladograms of areas and generated a single general cladogram of areas showing a separation in two large kingdoms Pantropical and Cold-Temperate, from the first two regions arise: Western Indian Ocean and Indo-West Pacific, of the second kingdom arise two regions: Magellanic-Antarctic and Boreal. The results obtained by Brooks parsimony analysis show congruence with what was found through the panbiogeographic method applied, as well as other studies using marine invertebrates to propose other endemic areas or other proposals for regionalization in the ocean.

Keywords: Biogeography, Cladistics, Inventory, Distribution maps, Marine biogeography, Marine molluscs, Occurrence records, Panbiogeography.

REGIONALIZACIÓN BIOGEOGRÁFICA MARINA CON BASE EN LA DISTRIBUCIÓN GLOBAL DE LAS FAMILIAS DE VETIGASTROPODA (MOLLUSCA: GASTROPODA)

I. INTRODUCCIÓN GENERAL

En la biología existen dos enfoques de estudio: la biología general y la biología comparada. Esta última estudia la diversidad biológica desde una perspectiva histórica (Nelson y Platnick, 1981), su objetivo de estudio es la reconstrucción de los patrones de semejanza que existen en la biodiversidad, tanto en la variedad de formas como en su distribución geográfica y temporal, y supone que a partir del análisis de ciertos caracteres es posible inferir las relaciones evolutivas entre las especies (Espinosa-Organista et al., 2002).

El estudio de la distribución de los seres vivos en el tiempo y espacio se denomina biogeografía (Morrone, 2009). Uno de sus objetivos principales es el describir y comprender los patrones de distribución geográfica de las especies o taxones supraespecíficos (Morrone, 2000). Además, puede analizar e interpretar dichos patrones bajo el supuesto de que los organismos tienen una historia común (Morrone, 2004).

Los estudios biogeográficos evolutivos tienen dos etapas distintas, la primera etapa es una conjetura sobre una historia común, lo que significa que diferentes taxones están integrados en el espacio y el tiempo (homología biogeográfica primaria), y la segunda se refiere a las pruebas cladísticas de la homología (homología biogeográfica secundaria) previamente propuestas como hipótesis (Morrone, 2004).

La panbiogeografía es un enfoque que enfatiza la dimensión espacial de la biodiversidad, hace posible comprender los patrones y procesos evolutivos (Craw et al., 1999). Postula una hipótesis de homología biogeográfica primaria, hace uso de la comparación de trazos individuales de diferentes taxones para detectar trazos generalizados, que posteriormente serán ordenados jerárquicamente en un sistema de clasificación biogeográfica (Morrone, 2013; Morrone y Escalante, 2016).

El Análisis de Parsimonia de endemismos que se conoce en inglés como Parsimony Analysis of Endemicity (PAE) se constituye de tres pasos esenciales: a) generación de trazos individuales, b) obtención de trazos generalizados y c) identificación de nodos panbiogeográficos (Morrone, 2014a). Los nodos panbiogeográficos representan áreas complejas, donde dos o más trazos generalizados se superponen, por lo que pueden interpretarse como zonas de convergencia tectónica y/o biótica (Morrone y Escalante, 2016).

Esta aproximación es útil en el ambiente marino, ya que puede ayudar a identificar la presencia de especies endémicas o reconocer a las especies ampliamente distribuidas, por lo que gracias a su aplicación se pueden obtener las afinidades geográficas de las especies. En este sentido, los nodos panbiogeográficos representan los límites filogenéticos y geográficos de los taxones de estudio (Heads, 1989). En el caso particular de los moluscos marinos, la mayoría de las especies y los datos disponibles están asociados al litoral (Keen, 1971; Abbott, 1974) y pocas de ellas se distribuyen en aguas profundas (Lee et al., 2019). Debido a que las áreas de distribución de estos organismos pueden ser muy diferentes, el uso de la panbiogeografía resulta ideal para poner asociar localidades de estudio distantes o donde no se tiene la información disponible y así poder reconocer los patrones de distribución de los moluscos marinos.

El PAE tiene diferentes aplicaciones, desde las ecológicas hasta la identificación de áreas de endemismo (Escalante, 2017). Una de sus aplicaciones más importantes considera los trazos generalizados, que son equivalentes a las áreas de endemismo en búsqueda de una hipótesis de homología biogeográfica, construye cladogramas basados en análisis de parsimonia de matrices de datos de presencia-ausencia de especies y taxones supraespecíficos (Morrone, 2014a), que permiten la identificación de componentes bióticos (Morrone, 2018).

A partir del cladograma más parsimonioso, es posible eliminar los taxones que soportan los clados y repetir el análisis hasta que no haya más sinapomorfías. Este procedimiento se conoce en inglés como Parsimony analysis of endemicity with progressive character elimination (PAE-PCE). Este método se puede utilizar para detectar la superposición de trazos generalizados y así encontrar nodos panbiogeográficos (Echeverry y Morrone 2010). El PAE identifica patrones de endemismo sucesivamente anidado para implementarse en regionalizaciones biogeográficas, así los cladogramas obtenidos pueden utilizarse en la elaboración de la jerarquía, distinguiendo en cada clado dichos niveles de jerarquización (Escalante, 2009; Escalante et al., 2017).

La biogeografía cladística elucida patrones históricos comunes de diferentes taxones, al utilizar datos filogenéticos y de distribución, asume una correspondencia entre los taxones y las áreas que habitan (Parenti y Ebach, 2009; Corral-Rosas y Morrone, 2017; López-García y Morrone, 2022). Este enfoque infiere relaciones al comparar los cladogramas con las áreas de distribución provenientes de diferentes hipótesis filogenéticas (Frota et al., 2020).

Su metodología considera los siguientes pasos: a) construir cladogramas de áreas a partir de los cladogramas taxonómicos de uno o varios taxones distintos, b) construir un cladograma resuelto de áreas para cada taxon a partir de los cladogramas de áreas y c) obtener un cladograma general de áreas a partir de la intersección de los cladogramas resueltos de áreas. Este último cladograma muestra una hipótesis de relación de las áreas bajo estudio (Morrone, 2000; Zunino y

Zullin, 2003). Estas metodologías (panbiogeografía y biogeografía cladística) en apariencia contradictorias, pueden ser compatibles y convertirse en fases de un mismo estudio biogeográfico. La panbiogegrafía evalúa el origen compuesto de las áreas y posteriormente y como resultado del análisis biogeográfico cladístico se puede reconocer la secuencia de fragmentación de las áreas (Morrone y Crisci, 1995; Morrone, 2001).

Una de las aplicaciones de estos dos enfoques de la biogeografía es poder analizar los patrones de distribución de los taxones, ya que son buenos indicadores de condiciones ambientales, con esta información, se pueden proponer distintos sistemas de clasificación de la superficie terrestre o marina; uno de ellos es la regionalización, que es un sistema, articulado en categorías y ordenado en forma jerárquica (Zunino y Zullini, 2003).

La regionalización en biogeografía es un sistema con jerarquías que categoriza áreas geográficas con respecto a su biota (Escalante, 2009). La jerarquía biogeográfica se presenta en términos de reinos, regiones, dominios, provincias y distritos, donde su unidad básica es la provincia (Morrone, 2014b), aunque también se pueden distinguir categorías intermedias como las subregiones o subdominios con base en las características compartidas (Escalante, 2009). Las unidades biogeográficas se basan en distintos taxones y comunidades endémicas, donde la representación de las regiones se lleva a cabo en mapas de áreas naturales o áreas de endemismo (Morrone, 2018).

Los esquemas de regionalización tradicionales han utilizado diferentes criterios y muchos de ellos están basados solo en la medición de las similitudes que exhiben (Escalante, 2009). Recientemente, los estudios enfocados a desarrollar esquemas de regionalización tienen como objetivo construir sistemas naturales de regionalización (Espinosa et al., 2001; Morrone et al., 2002). En términos de la biogeografía histórica, una región natural está relacionada con la detección de un origen común de las biotas u homología biogeográfica (Morrone, 2001, 2005).

Los moluscos son un grupo muy antiguo que se originó en el periodo Cámbrico hace 541 millones de años (Valentine et al., 1999; Cohen et al., 2013). A diferencia de muchos taxones, el phylum Mollusca es uno de los grupos animales más abundantes y diversos en el ambiente marino abarcando las zonas tropicales y templadas del mundo (Williams et al., 2008; Brusca et al., 2023). Sin embargo, en las zonas polares las especies de moluscos no se distribuyen uniformemente (Guzmán et al., 1998). La distribución de los moluscos en los océanos depende de varios factores, los fundamentales son: capacidad de dispersión, corrientes marinas, desarrollo larvario, profundidad, salinidad, temperatura, turbulencia (Díaz-Merlano y Puyana-Hegedus, 1994), interacciones ecológicas y cambios antropogénicos, los cuales tienen variaciones en el tiempo evolutivo (Ávila y Malaquias, 2003; Linse et al., 2006). Cada especie ocupa un área geográfica con condiciones particulares donde sobrevive, como la mayoría de los organismos marinos, los moluscos están restringidos por sus capacidades de osmorregulación y sus conjuntos enzimáticos, que son susceptibles a los cambios en los factores ambientales, mismos que modelan su distribución (Camus, 2001; Petuch, 2013). En ningún phylum esto ha sido demostrado mejor que con los moluscos (Linse et al., 2006) por lo que han servido por décadas como modelo para observar los patrones de diversidad en el bentos (Shantharam y Baco, 2020).

Se ha propuesto que los organismos marinos están más ampliamente distribuidos que las especies terrestres porque experimentan menos barreras físicas para su dispersión (Linse et al., 2006). Sin embargo, la disposición de los continentes y océanos representan barreras (Blum, 1989), que generan gradientes ambientales que se constituyen de conjuntos de especies propios (Briggs, 1995a; Longhurst, 1998).

II. ANTECEDENTES

La literatura malacológica para la subclase Vetigastropoda a nivel global es muy amplia, uno de los primero estudios que se pueden mencionar al respecto es el de Lebrun et al. (1856), sobre las conchas del emperador Hiroito y que han continuado hasta fechas recientes con el trabajo de Cunha et al. (2021) sobre los aspectos filogenómicos de 41 géneros dentro de esta subclase.

En general, los trabajos sobre la subclase Vetigastropoda se han enfocado a cuestiones de sistemática y taxonomía, la mayoría de ellos son listas de especies y estudios faunísticos que en algunos casos cuentan con datos geográficos de varias localidades a lo largo del mundo (Probert y Wilson, 1984; Guzmán et al., 1998; Dolorosa y Schoppe, 2008; Agudo-Padrón et al., 2009; Brown, 2011; Kang et al., 2013; Ávila-Poveda et al., 2014; Breves y Moraes, 2014; Ojeda et al., 2014; Barroso et al., 2016; Velásquez et al., 2016; Vicencio de la Cruz et al., 2017; Aldea et al., 2020), otros han abordado la propuesta de nuevos géneros o especies para la subclase (Kuroda y Habe, 1954; Kuroda y Kawamura, 1956; Geiger, 2006; Warrén y Bouchet, 2009; Petuch y Berschauer, 2017). También existen estudios con enfoques hacia aspectos ecológicos de miembros de la subclase Vetigastropoda (Aguilera, 2011; Flores-Garza et al., 2011; Aguilar-Estrada, 2017; Aguilar-Estrada et al., 2017), así como estudios sobre las características bioquímicas de este grupo de moluscos (Fujii et al., 2011; Martin et al., 2011), también los que tratan cuestiones que se relacionan con la obtención de cariotipos (Nishikawa, 1962; Wang et al., 1988) y otros trabajos sobre estudios moleculares que intentan resolver las relaciones de ancestría común al interior de la subclase (Geiger y Thacker, 2005; Williams et al., 2010; Kano et al., 2016; Cunha et al., 2019; 2021; Uribe et al., 2019; Dornellas et al., 2020).

Organismos marinos en estudios biogeográficos

Los estudios que toman en cuenta a los organismos marinos son escasos; en general, se han realizado trabajos con organismos marinos particularmente vertebrados, donde se puede mencionar los de peces arrecifales (Floeter et al., 2008; Kulbicki et al., 2013; Cowman et al., 2017; Siquiera et al., 2019) y mamíferos (Scheel et al., 2014; Holt et al., 2020; Liu et al., 2021).

Existen estudios biogeográficos que se han realizado en diferentes grupos de invertebrados bentónicos, como los crustáceos (Barnwell y Truman, 1984; Poupin, 2008; Pepato et al., 2019), corales (Reyes-Bonilla y Cruz-Piñón, 2000), esponjas (Vega et al., 2012), poliquetos (Reuscher y Shirley, 2014), equinodermos (Martínez-Melo et al., 2014; Caballero-Ochoa et al., 2017) e incluso en otros organismos marinos como las macroalgas (Hernández et al., 2017; 2021; Vilchis et al., 2018).

Los moluscos en estudios biogeográficos

Los estudios biogeográficos elaborados con moluscos son pocos, se puede mencionar el trabajo de Bertsch (2010), quien realizó una revisión comparativa con la presencia regional y provincial de heterobranquios entre las costas de Punta Concepción, California y Punta Aguja, Piura, Perú. También se cuenta con el estudio de Farfán-Beltrán (2016) con bivalvos, donde se aplicó un análisis de parsimonia de endemismos sobre las especies de bivalvos del golfo de México. Otros con moluscos gasterópodos como el de García-Cárdenas (2016) quien estudió la distribución geográfica de gasterópodos en Veracruz y el Atlántico occidental, obtuvo dos grupos de subprovincias zoogeográficas: el grupo 1 conformado por la subprovincia del golfo de México, Caroliniense y Brasileña; y el grupo 2 conformado por Antillas Mayores, Antillas Menores, Nica-Colombiana y Colombo-Venozolana. El estudio de García y Bertsch (2009), sobre la diversidad y distribución de opistobranquios del océano Atlántico realizado con más de 1,000 especies de este grupo donde se muestra una separación latitudinal y longitudinal de las áreas biogeográficas.

Ortigosa-Gutiérrez (2009) recopiló datos de la distribución geográfica de 533 especies de opistobranquios con el fin de ubicar geográficamente la costa de Yucatán en la Región del Atlántico Oeste Tropical, para ello, realizó un Análisis de Parsimonia de Endemismo, cuyos resultados coinciden con las regiones biogeográficas propuestas por los autores, como Ekman (1953), Briggs (1974, 1995b) y Salazar-Vallejo (2000). También se pueden mencionar los estudios de Gosliner y Draheim (1996) con diferentes especies de heterobranquios en la zona del Indo-Pacífico, así como el de Jensen (2007) con especies del orden Saccoglossa donde se asocia a los miembros de este grupo con las regiones biogeográficas a nivel global.

Por el contrario, los estudios para moluscos vetigastrópodos son escasos y la información con respecto a la distribución de la subclase en el planeta se encuentra dispersa. Sin embargo, se pueden mencionar los estudios como el de Geiger (1999) donde se presentan datos acerca de la distribución de 56 especies de abulones (Haliotidae), donde se proporcionó información para explicar el lugar de origen de esta familia en el mundo. Otro estudio es el de Cunha et al. (2019), en el que se integró la información de biología molecular, los datos geográficos y datos sobre fósiles para reconstruir la filogenia de 27 géneros pertenecientes a la familia Fissurellidae, con la finalidad de estimar las diferentes rutas de dispersión en el océano a nivel mundial.

Análisis de Parsimonia de Endemismos (PAE)

El PAE se aplicó originalmente utilizando localidades como unidades (Rosen, 1988; Rosen y Smith, 1988). Otros autores han implementado este método para evaluar las relaciones entre áreas de endemismo predeterminadas, celdas, cuencas hidrológicas e islas reales y virtuales (Morrone, 2014a). En el mundo el PAE se ha utilizado con distintos grupos de organismos la mayoría de los cuales son terrestres (Raxworthy y Nussbaum, 1996; Bisconti et al., 2001; García-Barros et al., 2002) como aves (Cardoso-Da Silva et al., 2004; Huang et al., 2010; Oliveira et al., 2017) mamíferos (Cardoso-Da Silva, 1996; Morrone y Escalante, 2002; Goldani et al., 2006) y plantas (Posadas et al., 1997; Luna-Vega et al., 2000; Trejo-Torres y Ackerman, 2001; Cavieres et al., 2002; Méndez-Larios et al., 2005).

Con respecto a los organismos marinos, el PAE se han implementado en los corales del género *Pacifigorgia* en el Pacífico americano (Vargas et al., 2008), camarones de la familia Pontonidae en el Indo-Pacifico (De Grave, 2001), isópodos en el Pacífico Oriental (Espinosa-Pérez et al., 2009), hidrozoarios del género *Oswaldella* en la Antártica (Marqués y Peña, 2010), cnidarios del océano Antártico (Miranda et al., 2013), anfípodos de las familias Caprellidae y Gammaridae en el suroeste del golfo de México (Winfield et al., 2006), así como con organismos que forman parte del zooplancton en humedales del Mediterráneo (Gilbert et al., 2014), otros con ascidias del Atlántico y Mediterráneo (Moreno et al., 2014). Los estudios que implementan el PAE han sido útiles para analizar los patrones de distribución de diversos grupos, en general este método ha resultado conveniente debido a que es sencillo de aplicar y se requieren de pocos datos (puntos de ocurrencia) para poder llevarse a cabo. Además, es comparable, ya que es la metodología más utilizada para reconocer áreas de endemismo o trazos generalizados (Morrone, 2015). Sin embargo, son escasos los estudios que hayan utilizado a los moluscos para hacer un análisis de parsimonia de endemismos.

Panbiogeografía

Los estudios panbiogeográficos se han aplicado en su mayoría a taxones terrestres y de agua dulce como crustáceos, peces y plantas (Huidobro et al., 2006; Herrera-Vázquez et al., 2008; Echeverry y Gallo, 2015; Cavalcanti et al., 2019); mientras que los trabajos con taxones marinos son mucho menos y se han llevado a cabo con distintos grupos como macroalgas, crustáceos, peces bruja, mamíferos, peces de arrecife, tiburones y gusanos planos (Aguilar-Aguilar y Contreras-Medina, 2001; Heads, 2005; Cavalcanti y Gallo, 2008; Celis-Villalba, 2009; Espinosa-Pérez et al., 2009; Gallo et al., 2010; Martínez-Castro, 2014). El uso de la panbiogeografía con especies de moluscos marinos podría representar una ventaja, ya que es un grupo muy antiguo, con un registro fósil que se remonta al Cámbrico (Valentine et al., 1999; Cohen et al., 2013). Son uno de los taxones más abundantes en los litorales a nivel mundial (Colman, 1940; Aguilera, 2011), habitan todo tipo de ambientes y tienen hábitos alimenticios variados. (Hickman et al., 2001).

Biogeografía cladística

Los estudios sobre biogeografía cladística se han implementado principalmente en organismos terrestres (López-García y Morrone, 2022) como plantas (Crisp et al., 1995; Contreras-Medina y Luna-Vega, 2002), vertebrados (Ron, 2000; Chakrabarty, 2004), insectos (Choi, 2000) y moluscos continentales (Craw, 2001). Los estudios sobre taxones marinos se han enfocado en organismos como las macroalgas (Cheshire et al., 1995), corales (Wallace et al., 1991; Pandolfi, 1992; Santini y Winterbottom, 2002), artrópodos (Watling y Thurston, 1989; Moller, 1991; De Grave, 2001), peces (Mooi y Gill, 2002; Parenti, 2008; Frota et al., 2020), esponjas (van Soest y Hajdu, 1997; Fernández et al., 2012), equinodermos (Ghiold y Hoffman, 1989), poliquetos (Glasby, 1999; Glasby y Alvarez, 1999; Garraffoni et al., 2006) y nemertinos (Härlin, 1996), por lo que sería interesante contrastar los análisis disponibles sobre otros grupos de invertebrados marinos, con la información resultado de esta investigación, ya que se trata de uno de los grupos más importantes a nivel ecológico y biogeográfico en los océanos del planeta.

Regionalización biogeográfica

Los estudios sobre regionalización que se han desarrollado establecen regionalizaciones biogeográficas en zonas terrestres (Morrone, 2015). Se pueden mencionar los estudios de Peters y Thackway (1998), quienes realizaron una propuesta de regionalización basada en 212 especies de vertebrados y plantas de Tasmania, donde se reconocen nueve regiones para ese sitio. Procheş (2005) quien estudió las especies de murciélagos a nivel mundial, el autor encontró diez regiones que se relacionan con regiones y subregiones faunísticas y florísticas aceptadas por otros autores. González-Orozco et al. (2013) realizaron un estudio con el género *Acacia* en Australia, donde se propusieron cinco grandes regiones biogeográficas para dicho género, estas biorregiones fueron muy similares a los biomas reconocidos en esa isla.

Los estudios sobre regionalización en el ambiente marino son escasos, ya que solo se pueden mencionar algunos trabajos en sitios específicos como los realizados con macroinvertebrados en Australia por Ahyong (2017) quien propuso cinco regiones distintas para este sitio: Damperiana, Gran Barrera de Coral, Solanderiana, Peroniana y Flindersiana; algunos con taxones en particular como el trabajo de Jirkov (2013) quien estudió 157 especies de poliquetos del mar de Barents, en el océano Ártico, el autor propuso para esta zona siete provincias biogeográficas distintas. Denisenko y Grebmeier (2015) realizaron un estudio con 204 especies de briozoarios, donde distinguieron cinco subregiones en el Mar de Chukotka en el Ártico.

Hattab et al. (2015) elaboraron un estudio de regionalización de la zona costera del Mediterráneo empleando 203 especies de peces costeros, en el que analizaron la información con análisis multivariados, gracias a los que observaron separaciones claras entre las regiones norte y sur, así como una disyunción entre las áreas costeras y oceánicas. Briggs y Bowen (2012) llevaron a cabo una propuesta de regionalización para los océanos a nivel global, las regiones proporcionadas en dicho trabajo han sido bien definidas y se han delimitado con la información disponible para especies de peces. Una de las regionalizaciones más importantes es la de Spalding et al. (2007), en la que se propusieron 12 reinos, 62 provincias y 232 ecorregiones marinas para la zona de la plataforma continental con organismos pelágicos y bentónicos. Sin embargo, los estudios con otro tipo de organismos como los invertebrados marinos son escasos, se pueden mencionar los realizados con anfípodos como el de Arfianti y Costello, (2020) quienes trabajaron con 4876 especies y reconocieron 12 regiones biogeográficas a nivel mundial. El estudio de van Soest y Hadju (1997) con esponjas, donde se reconocieron cinco grandes áreas a nivel global a partir de la información de más de 4000 especies de esponjas. Wallace et al. (1991) propusieron una regionalización biogeográfica con especies del género *Acropora* para la zona del Indo Pacífico. Glasby (2006) hizo una regionalización con base en 346 especies de poliquetos a nivel mundial donde se reconocieron 24 áreas con base en los endemismos de esas especies.

III. PLANTEAMIENTO DEL PROBLEMA

Existen pocos estudios sobre regionalización con invertebrados marinos, la mayoría de ellos se han llevado a cabo con especies de peces (Briggs y Bowen, 2012) o con datos sobre la biota bentónica y pelágica (Spalding et al., 2007). Tomando como base los estudios previos de Glasby (2006, poliquetos), así como los trabajos sobre la distribución geográfica de invertebrados marinos, surge la necesidad de ampliar la información hasta ahora obtenida y contrastar dichas propuestas de regionalización utilizando un taxón diferente como los moluscos, particularmente con la subclase Vetigastropoda la cual es un grupo con gran riqueza de especies, que se distribuye tanto en zonas costeras como en aguas profundas a lo largo de distintas latitudes en el planeta; dichas características lo convierten en un taxón interesante para llevar a cabo una regionalización a nivel global.

IV. JUSTIFICACIÓN

Existen estudios que permiten identificar a nivel global los patrones de distribución de las especies de invertebrados marinos; sin embargo, no existe una regionalización actual y detallada que se aplique a todo el planeta con base en moluscos marinos, por lo que resulta importante corroborar, modificar o hacer una nueva propuesta de regionalización a nivel global, ya que los moluscos son un grupo ampliamente distribuido en los océanos del planeta con gran importancia ecológica y tienen su distribución en hábitats diferentes a los de otros organismos como los peces con los que se han elaborado la mayoría de las regionalizaciones. Se propone tomar como punto de partida la información disponible sobre la distribución de las familias más diversas para la subclase Vetigastropoda (Calliostomatidae, Fissurellidae, Turbinidae y Trochidae) como indicador de los patrones de distribución de esta subclase de moluscos, con lo cual se podría asumir que una regionalización derivada de este estudio será un aporte importante al conocimiento de la biogeografía marina.

V. OBJETIVOS

General

Realizar una propuesta de regionalización biogeográfica global con base en los patrones de distribución de taxones de las familias de Vetigastropoda, e inferir las relaciones entre los taxones y las áreas que habitan mediante un análisis biogeográfico cladístico.

Particulares

- Analizar el estado actual del conocimiento sobre la distribución geográfica de Vetigastropoda a nivel global utilizando información proveniente de colecciones científicas, bases de datos y literatura especializada.
- Emplear el método de análisis de trazos para generar una regionalización sobre la distribución geográfica de las familias de Vetigastropoda.
- Realizar el análisis biogeográfico cladístico con base en las filogenias disponibles de Vetigastropoda e inferir las relaciones entre los taxones y las áreas que habitan.

Capítulo I

Geographical distribution of marine Vetigastropoda (Mollusca) of the world

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enviado a *Revista Mexicana de Biodiversidad*

Geographical distribution of marine Vetigastropoda (Mollusca:Gastropoda) of the world

Distribución geográfica de Vetigastropoda marinos (Mollusca:Gastropoda) del mundo

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Abstract

Vetigastropoda has around 4000 species that are distributed throughout the planet, which represent an important and ancient taxonomic group of marine gastropods. However, knowledge about their species richness and distribution on the planet is dispersed and has not been synthesized so far. The goals were to analyze the geographical distribution and to evaluate the knowledge of this subclass in the world. A database of 8700 records in literature and collections was revised. Distributions were analyzed with QGIS software. Species richness was estimated by marine regions in the world. Vetigastropoda have 937 species, Fissurellidae (204 spp.), Calliostomatidae (116 spp.), Haliotidae (65 spp.) are best representative. The genera that are widely distributed are *Anatoma* (Anatomidae), *Calliostoma* (Calliostomatidae), *Haliotis* (Haliotidae). The marine regions with the highest number of species are those situated in the Indo-Pacific Ocean.

Keywords: Biodiversity; Distributional area; Inventory; Marine biogeography; Molluscs; Points of occurrence.

Resumen

Vetigastropoda tiene alrededor de 4000 especies que se distribuyen por todo el planeta, que representan un importante y antiguo grupo taxonómico de gasterópodos marinos. Sin embargo, el conocimiento sobre la riqueza y distribución de sus especies en el planeta está disperso y no se ha sintetizado hasta ahora. Los objetivos fueron analizar la distribución geográfica y evaluar el conocimiento de esta subclase en el mundo. Se revisó una base de datos de 8700 registros en literatura y colecciones. Se analizaron distribuciones con software QGIS. La riqueza de especies fue estimada para las regiones marinas del mundo. Vetigastropoda tiene 937 especies, Fissurellidae (204 spp.), Calliostomatidae (116 spp.), Haliotidae (65 spp.) son las más representativas. Los géneros que están ampliamente distribuidos son *Anatoma* (Anatomidae), *Calliostoma* (Calliostomatidae), *Haliotis* (Haliotidae). Las regiones marinas con mayor número de especies son las situadas en el Océano Indopacífico.

Introduction

Among the less-studied taxa of molluscs, Vetigastropoda has around 38 families and 4000 living species and other extinct ones (Cunha et al. 2021). This clade evolved in the Cambrian/ Ordovician and was the most common gastropod group in the Palaeozoic (Fryda et al. 2008). Vetigastropoda (brushed snails) are marine organisms, are limpet-like, coiled or with a slit shell (Heller 2015). Inhabit from intertidal to the deep sea, including hydrothermal vents, cold seeps, skeletal remains of whales, even sunken wood (Ponder et al. 2019). They are distributed worldwide, almost at all latitudes, with wide geographical distribution (Aguilar-Estrada and Morrone 2022). Vetigastropoda were recognized as a natural group, but have been redefined several times ever since (Uribe et al. 2016). This clade includes five superfamilies, but recently other groups of uncertain phylogenetic position such as Lepetelloidea or Seguenzioidea were added to Vetigastropoda (Ponder et al. 2019).

Vetigastropoda (abalones, keyhole limpets and turban snails) are a large and morphologically diverse group of gastropods (Cunha et al. 2021). The species diversity of Vetigastropoda is higher in intertidal rocky shores and plays important roles in these zones (Miloslavich et al. 2013). Studies on Vetigastropoda have focused on: ecology (Alyakrinskaya 2010) physiology (Martin et al. 2011), genetics (Wang et al. 1988), molecular phylogeny (Uribe et al. 2019) and historical biogeography (Aguilar-Estrada and Morrone 2022).

The geographical distribution of Vetigastropoda at a global scale has been scarcely studied, so the literature for this subject is scattered. Systematic lists are available for several locations and faunistic studies, where some geographic data are presented (Dolorosa and Schoppe 2008, Velásquez et al. 2016). Only two studies exist on geographical distribution: Geiger (1999) on Haliotidae and Cunha et al. (2019) on Fissurellidae. Recently, Aguilar-Estrada and Morrone (2022) conducted a study on the distributional patterns of families of Vetigastropoda worldwide. The subclass Vetigastropoda can provide important information to know the origin and establishment of diversity of marine invertebrates in the world's oceans, due to the lack of works on geographic distribution of marine molluscs. Our objective was to evaluate the state of knowledge of the subclass Vetigastropoda at a global scale. Additionally, the presence of the species for each family on distributional maps is shown.

Materials and methods

Data gathering

We conducted a search and review of articles related to the richness, taxonomy, ecology and distribution of Vetigastropoda species, to obtain data on their geographical distribution, we also analyzed data from scientific collections (Table 1).

Database

A database of geographic and taxonomic data was made in spreadsheets. The data were refined and standardized, records that had no locality were searched in Google Earth for georeferencing. The nomenclatural update of Vetigastropoda species was made according to Bouchet et al. (2017) and WoRMS (Horton et al. 2023) to work with globally accepted species. Information collection is presented for vetigastropod species such as: family, habitat, records, species, genera and geographical distribution. The information collected for the families of Vetigastropoda was analyzed in QGIS 2.18 (QGIS Development Team, 2020). Distribution maps were developed for each family.

Results

We used 778 sources of information for families of Vetigastropoda. These references include articles, books, collections, and databases. The original database had about 25000 records, and most of them were deleted due to unconsciousness. The final analyzed database has 8700 unique records; each record is supported by scientific literature or information collections.

They were found: 937 species grouped in 251 genera and 34 families. We generated 29 family distribution maps for Vetigastropoda from this study. The families with the most species are Fissurellidae (204), Calliostomatidae (116) and Haliotidae (65). Fissurellidae (1924), Haliotidae (1140), Turbinidae (1179) are the families with the most records. The genera that include widely distributed species are *Anatoma*, *Calliostoma*, *Haliotis*, and *Pyropelta*. Most of the families were found in coastal areas and to a lesser extent in deep areas (Phasianellidae, Collonidae and Seguenziidae). The families in this study live on different substrates, most are on rocky shore, soft bottoms substrates and corals. Some can be found in shark eggs, whale skeletons, vegetation, or submerged wood. For the vertical distribution, 30% of the families are located in shallow zones (intertidal to subtidal) and Cataegidae, Chilodontaidae, Colloniidae, Eucyclidae and Larochaeidae are in depths greater than 3000 m (hydrothermal vents or methane infiltrations).

The distribution data for the Vetigastropoda families of this work are presented below as North-East Pacific (NEP), Central-East Pacific (CEP), South-East Pacific (SEP), North-West Atlantic (NWA), Central-West Atlantic (CWA), South-West Atlantic (SWA), Mediterranean and Black Sea (MBS), North-East Atlantic (NEA), Central-East Atlantic (CEA), West Indian Ocean (WIO), East Indian Ocean (EIO), North-West Pacific (NWP), Central-West Pacific (CWP), Antarctic Atlantic (ANA).

Fissurellidae (Fig. 1)

Habitat: On rocky from 0-1000 m.

Records: 1924

Genera: 36

Species: 204

Distribution: NEP, CEP, SEP, NWA, CWA, SWA, MBS, NEA, CEA, WIO, EIO, NWP, CWP (Abubakr, 2004; Agudo-Padrón, 2015; Agudo-Padrón et al., 2009; Aguilar-Estrada et al., 2017; Al-Khayat, 1997; Bartsch, 1915; Benkendorfer and Soares-Gomes, 2009; Boyle et al., 2016; Cavallari et al., 2016; Demir, 2003; El-Sorogy et al., 2016; Fernández et al., 2014; Grove, 2008; Grove and de Little 2014; Habe, 1978; Harasewych et al., 1997; Herbert, 2015; Hoenselaar and Dekker, 1998; Hylleberg and Kilburn, 2003; Keen, 1971; Kershaw, 1955; Kilburn, 1972; Mohanraj et al., 2011; Nakano and Sellanes, 2011; Olivares-Paz et al., 2011; Sanpanich and Duangdee, 2013; Siqueira-Dornellas and Simone, 2011; Silva-Absalao, 1989; Souza and Matthews-Cascon, 2019; Velásquez et al., 2016; Wells et al., 2001; Yamamoto and Handa, 2011).

Haliotidae (Fig. 2)

Habitat: Rocky intertidal zone to subtidal.

Records: 1140

Genera: 1

Species: 65

Distribution: NEP, CEP, SEP, CWA, SWA, MBS, NEA, CEA, WIO, EIO, NWP, CWP, SWP (Abubakr, 2004; Bartsch, 1915; Demir, 2003; Hylleberg and Kilburn, 2003; Kershaw, 1955; Kilburn, 1972; Grove, 2008; Grove and de Little, 2014; Herbert, 2015; Rogers-Bennett et al., 2016; Sanpanich and Duangdee, 2013; Seamone and Boulding, 2011; Singhakaew, 2003; Wells et al., 2001).

Addisonidae (Fig. 3)

Habitat: Deep areas on shark eggs.

Records: 9

Genera: 1

Species: 3

Distribution: CEP, SWA, NEA, MBS (Barbosa-Lima et al., 2016, Siqueira-Dornellas and Simone, 2011).

Lepetellidae (Fig. 4)

Habitat: Deep-water on coral or tubes of polychaetes.

Records: 5

Genera: 2

Species: 4

Distribution: SEA, EIO (Herbert, 2015, Kershaw, 1955, Prashard and Rao, 1934).

Pseudococculinidae (Fig. 5)

Habitat: Submerged wood.

Records: 6

Genera: 5

Species: 5

Distribution: NEP, CEP, CWP, SWA, SEA (Siqueira-Dornellas and Simone 2011; Warén and Bouchet 2009).

Pyropeltidae (Fig. 6)

Habitat: Deep waters in hydrothermal vents or on whale bones.

Records: 50

Genera: 1

Species: 6

Distribution: NEP, CEP, CWP, CEA (Warén and Bouchet, 2009).

Lepetodrilidae (Fig. 7)

Habitat: Deep waters in hydrothermal vents.

Records: 195

Genera: 4

Species: 14

Distribution: NEP, CEP, CWP, CEA (Warén and Bouchet, 2009).

Sutilizonidae (Fig. 8)

Habitat: In deep waters associated with hydrothermal vents.

Records: 4

Genera: 1

Species: 1

Distribution: NEP (Geiger 2019).

Anatomidae (Fig. 9)

Habitat: Sandy bottoms (200-1000 m).

Records: 272

Genera: 1

Species: 44

Distribution. NEP, CEP, SEP, CWA, SWA, MBS, NEA, CEA, WIO, EIO, NWP, CWP, SWP (Benkendorfer and Soares-Gomes, 2009; Demir, 2003; Grove and de Little, 2014; Herbert, 2015; Keen, 1971; Kershaw, 1955; Oliveria et al., 2018; Silva-Absalao, 1989).

Larochaeidae (Fig. 10)

Habitat: Deep waters in hydrothermal vents.

Records: 14

Genera: 2

Species: 4

Distribution: CEP, CWP, EIO (Geiger, 2008).

Scissurellidae (Fig. 11)

Habitat: Intertidal zone, sandy bottoms (10-20 m).

Records: 666

Genera: 5

Species: 54

Distribution: NEP, CEP, SEP, NWA, CWA, SWA, MBS, NEA, CEA, WIO, EIO, NWP, CWP, SWP, ANA (Abubakr, 2004; Bartsch, 1915; Benkendorfer and Soares-Gomes 2009; Demir, 2003; Grove 2008; Grove and de Little, 2014; Hardy, 1915; Herbert, 2015; Keen 1971; Kershaw, 1955; Siqueira-Dornellas and Simone, 2011).

Pleurotomariidae (Fig. 12)

Habitat: On rocks or reef areas.

Records: 133

Genera: 4

Species: 23

Distribution: CEP, CWA, SWA, SEA, EIO, CWP, NWP (Agudo-Padrón et al., 2009; Carvalho-Rios and Ramos-Matthews, 1968, Goodfriend et al., 1995; Grace et al., 2000; Harasewych et al., 1997; Healy and Harasewych, 1992; Herbert, 2015; Hylleberg and Kilburn, 2003; Okutani and Goto 1983, 1985; Petuch and Berschauer, 2017; Siqueira-Dornellas and Simone, 2011).

Cataegidae (Fig. 13)

Habitat: Common in deep-water methane infiltration zones.

Records: 19

Genera: 2

Species: 4

Distribution: CEP, CWA (Amon et al., 2017).

Chilodontaidae (Fig. 14)

Habitat: From 0-2000 m.

Records: 158

Genera: 7

Species: 40

Distribution: CEP, SEP, CWA, SWA, MBS, SEA, WIO, EIO, NWP, CWP (Abubakr, 2004; Al-Naser et al., 2010; Al- Khayat, 1997; Bartsch, 1915; Benkendorfer and Soares-Gomes, 2009; El-Sorogy et al., 2016; Grove, 2008; Grove and de Little, 2014; Habe and Kosuge, 1970; Hoenselaar and Dekker, 1998; Keen, 1971; Kershaw, 1955; Kilburn, 1972, 1977; Hylleberg and Kilburn, 2003; Mohanraj et al., 2011; Moonlenbeek and Faber, 1989; Ramses, 2014; Sanpanich and Duangdee, 2013; Silva-Absalao, 1989, 2009; Wells et al., 2001).

Eucyclidae (Fig. 15)

Habitat: Mud bottoms (500 to 1100 m).

Records: 95

Genera: 7

Species: 17

Distribution: NEP, CEP, SEP, MBS, CEA, WIO, NWP, CWP (Abubakr, 2004; Keen, 1971; Nakano and Sellanes, 2011; Veliz and Vasquez, 2000; Warén and Bouchet 2009).

Seguenziidae (Fig. 16)

Habitat: In sediments (200-1000 m).

Records: 170

Genera: 17

Species: 38

Distribution: CEP, CWA, SWA, NEA, SEA, WIO, EIO, CWP, SWP Kershaw 1955, Kilburn 1977, Grove 2008, (Agudo-Padrón et al., 2009; Benkendorfer and Soares-Gomes, 2009; Cavallari et al., 2016; Grove and de Little, 2014; Hardy, 1915; Lima et al., 2013, 2014; Oliveria et al., 2018; Salvador et al., 2014; Silva-Absalao, 1989; Siqueira-Dornellas and Simone, 2011).

Angariidae (Fig. 17)

Habitat: Intertidal to subtidal on rocky or algae near coral reefs.

Records: 170

Genera: 17

Species: 38

Distribution: WIO, EIO, NWP, CWP (Cavallari et al., 2016; Hylleberg and Kilburn, 2003; Sanpanich and Duangdee, 2013; Wells et al., 2001).

Areneidae (Fig. 18)

Habitat: Coral bottoms (50-120 m).

Records: 93

Genera: 2

Species: 28

Distribution: CEP, CWA, SWA, SEA, EIO (Agudo-Padrón, 2015; Bartsch, 1915, Benkendorfer and Soares-Gomes 2009, Siqueira-Dornellas and Simone 2011).

Calliostomatidae (Fig. 19)

Habitat: Soft bottoms, rocky, coralline algae (0-3000 m).

Records: 601

Genera: 13

Species: 116

Distribution: NEP, CEP, SEP, CWA, SWA, MBS, NEA, CEA, WIO, EIO, NWP, CWP, SWP, ANA (Abubakr, 2004; Agudo-Padrón et al., 2009; Azuma, 1975; Bartsch, 1915; Benkendorfer and Soares-Gomes, 2009; Cavallari et al., 2016; Demir, 2003; Grace et al., 2000; Grove, 2008; Grove and de Little, 2014; Habe and Kosuge, 1970; Hardy 1915; Keen, 1971; Kershaw, 1955; Kilburn, 1972; Kosuge and Oh-Ishi, 1970; Hylleberg and Kilburn, 2003; Okutani 1969; Sanpanich and Duangdee, 2013; Silva-Absalao, 1989; Siqueira-Dornellas and Simone 2011; Veliz and Vasquez, 2000; Wells et al. 2001).

Colloniidae (Fig. 20)

Habitat: Coral bottoms (60-1000 m).

Records: 114

Genera: 7

Species: 32

Distribution: NEP, CEP, NWA, SWA, MBS, SEA, EIO, WIO, NWP, CWP, SWP (Abubakr, 2004; Bartsch, 1915; Demir, 2003; Grove and de Little, 2014; Hylleberg and Kilburn, 2003; Kershaw 1955; Siqueira-Dornellas and Simone, 2011).

Conradiidae (Fig. 21)

Habitat: Rocks in subtidal areas.

Records: 9

Genera: 1

Species: 7

Distribution: CWP, SEP, EIO (Hardy, 1915; Kershaw, 1955).

Liotiidae (Fig. 22)

Habitat: Coral bottoms (0-260 m).

Records: 70

Genera: 12

Species: 28

Distribution: CEP, SEP, CWA, SWA, NEA, CEA, WIO, EIO, CWP (Abubakr 2004; Hylleberg and Kilburn, 2003; Grove and de Little, 2014; Kershaw 1955; Oliveria et al. 2018; Sakurai and Habe, 1977; Silva-Absalao, 1989; Wells et al., 2001).

Margaritidae (Fig. 23)

Habitat: Subtidal to deep sea (60-1200 m).

Records: 156

Genera: 4

Species: 20

Distribution: NEP, CEP, CWA, SWA, WIO, EIO, NWP, CWP, SWP (Agudo-Padrón, 2015; Nakano and Sellanes, 2011; Silva-Absalao, 1989; Simone and Cunha, 2006; Siqueira-Dornellas and Simone 2011).

Phasianellidae (Fig. 24)

Habitat: Soft bottoms with vegetation.

Records: 220

Genera: 5

Species: 20

Distribution: CEP, SEP, CWA, SWA, MBS, SEA, WIO, EIO, NWP, CWP (Abubakr, 2004; Agudo-Padrón et al., 2009; Bartsch, 1915; Benkendorfer and Soares-Gomes, 2009; Demir, 2003; Grove, 2008; Grove and de Little, 2014; Hardy 1915, Kershaw 1955, Silva-Absalao, 1989; Souza and Matthews-Cascon, 2019; Wells et al., 2001).

Skeneidae (Fig. 25)

Habitat: Deep areas in hydrothermal vents.

Records: 64

Genera: 5

Species: 28

Distribution: NEP, CEP, SWA, SEA, WIO, EIO, NWP, CWP (Ando and Habe, 1980; Bartsch 1915; Benkendorfer and Soares-Gomes, 2009; Grove, 2008; Grove and de Little, 2014; Habe, 1961; Kershaw 1955; Kilburn, 1977; Silva-Absalao 1989).

Solariellidae (Fig. 26)

Habitat: Soft sediments (200 to 1000 m).

Records: 45

Genera: 6

Species: 16

Distribution: NEP, CEP, SEP, NWA, SWA, SEA, EIO (Agudo-Padrón et al., 2009; Bartsch 1915; Benkendorfer and Soares-Gomes, 2009; Cavallari et al., 2016; Keen, 1971; Kershaw, 1955; Kilburn, 1977; Nakano and Sellanes, 2011; Schwabe et al., 2017; Siqueira-Dornellas and Simone, 2011).

Tegulidae (Fig. 27)

Habitat: Rocky and vegetation (0-20 m).

Records: 503

Genera: 8

Species: 41

Distribution: CEP, SEP, NWA, CWA, SWA, NEA, MBS, WIO, EIO, CWP (Abubakr, 2004; Agudo-Padrón et al., 2009; Fernández et al., 2014; Grace et al., 2000; Hylleberg and Kilburn, 2003; Prashard and Rao, 1934; Robertson, 2003; Sanpanich and Duangdee, 2013; Souza and Matthews-Cascon, 2019; Velásquez et al., 2016; Veliz and Vasquez, 2000; Wells et al., 2001; Yamamoto and Handa, 2011).

Trochidae (Fig. 28)

Habitat: From 0-3000 m.

Records: 706

Genera: 57

Species: 52

Distribution: CEP, SEP, SWA, MBS, CEA, WIO, EIO, NW, CWP (Abubakr, 2004; Agudo-Padrón et al., 2009; Al-Khayat, 1997; Bartsch, 1915; Benkendorfer and Soares-Gomes, 2009;

Colgan and Schreiter, 2011; Demir, 2003; El- Sanpanich and Duangdee, 2013; Grove, 2008; Grove and de Little, 2014; Habe, 1978; Hardy, 1915; Hoenselaar and Dekker, 1998; Hylleberg and Kilburn 2003, Kershaw 1955; Kilburn, 1972, 1977; Mohanraj et al., 2011; Siqueira-Dornellas and Simone, 2011; Sorogy et al., 2016; Veliz and Vasquez, 2000, Wells et al., 2001; Yamamoto and Handa, 2011).

Turbinidae (Fig. 29)

Habitat: Rocks, sand or mud in intertidal to subtidal zones

Records: 1179

Genera: 14

Species: 61

Distribution: NEP, CEP, SEP, NWA, CWA, SWA, MBS, NEA, CEA, WIO, EIO, NWP, CWP, SWP (Abubakr, 2004; Agudo-Padrón, 2015; Agudo-Padrón et al., 2009; Bartsch, 1915; Benkendorfer and Soares-Gomes, 2009; Cavallari et al., 2016; Demir, 2003; El-Sorogy et al., 2016; Fernández et al., 2014; Grove, 2008; Grove and de Little, 2014; Habe and Kosuge, 1970; Harasewych et al., 1997; Hayakawa et al., 2010; Hylleberg and Kilburn, 2003; Kershaw, 1955; Kilburn, 1972; Mohanraj et al., 2011; Sanpanich and Duangdee 2013; Souza and Matthews-Cascon, 2019; Tsuchida, 1978; Velásquez et al., 2016; Wells et al., 2001; Yamamoto and Handa, 2011).

Discussion

This work is a first attempt to compile the information available for the world of Vetigastropoda. The registered species represents approximately 20% of the 4000 recognized species of this group (Cunha et al., 2021). There is no work similar to this with marine molluscs to date, with the exception of Geiger (1999) with Haliotidae with 56 species, and that of Cunha et al. (2019) for Fissurellidae. The latter, however, does not have information for some subfamilies in the CEP, SEA and CWA where there are records for Fissurellidae and other families of the subclass.

It was found that 80% of the families are distributed on both margins of the Pacific Ocean (e. g. Western and Eastern). Santini and Winterbottom (2002), analyzing mollusk species, provide explanations for the geological events that led this group to expand into the Western Indo-Pacific. This region presents oceanographic barriers that limit the dispersal of species to other regions of the planet (Blum, 1989). In vetigastropod molluscs a wider distribution is presented, which is not restricted latitudinally, since many of the groups of this subclass occur in temperate and tropical zones. Unlike of those observed with fish in the Eastern Tropical Pacific, where temperature gradients represent barriers to the south and north (Robertson and Cramer, 2009). While the Eastern Pacific presents few oceanographic barriers, for this reason, vetigastropods could end up dispersing by different means to other, even distant, locations (Scheltema, 1971), these unexpectedly wide geographic distributions are the result of alternative dispersal mechanisms (Johnson et al., 2001) as: long duration of telepanic larvae (and hence larval drift), highly survival, “rafting” and “diving board” colonization. These larvae have a long-term development and serve as a means of dispersal over long distances, floating for up to four months and thus colonizing new environments (Scheltema, 1971), e. g. *Rochia nilotica* (Linnaeus, 1767) whose distribution range goes from Papua to New Caledonia thanks to this type of larva (Lemouellic and Chauvet, 2008). It has been proposed that planktotrophic larval development favors rapid dispersal and a wide geographic distribution due to the high capacity of the larvae to disperse by ocean currents to remote locations (Shuto, 1974), e. g. *Diodora* *cayenensis* (Lamarck, 1822) and *Lucapinella limatula* (Reeve 1850) have managed to spread from the Canary Islands to the Atlantic off the American coasts (Vermeij and Rosenberg, 1993).

The two previous contributions are notable efforts to understand initially the distribution patterns of the Vetigastropoda subclass; compared to 56 species and 27 genera from this studies the analysis of the richness and distribution of Vetigastopoda carried out in this work has provided information for almost a quarter of the total species recognized for this group of molluscs (Cunha et al., 2021). It should be noted that there are important areas that can function as centers of biodiversity, especially the Indo-West Pacific; this has been studied in fish and echinoderms (Carpenter and Springer, 2007, Saulsbury and Baumiller, 2022). Given the importance of mollusks in marine environments, their study should be undertaken, since the existence of other organisms in marine communities depends on them, since they are considered ecosystem engineers (Gutiérrez et al., 2003). Therefore, there is a need for an inventory of mollusc species in scenarios of biodiversity loss due to human activities (Sahidin et al., 2019).

The characteristics of the environment are a fundamental factor that determines the geographical distribution; abiotic factors are better known than biotic ones to explain the distribution patterns of molluscs (Vermeij, 1972). The habitats recorded for the Vetigastropoda families in this study can be explained by the environmental requirements that the species have in each of them (Díaz et al., 2015).

The abiotic characteristics of the environment are the fundamental factor that determines the geographic distribution; however, little is known about the influence of biotic factors on the distribution patterns of molluscs (Vermeij, 1972). The presence of the different habitats recorded for the families of Vetigastropoda in this study are mainly due to the environmental requirements that each of them has (Degnan et al., 2006; Díaz et al., 2015; Salas et al., 2014).

In general, the most common habitats where Vetigastropoda can be found are rocks, sand, and coral reefs (Lee et al., 2019). These substrates constitute the environments most affected by anthropic activities (He et al., 2019), which prevent the formation of complex marine communities such as coral reefs or the communities of macroalgae to which they are associated on the coasts (Kelaher et al., 2022). The loss of these places would have important effects on the number of species of this subclass worldwide, so a global inventory is still necessary.

There is few information on the biotic interactions that may have an effect on the geographic distribution of marine molluscs; however, latitudinal changes of *Tegula funebralis* (A. Adams, 1855) have been observed as a defensive mechanism against its predators (octopuses) that have caused this snail to move south off the coast of California (Fawcett, 1984). It has been proposed that the latitudinal gradients observed in marine invertebrates are correlated with the geographic distribution of coral reefs. The distribution limits of coral reefs have served to delimit the latitudinal intervals of bivalves and gastropods (Rex et al., 2005). Associations with coralline algae and abalone, e. g. *Haliotis laevigata* Donovan, 1808 and *H. iris* Gmelin, 1791 larvae are restricted to places with said algae as substrate, this alga-mollusc interaction could restrict the dispersal of these vetigastropods in different places (Shepherd and Turner, 1985).

Environmental features are not the same along a depth gradient. In general, the wider the vertical distribution of a species, the wider its geographic distribution (Benkendorfer and Soares, 2009). In gastropods, species that inhabit shallow waters have wider latitudinal distribution intervals, and occupy more biogeographic provinces, than species from deeper. Species that are tolerant of changes in depth throughout the water column have wider geographic ranges than species restricted to shallower areas (Harley et al., 2003). In this way, the presence of a species in a certain site is given by the availability of the habitat, which in turn is defined by environmental conditions, adaptations, physiology and interactions (Guzmán et al., 1998).

Other important factors related to the distribution of the species in shallow waters (oceanic circulation, tectonism and upwelling) could explain a greater diversification in littoral to subtidal habitats (Williams et al., 2013). Few families of Vetigastropoda inhabit deep areas (Lee et al., 2019); in general, it has been suggested that food availability may have been a limiting factor for the exploitation of these habitats (Williams et al., 2013). Other factors such as volcanic rocks, hot fluids (rich in metals), methane filtrations, can determine the colonization of different groups of invertebrates, including mollusks, which are adapted to deep water conditions, so these conditions have influenced the vertical distribution of Vetigastropoda families (Kiel, 2016).

The present study compiles the information so far available for the subclass Vetigastropoda with about 20% of the species recognized for this taxon. Future studies could gather additional information for other species, with data from other biological collections, field sampling or even database implementation, with which valuable and interesting information could be obtained for a more robust analysis leading to the recognition of current distribution areas.

This work tries to promote research on marine biogeography, a subject little studied with marine invertebrates. Inventory studies and collection of distributional data are the basis for undertake biogeographic studies, since the information collected can help us to know the distribution areas of the species or places where field work is needed. These studies can generate vital information to generate assessments on the state of conservation of priority areas for biological knowledge, because in some cases these types of areas suffer different effects from anthropic activities. The information available, it will be possible to create programs for conservation and management plans that contribute to the maintenance of natural resources globally in the face of climate change scenarios.

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Tables

Table 1. Collections consulted in the present study.

Collections	**Acronyms**
Colección Nacional de Moluscos, Instituto de Biología, UNAM, Mexico City	CNMO
Colección Malacológica Dr. Antonio García-Cubas, Instituto de Ciencias del Mar y Limnología, UNAM, Mexico City	COMA
Colección Regional de Invertebrados Marinos, Instituto de Ciencias del Mar y Limnología, UNAM, Mexico City	CRIM
The Academy of Natural Sciences of Drexel University, Philadelphia	ANSP
Invertebrate Zoology Collection, California Academy of Sciences, San Francisco	CAS
Mollusk Collection, Field Museum of Natural History, Chicago	FMNH
Malacology Collection, Museum of Comparative Zoology, Harvard University, Cambridge	MCZ
Invertebrate Zoology, Santa Barbara Museum of Natural History, Santa Barbara	SBMNH
Benthic Invertebrate Collection, Scripps Institution of Oceanography University of California, San Diego	BIC

Figure captions

Figure 1. Geographic distribution of Fissurellidae.

Figure 2. Geographic distribution of Haliotidae.

Figure 3. Geographic distribution of Addisonidae.

Figure 4. Geographic distribution of Lepetellidae.

Figure 5. Geographic distribution of Pseudococculinidae.

Figure 6. Geographic distribution of Pyropeltidae.

Figure 7. Geographic distribution of Lepetodrilidae.

Figure 8. Geographic distribution of Sutilizonidae.

Figure 9. Geographic distribution of Anatomidae.

Figure 10. Geographic distribution of Larochaeidae.

Figure 11. Geographic distribution of Scissurelidae.

Figure 12. Geographic distribution of Pleurotomariidae.

Figure 13. Geographic distribution of Cataegidae.

Figure 14. Geographic distribution of Chilodontaidae.

Figure 15. Geographic distribution of Eucyclidae.

Figure 16. Geographic distribution of Seguenziidae.

Figure 17. Geographic distribution of Angariidae.

Figure 18. Geographic distribution of Areneidae.

Figure 19. Geographic distribution of Calliostomatidae.

Figure 20. Geographic distribution of Colloniidae.

Figure 21. Geographic distribution of Conradiidae.

Figure 22. Geographic distribution of Liotiidae.

Figure 23. Geographic distribution of Margaritidae.

Figure 24. Geographic distribution of Phasianellidae.

Figure 25. Geographic distribution of Skeneidae.

Figure 26 Geographic distribution of Solariellidae.

Figure 27. Geographic distribution of Tegulidae.

Figure 28. Geographic distribution of Trochidae.

Figure 29. Geographic distribution of Turbinidae.

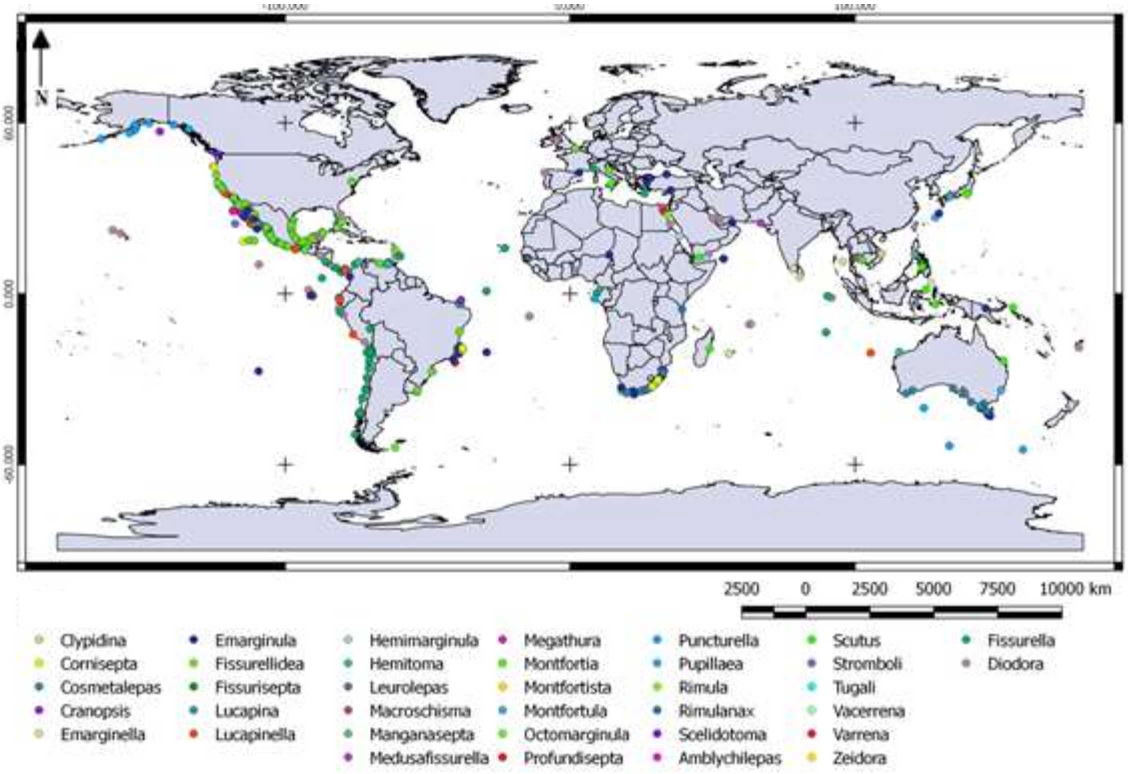

Figure 1. Geographic distribution of Fissurellidae.

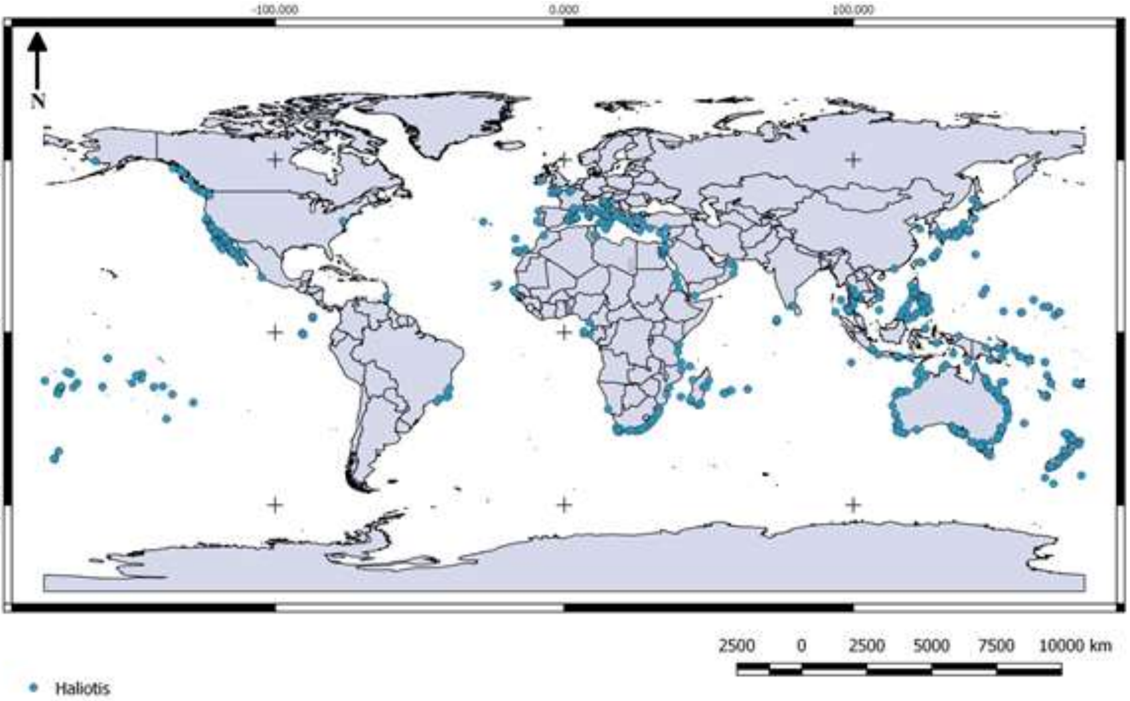

Figure 2. Geographic distribution of Haliotidae.

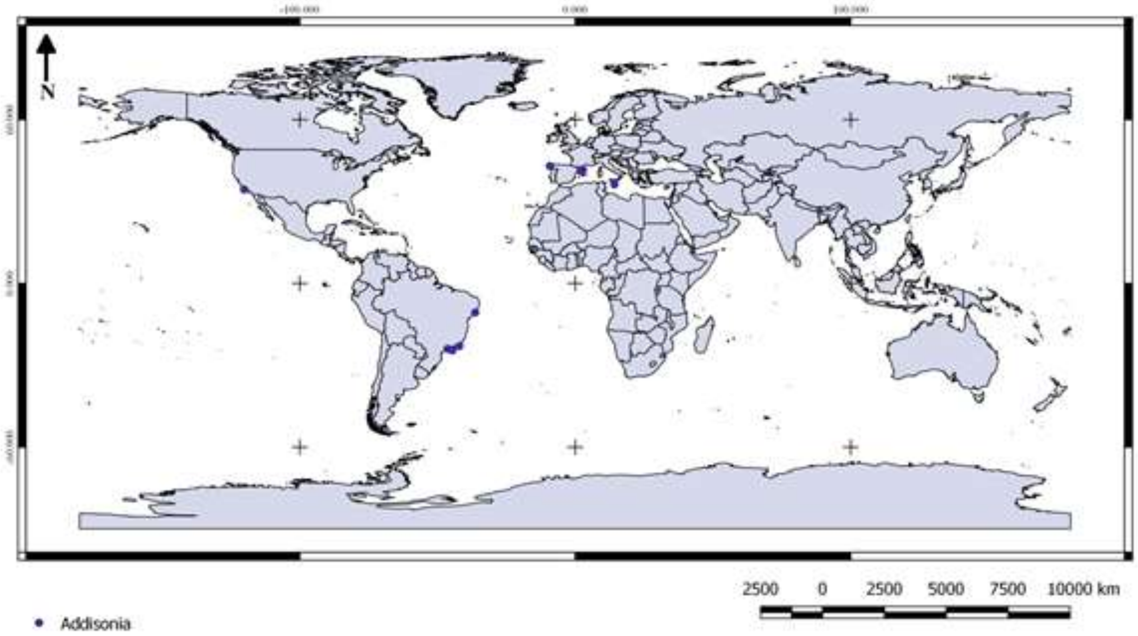

Figure 3. Geographic distribution of Addisonidae.

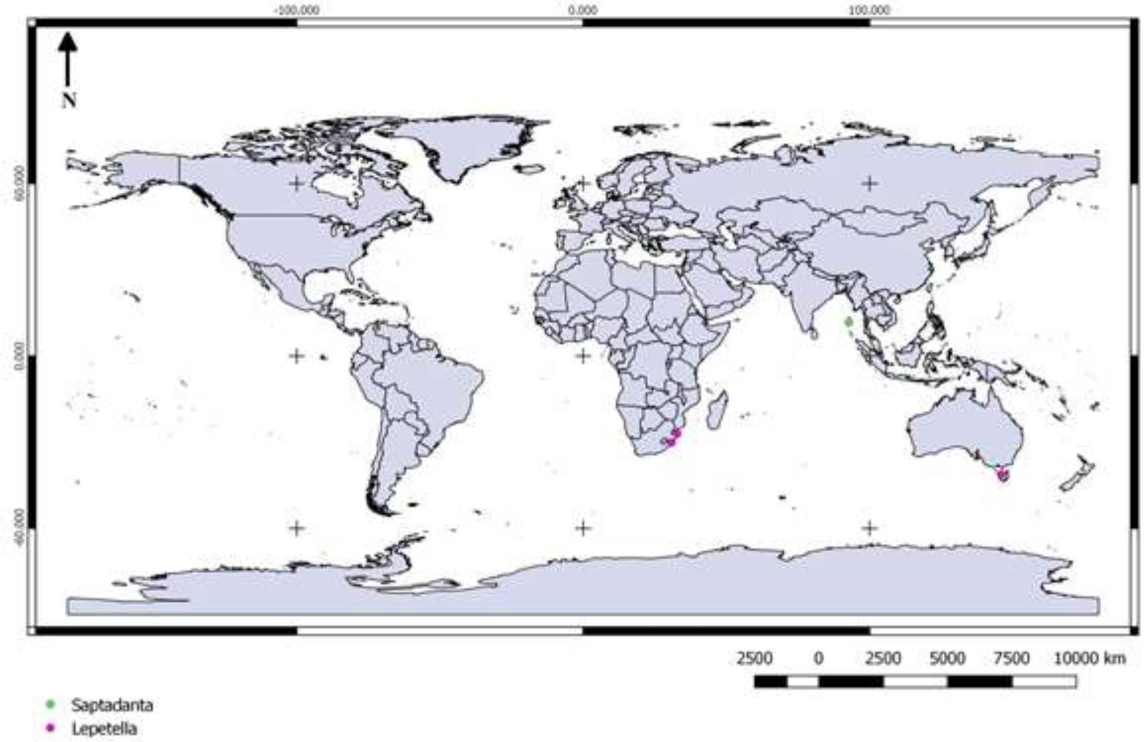

Figure 4. Geographic distribution of Lepetellidae.

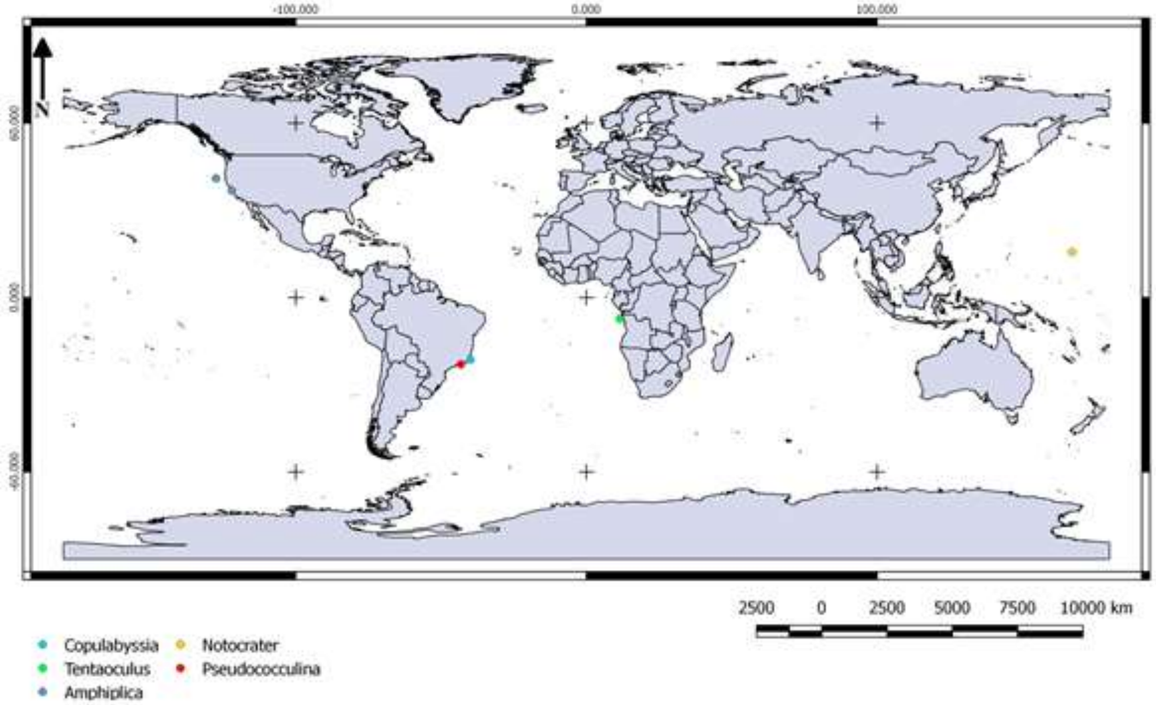

Figure 5. Geographic distribution of Pseudococculinidae.

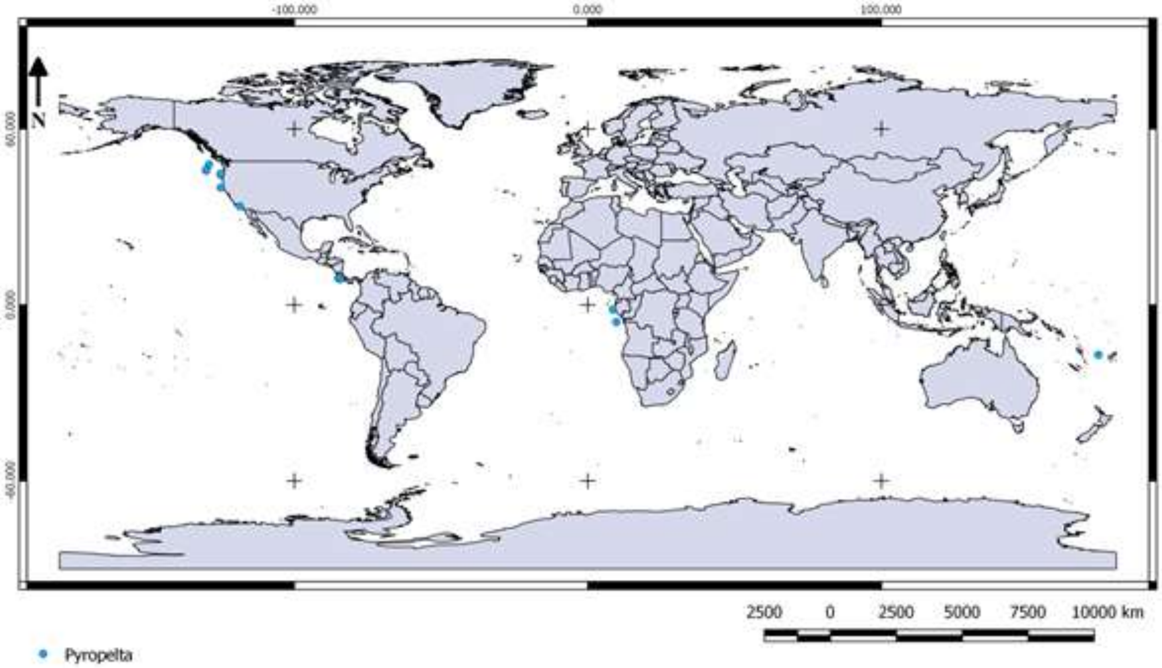

Figure 6. Geographic distribution of Pyropeltidae.

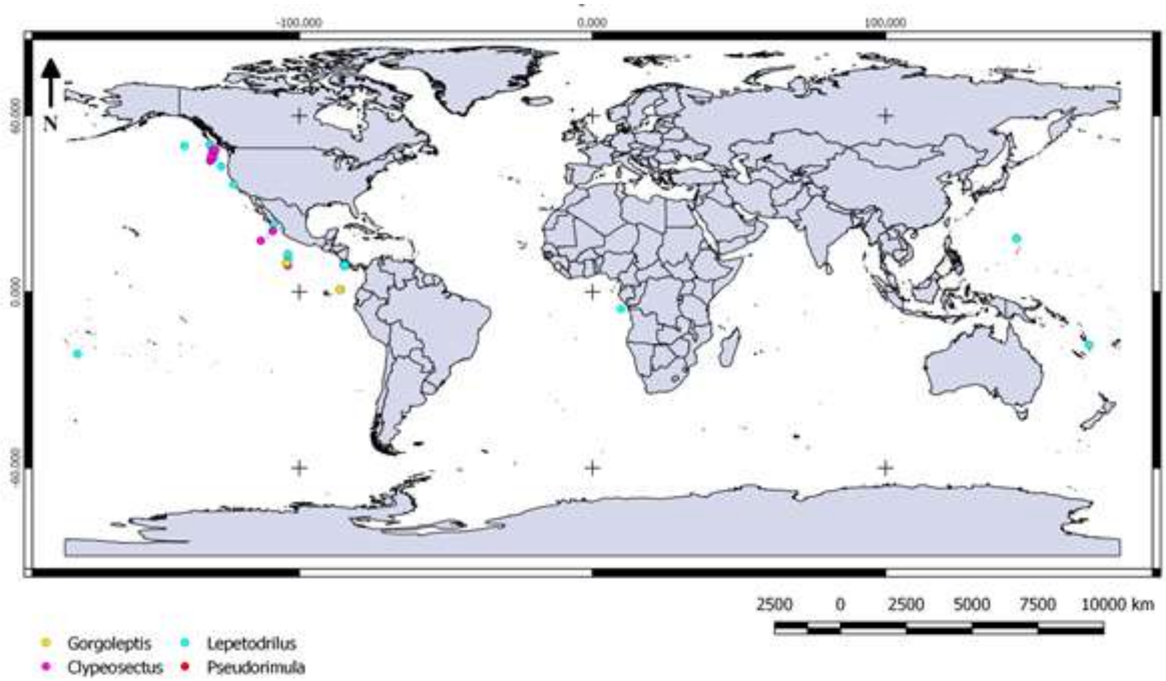

Figure 7. Geographic distribution of Lepetodrilidae.

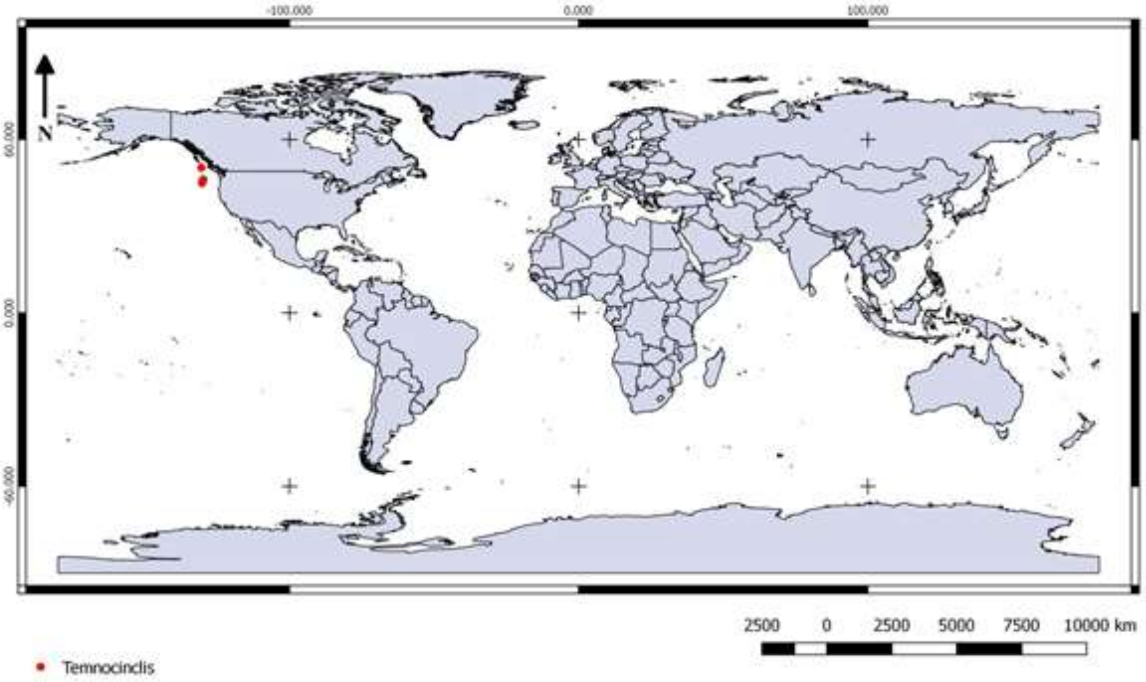

Figure 8. Geographic distribution of Sutilizonidae.

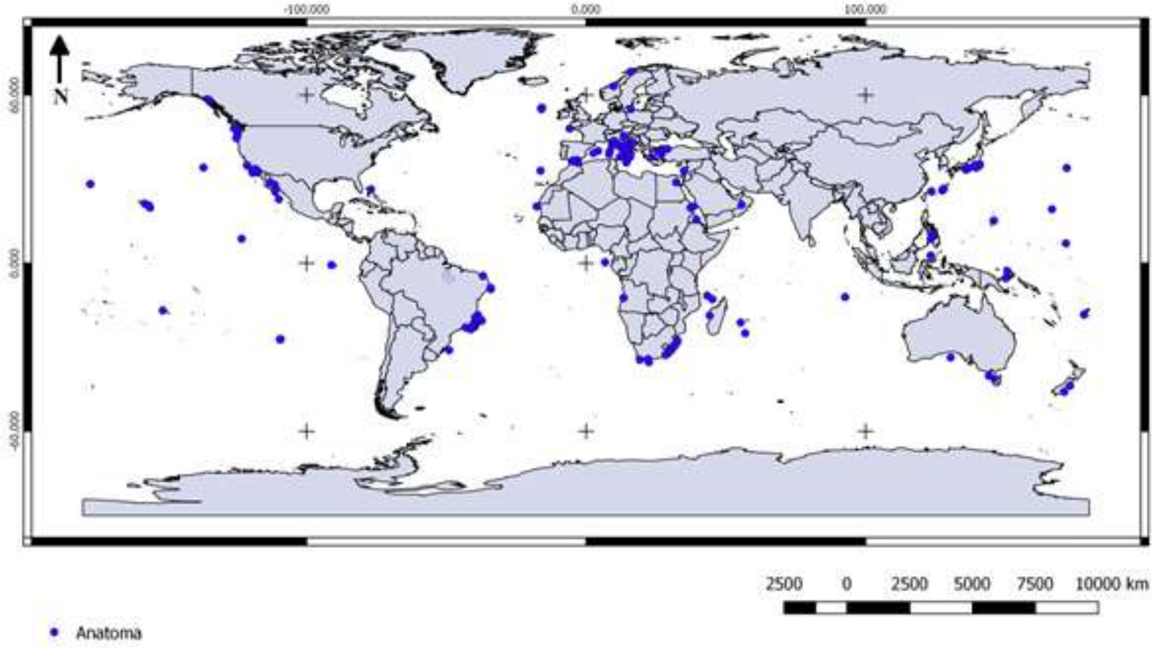

Figure 9. Geographic distribution of Anatomidae.

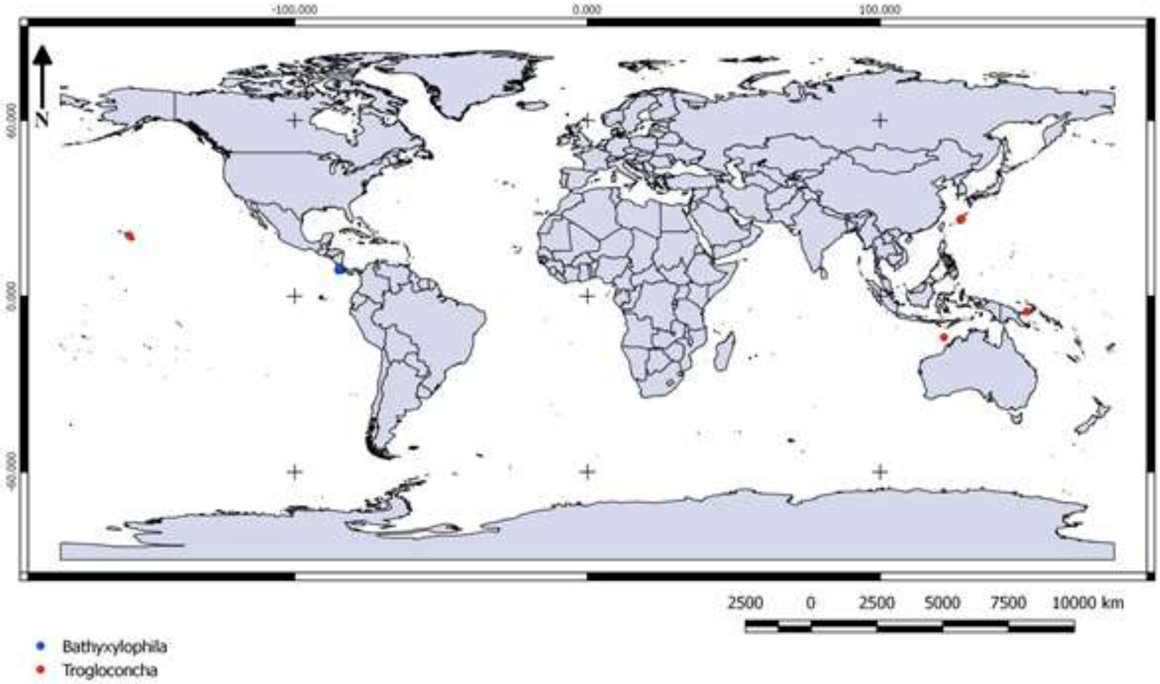

Figure 10. Geographic distribution of Larochaeidae.

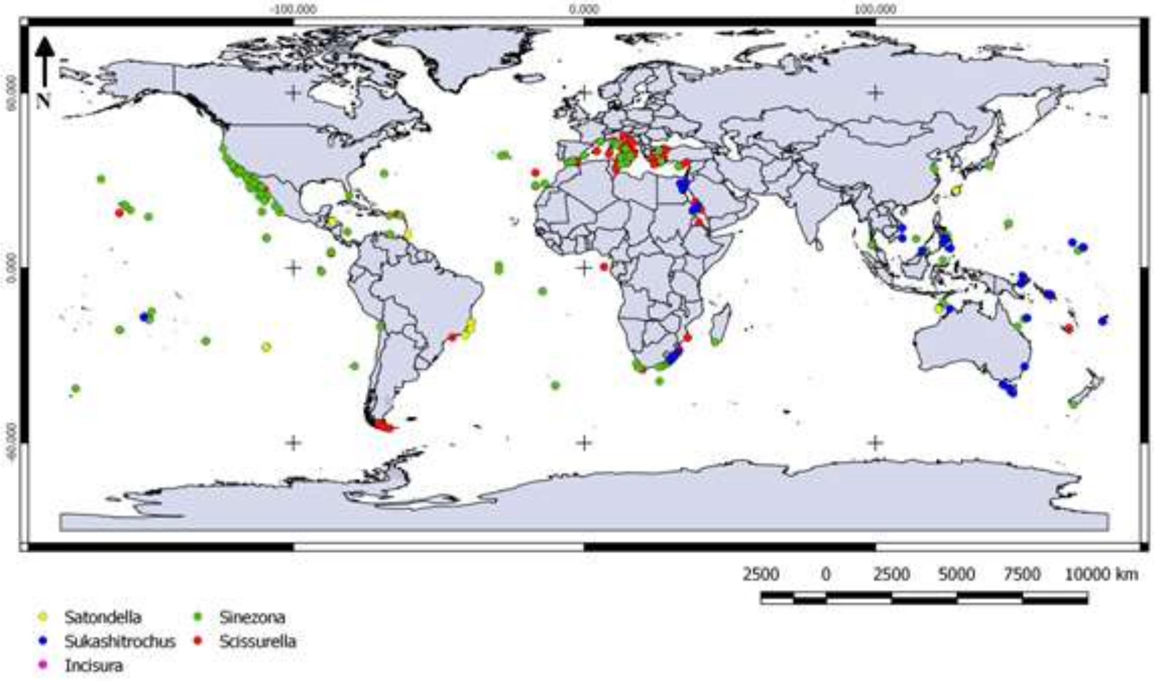

Figure 11. Geographic distribution of Scissurelidae.

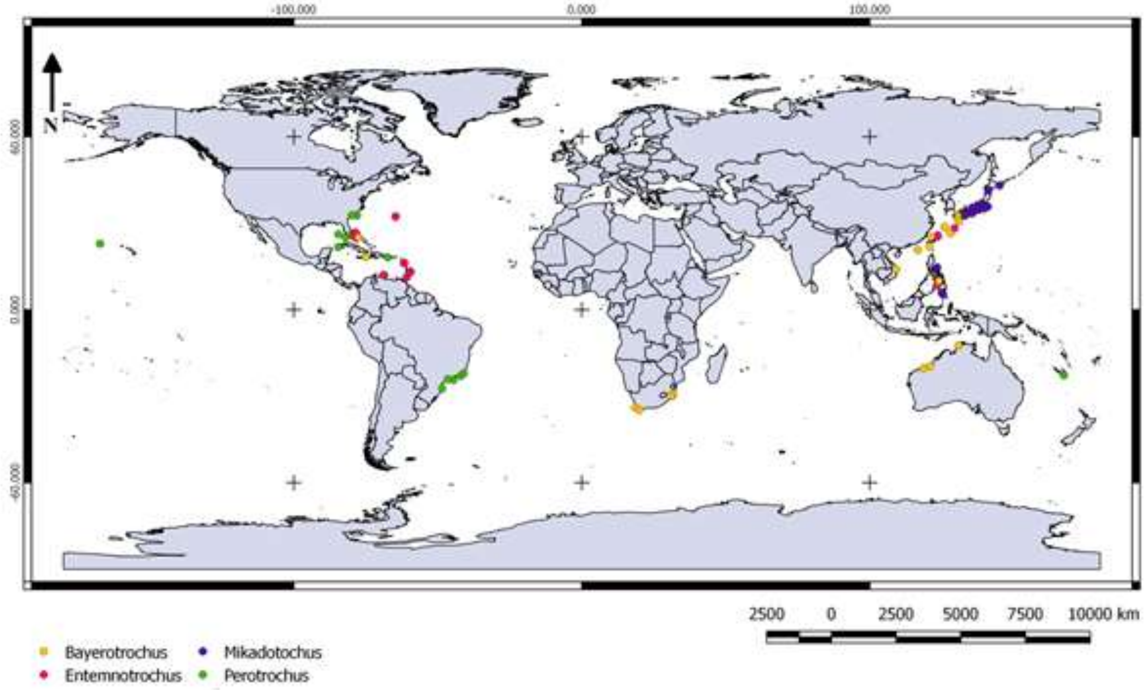

Figure 12. Geographic distribution of Pleurotomariidae.

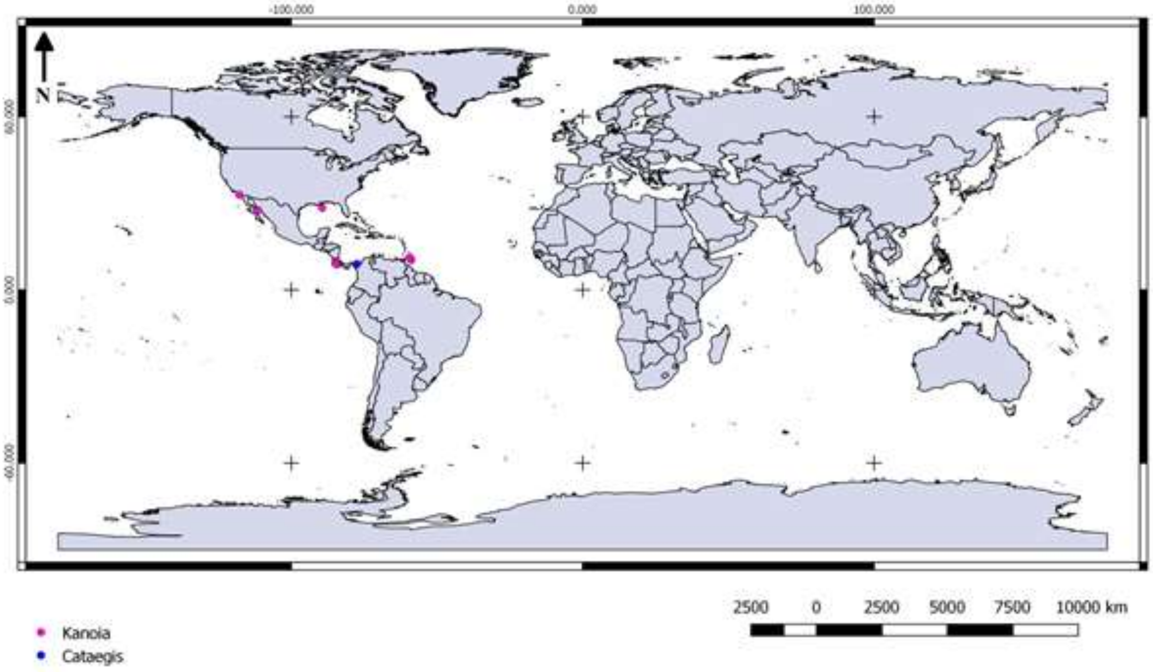

Figure 13. Geographic distribution of Cataegidae.

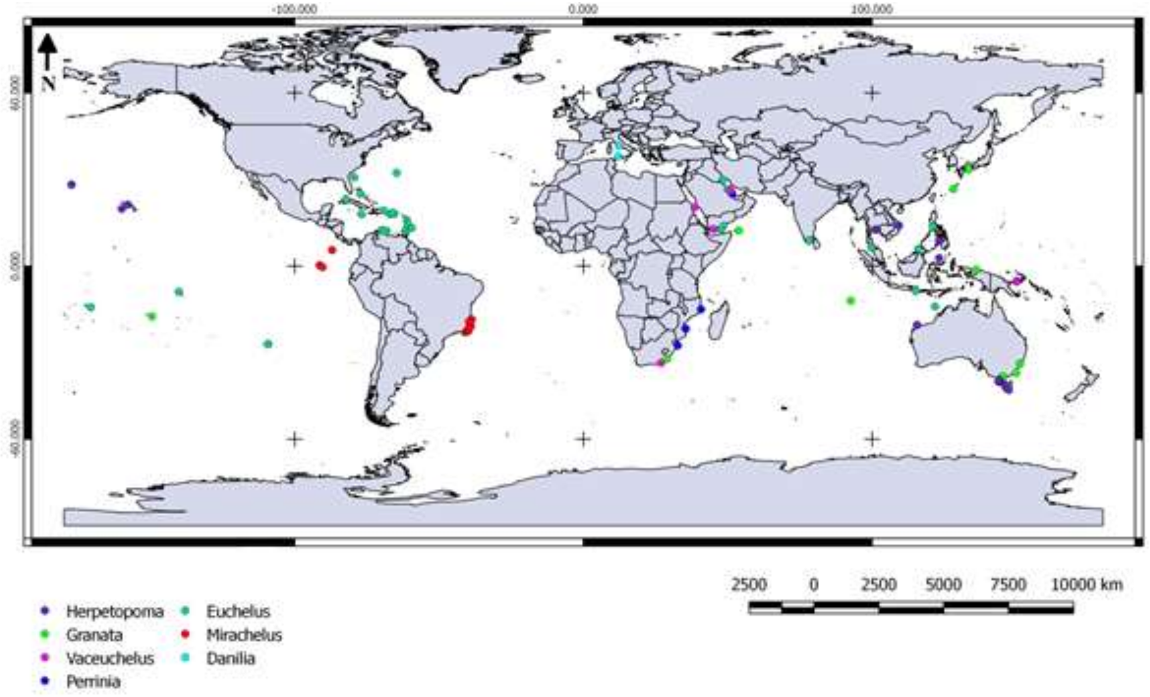

Figure 14. Geographic distribution of Chilodontaidae.

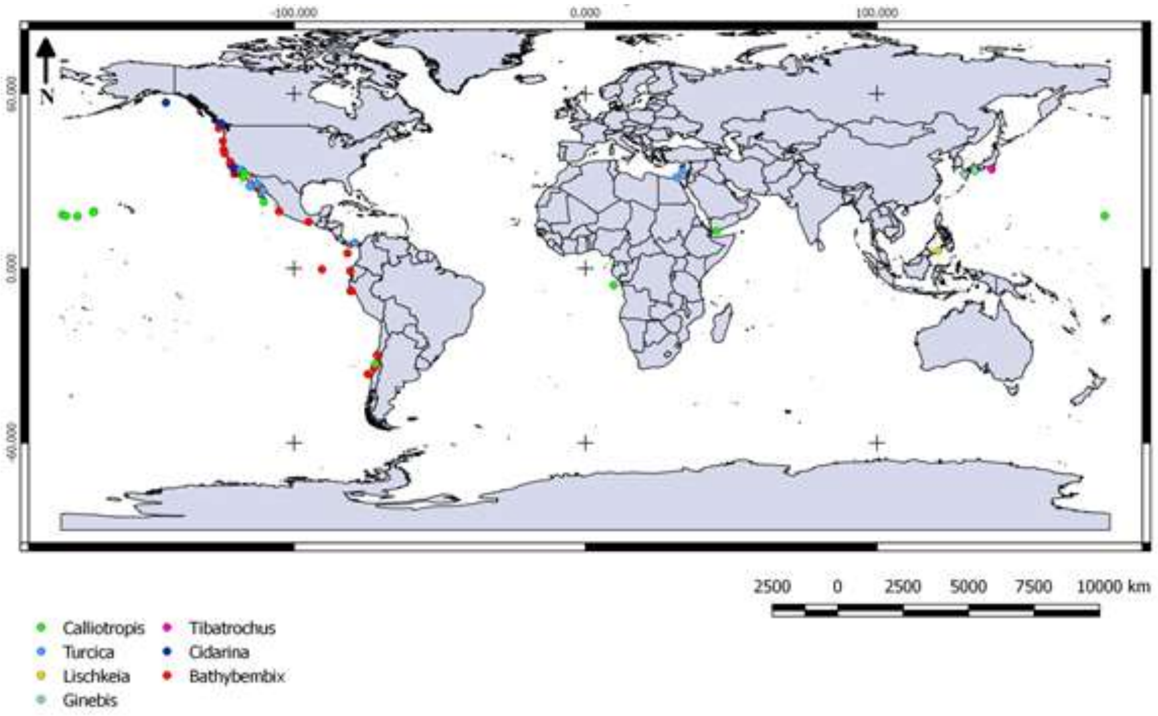

Figure 15. Geographic distribution of Eucyclidae.

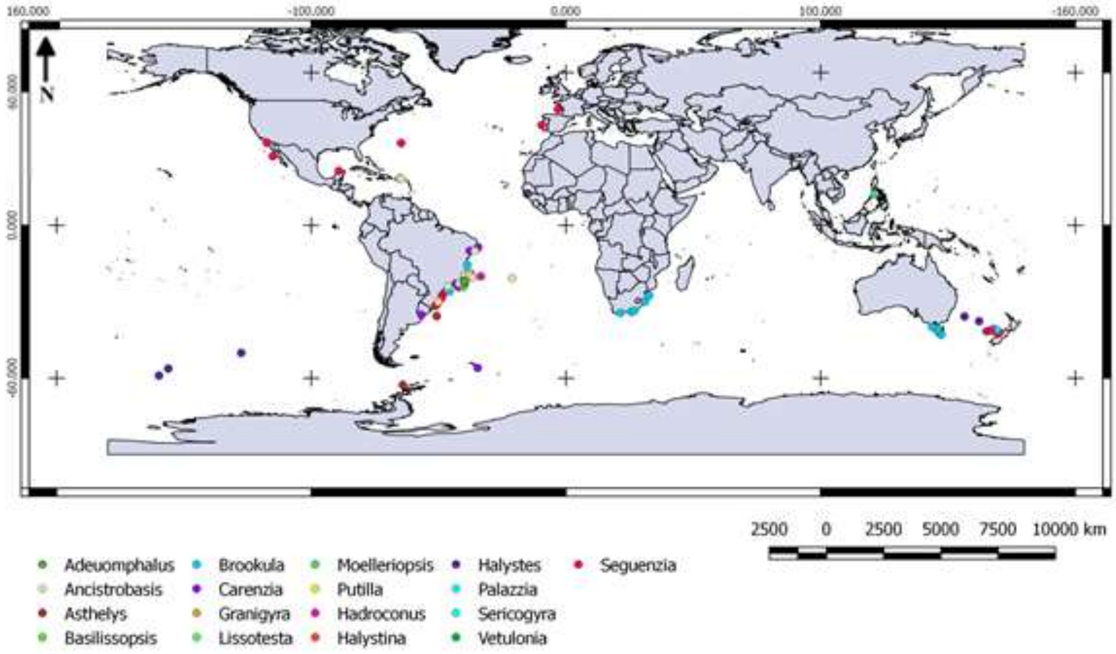

Figure 16. Geographic distribution of Seguenziidae.

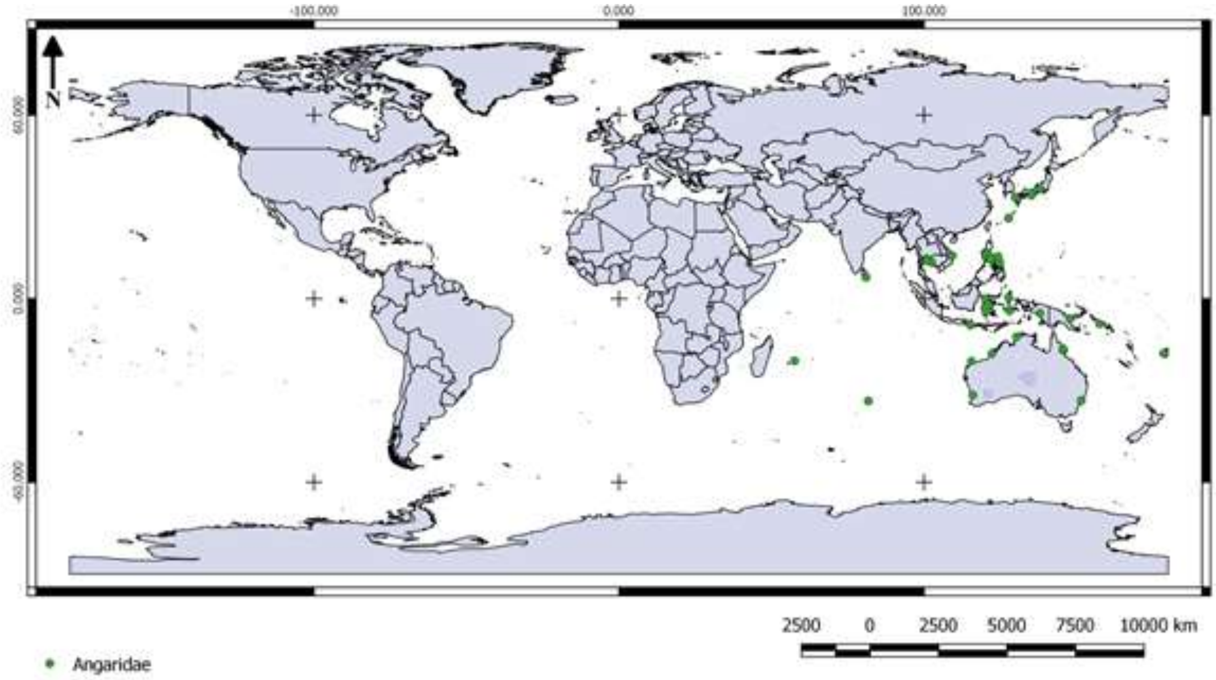

Figure 17. Geographic distribution of Angariidae.

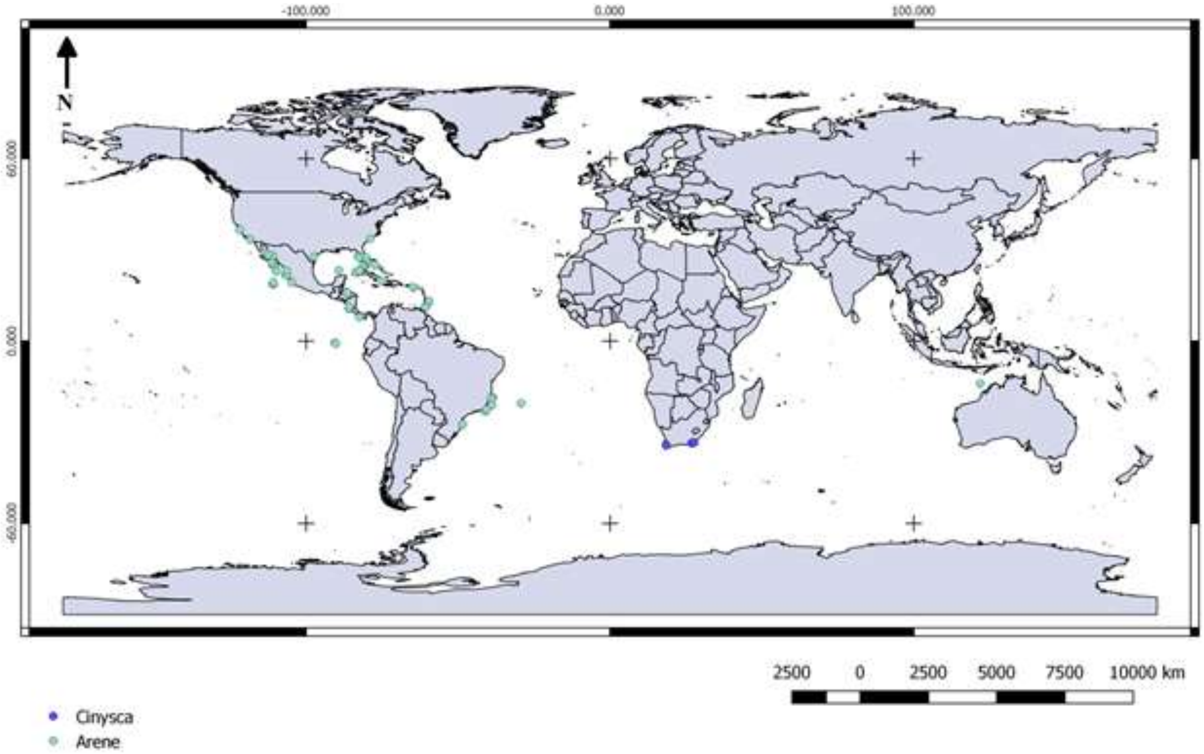

Figure 18. Geographic distribution of Areneidae.

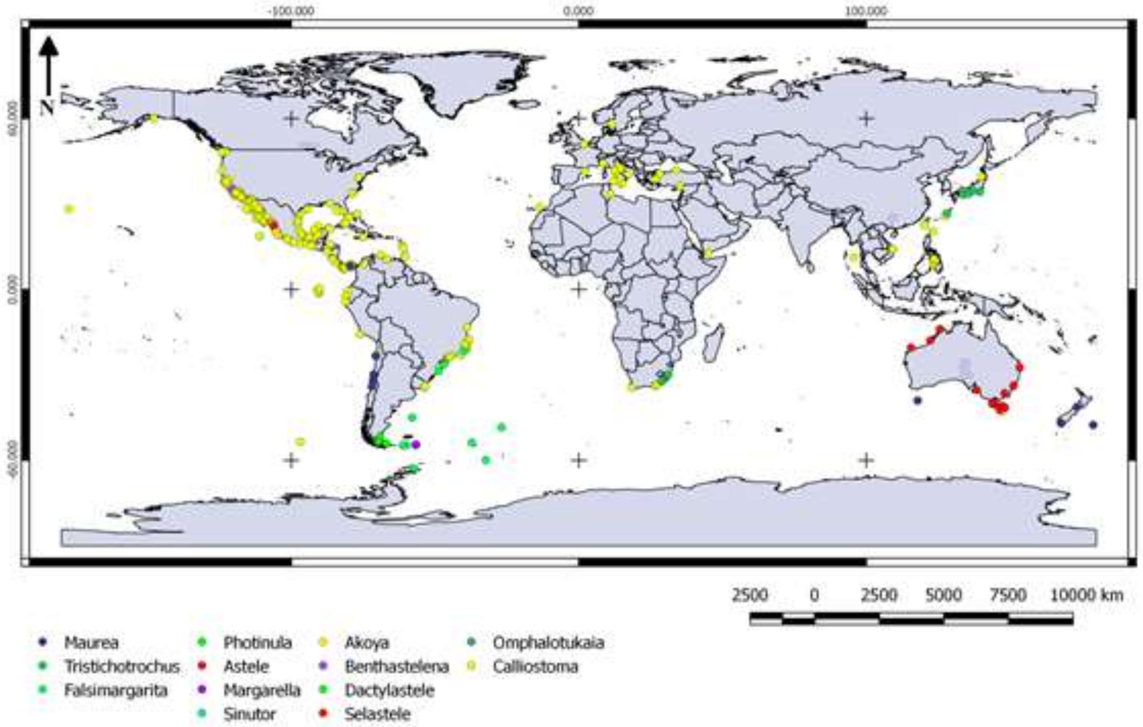

Figure 19. Geographic distribution of Calliostomatidae.

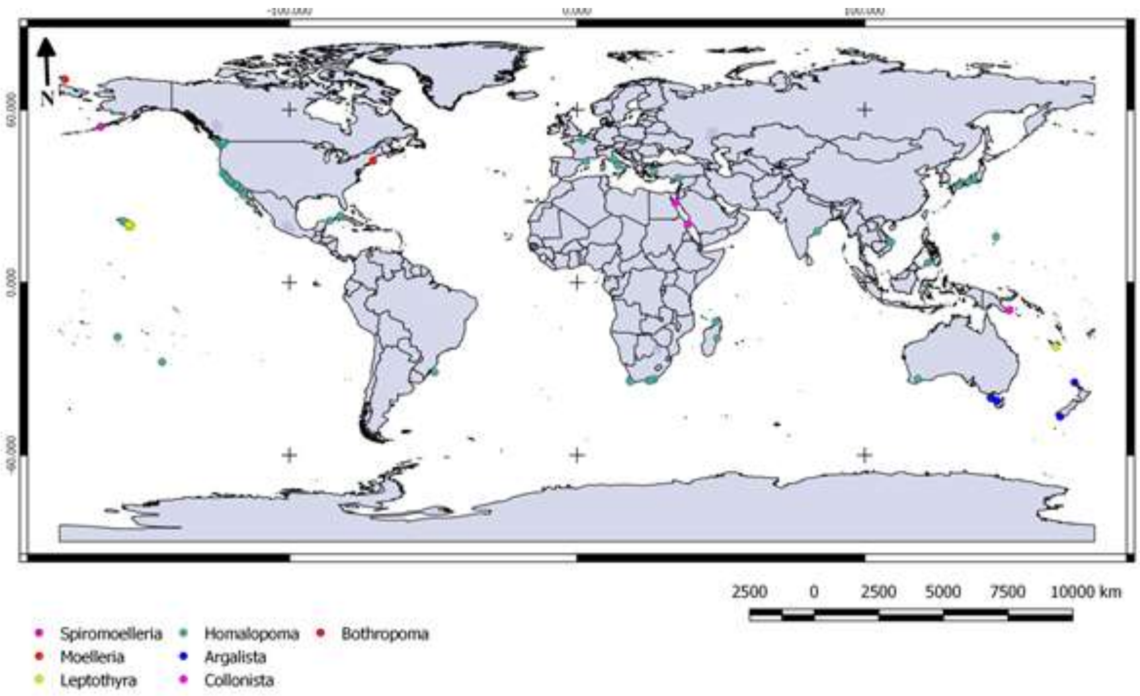

Figure 20. Geographic distribution of Colloniidae.

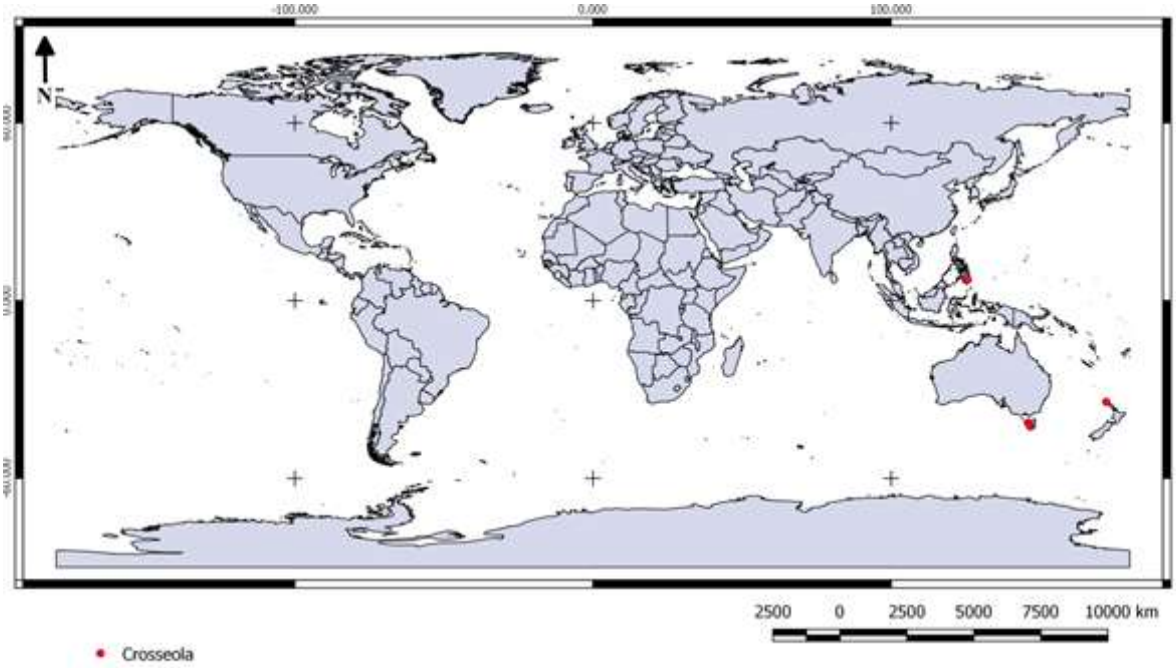

Figure 21. Geographic distribution of Conradiidae.

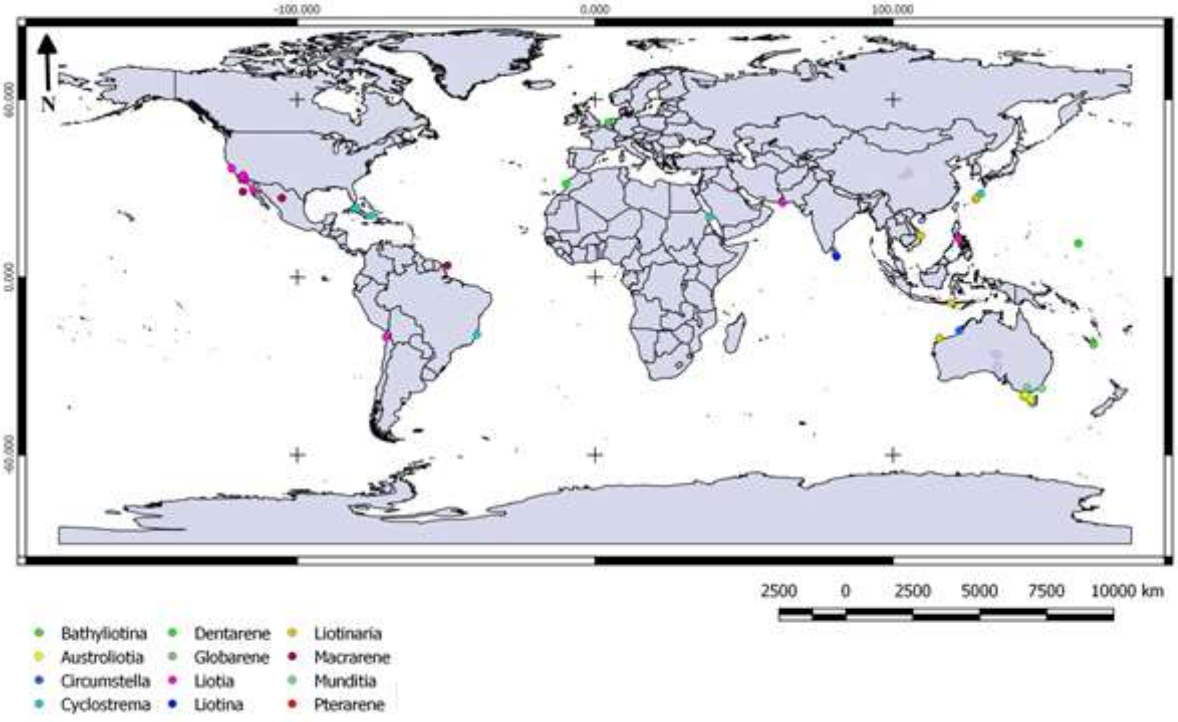

Figure 22. Geographic distribution of Liotiidae.

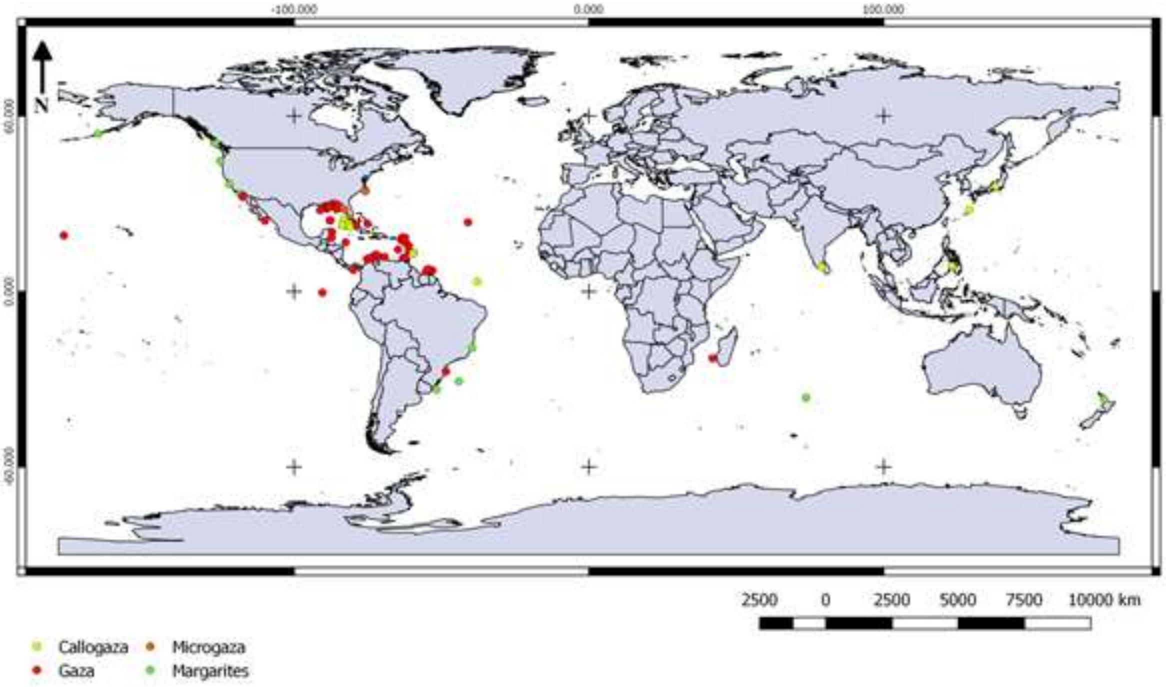

Figure 23. Geographic distribution of Margaritidae.

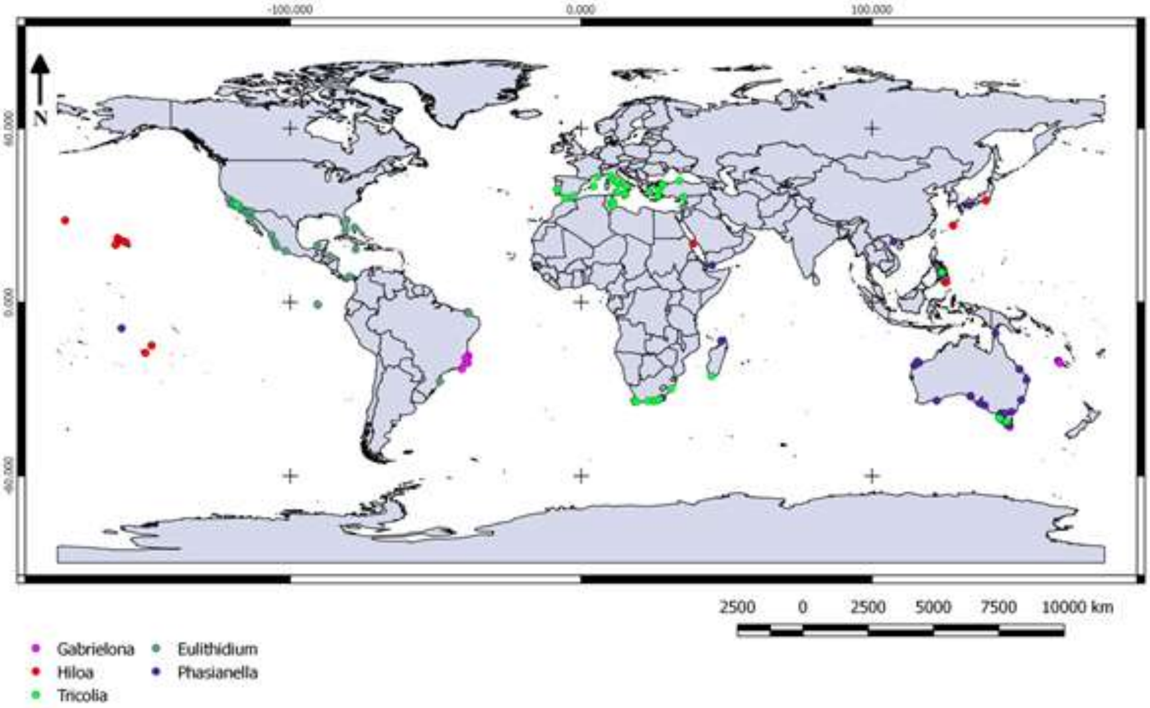

Figure 24. Geographic distribution of Phasianellidae.

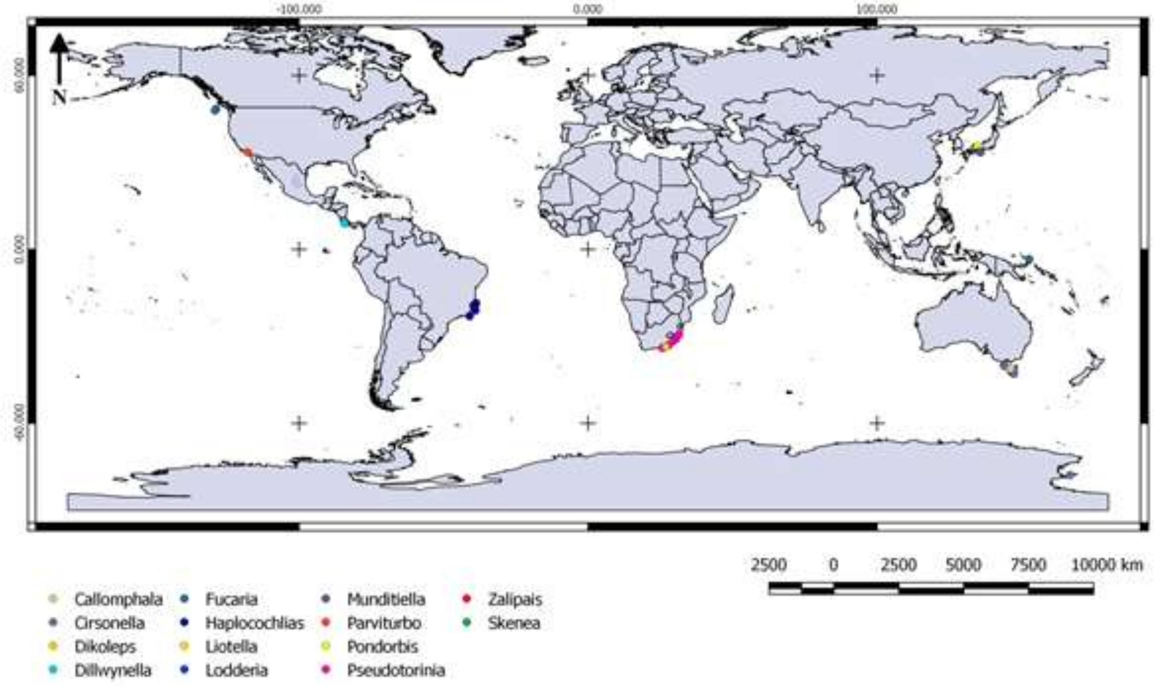

Figure 25. Geographic distribution of Skeneidae.

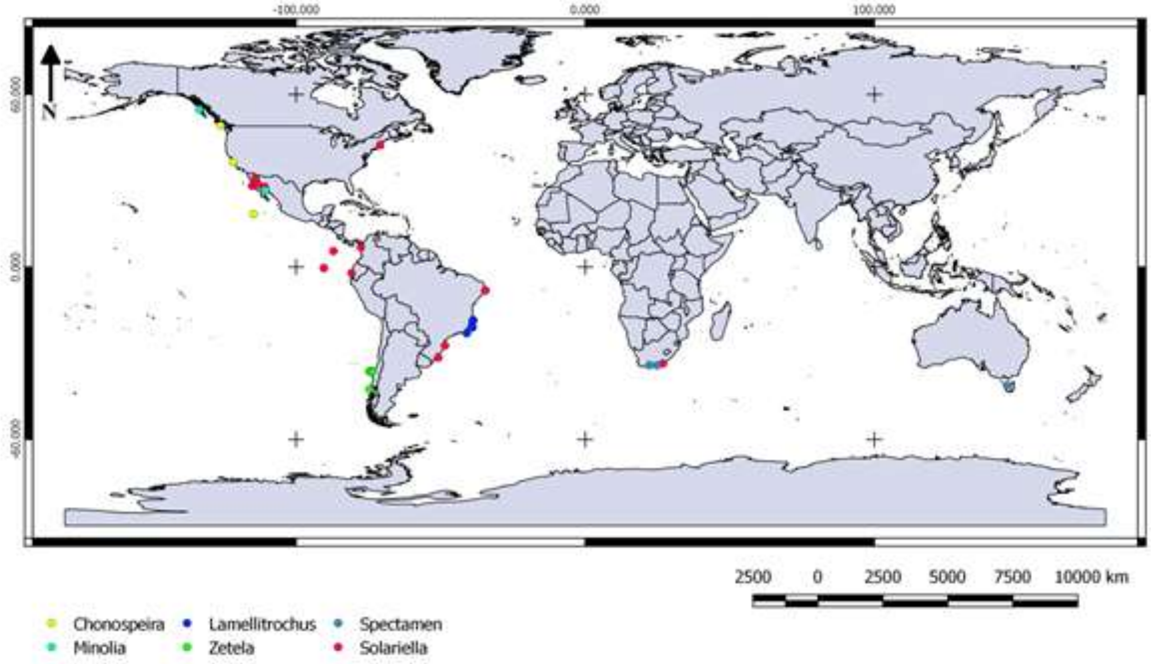

Figure 26. Geographic distribution of Solariellidae.

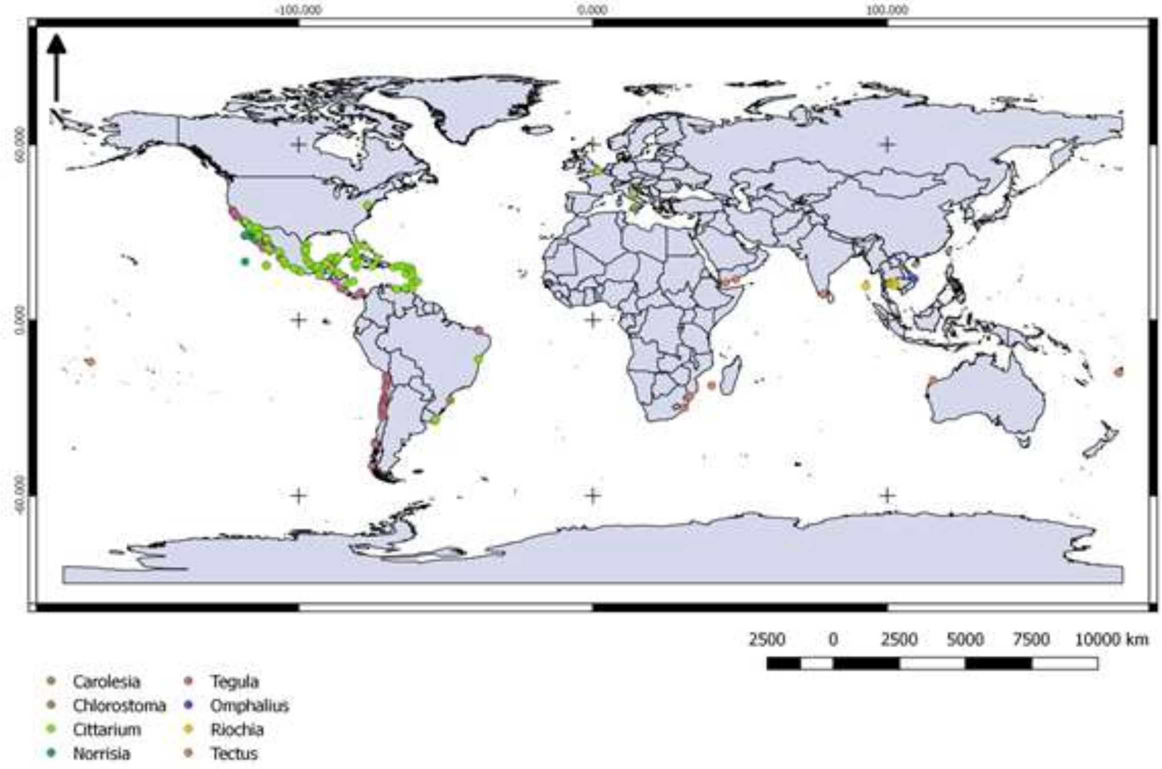

Figure 27. Geographic distribution of Tegulidae.

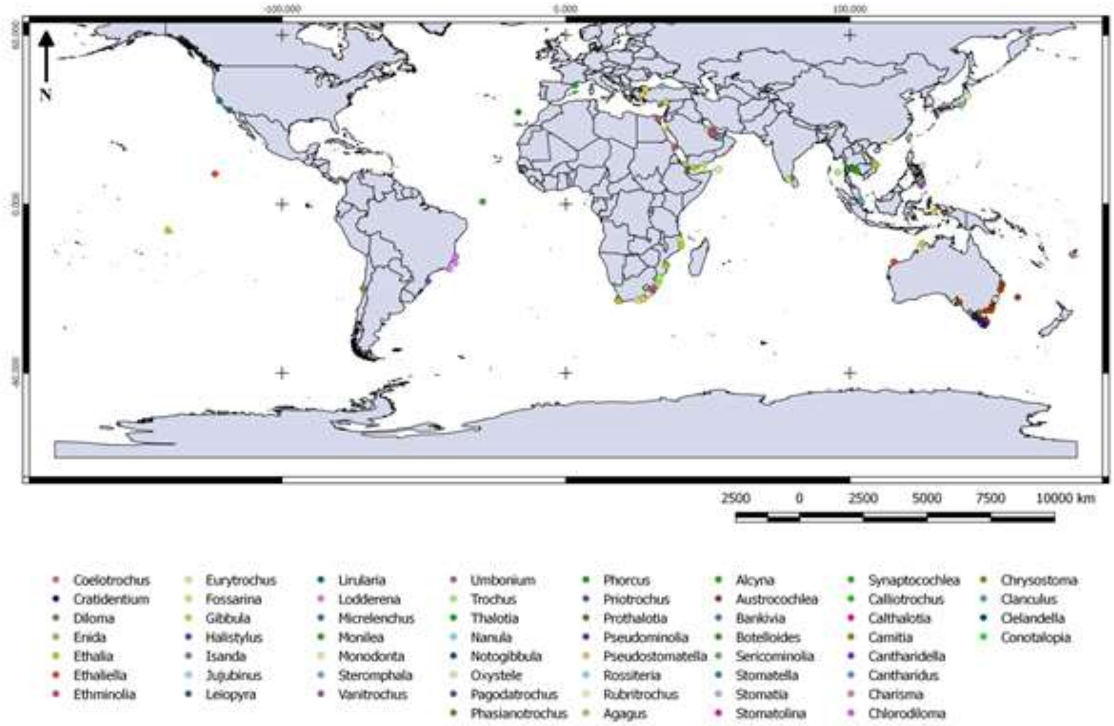

Figure 28. Geographic distribution of Trochidae.

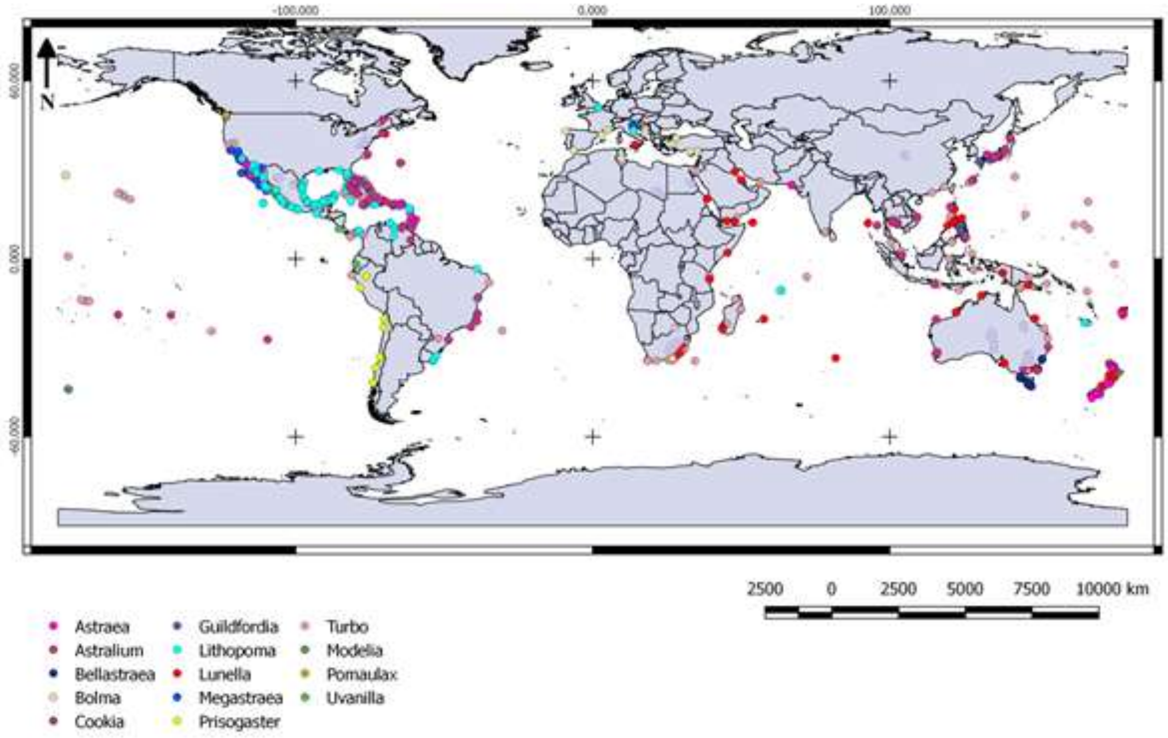

Figure 29. Geographic distribution of Turbinidae.

Supplementary material. Distributional data of de families in this study deposited in de malacological collections

Family Fissurellidae

BIC M12, M353, M376, M395, M448, M700, M790, M947, M977, M978, M1379, M2447, M2546, M2589, M2625, M2645, M3753, M3754, M3954, M7060, M8237, M11534, M12228, M12260, M13344, M13746, M14266, M14270, M14304, M14305, M14345, M14366; **CAS** 10804, 13298, 16675, 18040, 26406, 31984, 33361, 36324, 43928, 43990, 60386, 61711, 63634, 63739, 63821, 63829, 64610, 64711, 64713, 64730, 66181, 66753, 67709, 67710, 67713, 67714, 67717, 67718, 76344, 76356, 78549, 81125, 81332, 87363, 88265, 88626, 88627, 88631, 88654, 88687, 89553, 89572, 92219, 94477, 94484, 94547, 94548, 94550, 94553, 94561, 94567, 94568, 94569, 94572, 94574, 94575, 94577, 94606, 94654, 96259, 102346, 107270, 109967, 111567, 112267, 112597, 113709, 119029, 119314, 119822, 120133, 120257, 120281, 120284, 120490, 128261, 128262, 128377, 131428, 141571, 143431, 157430, 157595, 157723, 157995, 158002, 159229, 160935, 160936, 160942, 161796, 161802, 161836, 161880, 161914, 161915, 161916, 161920, 161921, 161923, 161924, 161925, 162121, 165426, 171909, 172470, 183611, 183616, 184825, 186239, 189402, 195011, 196286, 198768, 202087, 203122, 203291, 203292, 203296, 204107, 204108; **CNMO** 0369, 1096, 1492, 1493, 1494, 2264, 2951, 3792, 3803, 3950, 3954, 4111, 4113, 4637, 4638, 4692, 4693, 4694, 4697, 4748, 4754, 4781; 4849, 4931, **COMA**, 2020; **CRIM** 96, 664, 773, 774, 775, 1130, 1250, 1555, 1678, 1679, 1680, 1681, 1682, 1683, 1684, 1685, 1686, 2136, 2137, 2401, 5181, 5254, 94548, 94567, 94568, 94574, 113709, 183611, 142163; **SBMNH** 171652, 172143, 172196, 172280, 230103, 236704, 237357, 237359, 237448, 237471, 237478, 265771, 461770, 461812, 473699.

Family Haliotidae

BIC M11, M285, M317, M319, M432, M953, M967, M1006, M4781, M7620, M8226, M8833; **CAS** 20808, 20810, 21316, 21318, 21336, 21339, 21353, 21380, 21467, 21696, 21698, 21705, 21706, 21708, 21710, 21714, 21741, 21751, 28154, 44954, 44960, 44963, 44965, 57773, 60761, 60934, 64682, 64697, 64703, 64771, 65629, 66178, 66859, 67999, 68000, 68001, 68009, 69310, 69611, 71109, 71110, 71896, 73582, 76574, 78031, 78147, 78148, 78149, 78150, 78152, 81037, 81038, 81039, 81123, 81215, 81217, 83772, 83776, **SBMNH** 2202, 2239, 2331, 3296, 3511, 3833, 4880, 4884, 6172, 12590, 13689, 14167, 18863, 19074, 19084, 19085, 22025, 23119, 23120, 23131, 23655, 23722, 23915, 25867, 26127, 26128, 26228, 26229, 26233, 28151, 28305, 28306, 28308, 28309, 28312, 28315, 28320, 28324, 28325, 28350, 28360, 28937, 28938, 31463, 31464, 31502, 34846, 43449, 43470, 43472, 43489, 44469, 44470, 44471, 44473, 45268, 46553, 52706, 52707, 55172, 55232, 83393, 89059, 89241, 97998, 98036, 98173, 99680, 100047, 100049, 100634, 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472203, 472205, 472206, 472207, 474327, 616309, 616311, 616312, 616315, 616318,
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Family Addisonidae

CAS 41583; **MCZ** 378222, 372706, 372689, 378223.

Family Pseudococculinidae

BIC M13732; **MCZ** 378230, MCZ 378637.

Family Pyropeltidae

BIC M7929, M11977, M12013, M12024, M12036, M12044, M12097, M12242, M12244, M12261, M12420, M12421, M12422, M12423, M12425, M14882, M15553, M15584, M15591, M15667, M15678, M15700, M16105, M16157, M16171, M16231, M16361, M16408, M16434, M16467, M16470, M16529, M16546, M16559, M16560, M16568, M16572, M16577, M16580, M16685, M16874, M16920, M16935, M16957, M17849, M17850; **MCZ** 378706, 384402.

Family Lepetodrilidae

BIC M3974, M8156, M11751, M11754, M11755, M11758, M11767, M11778, M11900, M11905, M11916, M11965, M11973, M12020, M12057, M12099, M12224, M12225, M13140, M13141, M13143, M13144, M13147, M14405, M14413, M14415, M14444, M14446, M14449, M14451, M14452, M14453, M14454, M14460, M14465, M14466, M14467, M14470, M14641, M14643, M14648, M14653, M14661, M14663, M14670, M14677, M14682, M14698, M14700, M14708, M14710, M14712, M14723, M14746, M14815, M14816, M14822, M14829, M14830, M14834, M14886, M14893, M15336, M15342, M15350, M15401, M15477, M15511, M15515, M15517, M15518, M15521, M15538, M15545, M15549, M15554, M15555, M15559, M15560, M15563, M15582, M15594, M15615, M15641, M15653, M15665, M15674, M15675, M15687, M15795, M15796, M15797, M15804, M16142, M16146, M16159, M16163, M16179, M16226, M16233, M16248, M16253, M16273, M16276, M16283, M16286, M16324, M16326, M16362, M16365, M16367, M16379, M16388, M16396, M16407, M16416, M16418, M16464, M16473, M16479, M16486, M16558, M16565, M16571, M16573, M16578, M16579, M16607, M16628, M16639, M16652, M16655, M16665, M16676, M16683, M16732, M16770, M16926, M16934, M16936, M16992, M17476, M17477, M17480, M17483, M17487, M17731, M18165; **CAS** 85307, 85311, 85313, 85316, 85317, 85319, MCZ 297061, 297062 297063, 362067; **SBMNH** 83892, 83893, 348717, 348719, 348720, 348722, 348723, 348724, 348725, 452923, 452924, 452925, 452926, 452948, 452953, 452961, 452962, 452967, 452968, 452969, 452970, 452979, 452980, 452982, 452983, 470748, 615491, 615492, 615493, 615494, 615502, 615506, 615509, 615514, 615515, 615516.

Family Sutilizonidae

BIC M15550, M16557, M16569, M16299.

Family Anatomidae

BIC M1778, M1834, M1974, M1991, M2070, M2171, M2529, M12428; **SBMNH** 34531, 83432, 83433,83518, 85480, 103215, 133331, 133350, 133373, 140024, 140030, 140037, 149454, 149455, 149456, 149458, 149465, 149471, 149586, 149680, 149681, 149937, 149941, 153117, 170097, 170098, 170099, 170105, 170119, 170280, 170301,170308, 170310, 170315, 170320, 170322, 170331, 170332, 170333, 170337, 170338, 170339, 170347, 170438, 170557, 170604, 170605, 170671, 170754, 170767, 170823, 170824, 170826, 170829, 170830, 170831, 170857, 170862, 170891, 170895, 170896, 170904, 170927, 170953, 170957, 170961, 171036, 171073, 171077, 171127, 171128, 171129, 171162, 171176, 171189, 171198, 171208, 171210, 171211, 171215, 171216, 171217, 171254, 171258, 171270, 171273, 171277, 171281, 171302, 171303, 171304, 171305, 171305, 171308, 171310, 171321, 171327, 171336, 171337, 171340, 171341, 171342, 171351, 171358, 171359, 171364, 171367, 171376, 171377, 171378, 171385, 171391, 171395, 171396, 171405, 171424, 171435, 171492, 171520, 171534, 171551, 171578, 171589, 171590, 171591, 171601, 171631, 171632, 171633, 171634, 171635, 171639, 171640, 171641, 171642, 171791, 171810, 171980, 172019, 172020, 172319, 172358, 172372, 172388, 172389, 172390, 172402, 172428, 172429, 172532, 172545, 172556, 172558, 172617, 172621, 172629, 172630, 172645, 172646, 172647, 172648, 172652, 172657, 172668, 172725, 172726, 172755,172757, 172774, 172775, 172776, 72777, 172778, 172779, 172782, 172790, 172791, 172793, 172848, 172868, 172869, 172870, 172871, 230139, 230140, 230141, 230142, 230144, 230145, 230150, 230279, 266081, 266082, 266292, 266330, 266331, 345565, 350392, 350393, 424191, 452776, 454753, 454792, 454984, 455012, 460133, 460134, 469832, 469835, 470736, 471951, 471952, 471953, 471954, 471955, 471958, 617102, 617105, 617106, 617110, 61711.

Family Larochaeidae

BIC M16198, M16913, M16954, M12028, M12038; **SBMNH** 452835, 266150, 454761, 149464, 149468, 171487, 171550, 170735, 369510.

Family Scissurellidae

SBMNH 32218, 83540, 83541, 83542, 83545, 83549, 83704, 83705, 83706, 83707, 85110, 85111, 85112, 85113, 85114, 85115, 85116, 85117, 85118, 85119, 85121, 85122, 85123, 85124, 85126, 85127, 85128, 85129, 85130, 85131, 85132, 85133, 85134, 85135, 85137, 85138, 85139, 85140, 85141, 85142, 85143, 85144, 85145, 85146, 85147, 85148, 85149, 85150, 85152, 85153, 85154, 85155, 85158, 85159, 85162, 85163, 85164, 85165, 85166, 85167, 85169, 85171, 85172, 85173, 85174, 85175, 85176, 95777, 103982, 113929, 114004, 114111, 116210, 116311, 119692, 124050, 124543, 127586, 132624, 141271, 142247, 149459, 149460, 149461, 149462, 149463, 149466, 149467, 149469, 149470, 149472, 149866, 158113, 170100, 170101, 170102, 170103, 170107, 170109, 170224, 170225, 170230, 170233, 170234, 170235, 170238, 170239, 170242, 170244, 170266, 170267, 170268, 170275, 170276, 170277, 170278, 170279, 170281, 170282, 170284, 170297, 170298, 170299, 170300, 170302, 170303, 170309, 170312, 170313, 170314, 170316, 170317, 170318, 170321, 170324, 170325, 170326, 170327, 170329, 170340, 170348, 170349, 170350, 170360, 170393, 170394, 170395, 170396, 170397, 170398, 170399, 170400, 170401, 170402, 170441, 170442, 170443, 170444, 170445, 170473, 170474, 170477, 170478, 170485, 170495, 170500, 170510, 170529, 170532, 170558, 170559, 170577, 170578, 170579, 170601, 170603, 170606, 170607, 170608, 170609, 170639, 170647, 170648, 170672, 170703, 170730, 170731, 170733, 170734, 170739, 170740, 170756, 170768, 170771, 170772, 170791, 170792, 170798, 170799, 170800, 170801, 170814, 170816, 170817, 170819, 170820, 170821, 170822, 170828, 170835, 170852, 170856, 170860, 170861, 170863, 170864, 170865, 170867, 170868, 170869, 170870, 170871, 170872, 170881, 170883, 170884, 170892, 170893, 170894, 170897, 170900, 170901, 170926, 170932, 170944, 170945, 170946, 170947, 170948, 170949, 170950, 170954, 170955, 170958, 170959, 170960, 170962, 170963, 170965, 170967, 170972, 170973, 170974, 170976, 170977, 170978, 170997, 170998, 171001, 171002, 171011, 171012, 171022, 171024, 171032, 171038, 171058, 171068, 171069, 171070, 171071, 171072, 171076, 171078, 171125, 171126, 171133, 171140, 171159, 171160, 171161, 171174, 171175, 171195, 171196, 171197, 171209, 171212, 171213, 171214, 171218, 171219, 171220, 171221, 171261, 171271, 171272, 171274, 171275, 171276, 171278, 171282, 171283, 171284, 171285, 171286, 171287, 171288, 171290, 171291, 171292, 171293, 171294, 171295, 171296, 171297, 171298, 171309, 171311, 171312, 171313, 171314, 171315, 171316, 171317, 171318, 171319, 171325, 171326, 171331, 171332, 171333, 171334, 171335, 171347, 171348, 171349, 171350, 171360, 171361, 171365, 171366, 171368, 171370, 171371, 171372, 171374, 171375, 171379, 171381, 171382, 171383, 171384, 171386, 171388, 171390, 171392, 171393, 171394, 171397, 171398, 171399, 171400, 171401, 171402, 171403, 171404, 171406, 171407, 171408, 171409, 171410, 171415, 171416, 171417, 171420, 171421, 171422, 171423, 171436, 171437, 171438, 171439, 171440, 171441, 171442, 171443, 171444, 171445, 171446, 171447, 171448, 171457, 171458, 171459, 171460, 171461, 171462, 171463, 171490, 171515, 171516, 171517, 171518, 171519, 171529, 171530, 171531, 171532, 171533, 171542, 171543, 171544, 171545, 171546, 171547, 171548, 171549, 171574, 171576, 171577, 171588, 171627, 171628, 171629, 171630, 171636, 171637, 171638, 171643, 171644, 171645, 171646, 171648, 171729, 171747, 171748, 171749, 171750, 171752, 171765, 171780, 171781, 171792, 171811, 171812, 171824, 171981, 172006, 172018, 172318, 172323, 172324, 172325, 172347, 172369, 172370, 172371, 172376, 172386, 172387, 172392, 172401, 172427, 172446, 172468, 172493, 172526, 172527, 172540, 172541, 172542, 172544, 172546, 172547, 172548, 172557, 172559, 172560, 172603, 172606, 172607, 172618, 172620, 172623, 172642, 172649, 172650, 172651, 172653, 172654, 172655, 172656, 172667, 172670, 172678, 172679, 172705, 172710, 172716, 172719, 172724, 172731, 172732, 172733, 172787, 172798, 172849, 172851, 172860, 172862, 211378, 211379, 211380, 230138, 230148, 230152, 230153, 230154, 230157, 230159, 230160, 230161, 230163, 230164, 230165, 230166, 230167, 230170, 230171, 230172, 348009, 348010, 348011, 348012, 348769, 349056, 350876, 351025, 358511, 359317, 359327, 359440, 361473, 361481, 361482, 361483, 361702, 367143, 367144, 369506, 369508, 369511, 369513, 369525, 369527, 369533, 369614, 369615, 369616, 369617, 369619, 369622, 369623, 369625, 369626, 369694, 369696, 422861, 422862, 454307, 454308, 454311, 454312, 454313, 454315, 454318, 454319, 454320, 454321, 454322, 454323, 454325, 454326, 454329, 454330, 454331, 454332, 454333, 454334, 454416, 456685, 456686, 456687, 457459, 466815, 616283, 616284, 617103, 617104.

Family Pleurotomariidae

ANSP 267791, 85803, 139968, 189698, 219610, 240853, 240855, 240858, 240859, 240860, 240862, 276991, 282398, 302134, 359098, 359099, 372144, 388063, 397788, 400173, 403884, 403983, 405694, 405699, 405704, 405705, 405709, 405710, 405711, 405712, 405713, 410043, 410047, 413655, 425042, 425043, 425044, 425045, 425048, 425062, 425063, 426325; **CAS** 42304, 46342; **FMNH** 36723, 153703, 243513, 281434, 281435, 281440, 281441, 281443, 281445, 281446, 281447, 281448, 281449, 281451, 281452, 281454, 281456, 281457, 281487, 378860, 475314, 508935, 516406; **MCZ** 16825, 31620, 31621, 57925, 58836, 58837, 119057, 119057, 119058, 135025, 135025, 175025, 204456, 204457, 225246, 225248, 225871, 225871, 229643, 235398, 315180, 329272, 329273, 329273, 329275, 329277, 329278, 329278, 329279, 329280, 366653, 366654, 366655, 374931, 374933, 383057; **SBMNH** 155649, 422863, 470506.

Family Cataegidae

BIC M11975, M12052, M14400, M16846, M14303, M17028, M14419, M16919, M14395, M13149, M17726, M17725; **MCZ** 296111; **SBMNH** 149781.

Family Chilodontaidae

BIC M13808; **CAS** 66823, 165228, 188360; **MCZ** 205895; **SBMNH** 32221, 142329, 142389, 142390, 156679, 159546, 159877, 171619, 236921, 237017, 237019, 237020, 237021, 237023, 237039, 237040, 237081, 237169, 237178, 366680, 369023, 369531, 452880, 452882, 466950, 467541, 467555, 470893, 470954, 471939, 473156, 473817.

Family Eucyclidae

BIC M16, M445, M765, M766, M767, M768, M769, M770, M771, M772, M773, M1074, M1077, M1092, M1511, M1587, M1588, M1593, M1600, M2110, M2237, M2319, M2341, M2353, M2359, M2370, M2382, M2399, M2429, M2442, M2455, M2468, M2761, M3579, M3602, M3904, M3949, M7097, M7430, M7439, M7771, M7883, M8174, M8180, M11543, M11653, M11683, M11697, M12128, M17722, M17738; **CAS** 93213, 116970, 119223, 119311, 120082, 120146, 161771; **SBMNH** 31762, 36147, 99923, 130047, 145969, 152186, 237002, 237003, 345571, 349119, 349122, 349128, 349139, 350399, 358474, 459366, 459598, 470953, 472210.

Family Seguenziidae

BIC M1837, M1865, M2294; **MCZ** 22406.

Family Angariidae

MCZ 249572, 215198, 224378, 224308, 224607, 179381, 96733, 249525, 96732, 224664, 225079; 386155, 386154, 386154, 205891, 154809, 164836, 158319, 158463, 238491, 271624, 266194, 249568, 281824, 158325, 374057, 249571, 158337, 158330.

Family Areneidae

MCZ 7602, 7604, 7605, 7609, 7611, 7615, 101537, 101542, 153242, 162645, 168347, 168349, 179060, 179061, 179063, 207131, 208163, 208176, 208180, 208181, 233677, 244429, 254386, 254387, 254388, 258913, 298595, 298606, 299360, 325340, 325343, 379206; **SBMNH** 15290, 27160, 32220, 33981, 34830, 82028, 82078, 98375, 129644, 141465, 141466, 141467, 141468, 151803, 152933, 153107, 154482, 154494, 154669, 160930, 230515, 230516, 230524, 367189, 369530, 424319, 424320, 424321, 459900, 469301, 469779, 469788, 472057, 616286.

Family Calliostomatidae

BIC M440, M509, M554, M714, M2140, M2338, M2452, M2541, M2789, M3565, M3605, M3609, M3613, M4309, M8074, M10253, M10268, M11537, M12668, M12675, M12968, M13002, M13089, M13095, M13361, M13605, M13989, M14084, M17502; **CNMO** 1496, 2394, 3786; **COMA** 2020; **CRIM**: 557, 740, 1211, 1324, 1474; 1475, 1556, 1692, 1693, 1925, 1926, 1927, 1928, 1929, 2142; MCZ 40459, 66267, 83291, 85094, 85099, 104554, 104555, 188337, 204641, 297051, 297052, 359442, 362011; **SBMNH** 33966, 34511, 34762, 35158, 81193, 81194, 81195, 81206, 81207, 81208, 81234, 81235, 82020, 98241, 98426, 99921, 99922, 99924, 103209, 140246, 141126, 141266,142261, 145162, 145218, 145219, 145221, 145222, 145224, 145226, 145899, 145993, 146000, 146005, 149306, 152163, 152167, 152197, 152198, 152339, 152344, 152469, 152499, 152690, 152776, 152964, 152977, 153299, 153301, 153323, 153335, 153336, 153382, 153383, 153386, 153411, 153412, 153413, 153502, 153504, 153558, 154226, 154247, 154296, 154353, 154497, 154498, 154501, 154502, 154937, 154949, 155424, 155564, 156843, 157049, 157064, 157105, 157106, 157403, 157464, 157465, 157491, 157918, 157919, 158742, 159009, 159118, 159255, 159398, 159442, 159519, 159574, 159626, 159667, 159702, 159734, 159965, 160858, 160875, 160902, 160921, 160922, 210483, 211066, 212102, 212105, 212106, 230574, 230575, 230576, 235323, 236623, 236624, 236625, 236626, 236627, 236628, 236629, 236630, 236631, 236632, 236633, 236634, 236635, 236636, 236882, 236883, 236884, 236885, 236886, 236887, 236888, 236889, 236890,236891, 236892, 236893, 236894, 236896, 236897, 236898, 236906, 236907, 236908, 236909, 236910, 236911, 236912, 236913, 236914, 236915, 236923, 236924, 236925, 236926, 236927, 236928, 236929, 236930, 236931, 236932, 236933, 236934, 236935, 236936, 236937, 236938, 236939, 236940, 236941, 236942, 236943, 236944, 236945, 236946, 236947, 236948, 236949, 236950, 345577, 349125, 349136, 349137, 349138, 349141, 349144, 349146, 349147, 349153, 349155, 349157, 349158, 349297, 350402, 350403, 350404, 353516, 353517, 353518, 358399, 361562, 361676, 361691, 361706, 361756, 361811, 366730, 366842, 366864, 366944, 366955, 367017, 367378, 425048, 453129, 454508, 454694, 454698, 454705, 454706, 459370, 459895, 460122, 464679, 465105, 465116, 465167, 466606, 467608, 468295, 468296, 468380, 468739, 468817, 470316, 472064, 472600, 472767, 472778, 472785, 472816, 473066, 473136, 473140, 473143, 473151, 473155, 473157, 473184, 473185, 473186, 473282, 473571, 473573, 473578, 474180, 613698, 614291, 615265, 615698, 616622, 616623.

Family Colloniidae

BIC M14086, M14350; **CAS** 13481, 27109, 28756, 33366, 61786, 64307, 102982, 105808, 120439, 122470, 127885, 130443, 131402, 131403, 157605, 160878, 161817, 161819, 161918, 184645, 203119; **MCZ** 7531, 7534, 7539, 29024, 31932, 36712, 42733, 48184, 55898, 55899, 61824, 69097, 78179, 84685, 86230, 87863, 101121, 102484, 176012, 208190, 208191, 208195, 208196, 208198, 208203, 225488, 234954, 239503, 245259, 245261,245281, 252871, 264525, 265022, 292842, 325348, 325352, 325356, 325358, 325359, 325360, 325361, 325363, 325366, 325373, 325377, 325379, 325380, 325387, 325388, 325392, 325394, 329947, 336261, 336262, 336263, 336266, 336267, 336273, 342167, 342168, 349185, 359061, 370541, 373884, 378510, 378511, 383827.

Family Conradiidae

MCZ 23093, 23094, 247276, 247277, 247278; **SBMNH** 452716, 615430.

Family Liotiidae

BIC M3724, M3725, M8231; **MCZ** 50805, 51581, 62372, 83647, 89837, 89838, 89878, 99444, 160509, 160510, 160512, 160513, 160514, 160515, 160516, 160517, 208158, 208184, 221236, 277427, 314226, 325396, 325398, 325400, 329924, 342169, 376874, 378254, 383918, 383920, 383925, 383927, 383969, 386122, 386207, 386214.

Family Margaritidae

BIC M1861, M1944, M1995, M2066, M2251, M2430, M2762, M2792, M3636, M3651, M8883, M12437, M14373; **MCZ** 7541, 7542, 7543, 7544, 7549, 7550, 27907, 68422, 104580, 104683, 104799, 125460, 135005, 135006, 135045, 135151, 135152, 135153, 135154, 135155, 135157, 135158, 135159, 135160, 135161, 145911, 150902, 187729, 187730, 187731, 187943, 196333, 206285, 207126, 226820, 271140, 271141, 271142, 271143, 288095, 291335, 291336, 291337, 291338, 291339, 291340, 291341, 291342, 291343, 291344, 291345, 291346, 291347, 291348, 291349, 291350, 291351, 291352, 291353, 291354, 291355, 291356, 291357, 291358, 291359, 291360, 291361, 291362, 291363, 291364, 291365, 291366, 291367, 291368, 291369, 291370, 291371, 291372, 291373, 291374, 291375, 291376, 291377, 293798, 294918, 294919, 302532, 315676, 331872, 374880.

Family Phasianellidae

BIC M4431, M13499, M14374; **MCZ** 186165, 293721; **SBMNH** 32228, 81256, 82708, 82709, 89132, 141274, 141275, 141488, 141489, 142166, 142167, 142168, 142275, 145587, 151826, 151839, 151840, 151841, 151842, 151843, 151844, 151845, 151846, 152979, 154489, 154490, 155062, 155378, 155777, 158364, 159665, 159715, 159732, 160890, 164059, 210715, 230083, 230084, 230990, 237087, 237118,237119, 237120, 237121, 237122, 237123, 237124, 237125, 237126, 237127, 237130, 237131, 237132, 237133, 237134, 237135, 237136, 237137, 237138, 237139, 237140, 237141, 237142, 237143, 237144, 237145, 237146, 237147, 237148, 237149, 237150, 237151, 237152, 237153, 237154, 237155, 265931, 266028, 266284, 348792, 349197, 349198, 349219, 349221, 356951, 361515, 361519, 361534, 361535, 361560, 361561, 361613, 361631, 361682, 361704, 361705, 366850, 367028, 367063, 367532, 367673, 424374, 424870, 424969, 424976, 453232, 453303, 453790, 453898, 453959, 454457, 454760, 454999, 455033, 455034, 455068, 459425, 470317, 471433, 471470, 471890, 471901, 472122.

Family Skeneidae

BIC M10850, M11752, M11781, M14733, M15365, M16536, M17884; **MCZ** 50806, 101990.

Family Solariellidae

BIC M11660; **MCZ** 156385.

Family Tegulidae

BIC 191, 304, 340, 344, 348, 356, 361, 374, 386, 420, 684, 964, 972, 1017, 1032, 1130, 1139, 1271, 1527, 1635, 3514, 3521, 3522, 3532, 3533, 3534, 3535, 3546, 3547, 3555, 3556, 3966, 7016, 7028, 7169, 7591, 7634, 7753, 7859, 7893, 7948, 8013, 8087, 8631, 8634, 8870, 9156, 9873, 11252, 13165, 13992, 13993, 13995, 13996, 14001, 14002, 15010, 15309, 15313, 16353; **COMA** 2020; **CNMO** 1504, 1510, 1570, 1574, 1575, 2632, 2633, 4064, 4741, 4749, 4762, 4764, 4769, 4843; **CRIM** 499, 743, 744, 745.

Family Trochidae

BIC M3657, M6435, M13500, M14090, M14297, M14339, M14985; **MCZ** 38045, 378644; **SBMNH** 157393, 157463, 157537, 157538, 157600, 157693, 159896, 164024, 237075, 237076, 237164, 237207, 358716, 366845, 367031, 368993, 468367, 472766, 473061, 615686, 615699.

Family Turbinidae

BIC M347, M354, M367, M605, M607, M691, M692, M725, M799, M909, M991, M1022, M1085, M1526, M2621, M4252, M4262, M4263, M4267, M4316, M7020, M7038, M7166, M7949, M8360, M11379, M13498, M13929, M13998, M13999, M14000, M14109, M14127, M14213, M14359, M14937, M17856.

CNMO 1221, 1449, 1473, 1500, 1501, 1505, 1506, 1507, 1521, 1522, 1562, 1567, 1568, 1595, 2309, 2440, 2948, 2949, 4188, 4755, 4858, 4860, 5482, **CRIM**:5178; **MCZ** 2622, 2624, 2626, 21059, 23118, 23457, 23940, 23942, 28747, 29482, 29483, 29724, 32043, 35688, 35702, 36004, 36007, 36009, 36010, 37935, 37937, 37938, 37941, 37945, 37948, 37949, 37953, 37954, 37962, 37963, 37968, 38025, 38030, 38115, 40507, 42717, 42720, 42728, 49063, 49074, 54649, 56106, 56714, 57406, 57559, 57622, 57634, 57856, 57878, 59464, 60059, 60556, 60570, 62408, 62636, 62670, 62837, 62846, 62847, 63381, 63383, 64699, 64722, 66134, 66285, 66353, 66357, 67055, 67275, 67310, 67667, 68085, 69169, 69488, 70220, 70326, 71008, 71584, 71590, 71592, 71624, 73493, 73494, 73551, 73552, 73553, 73554, 73555, 75494, 75886, 75893, 75902, 76713, 77730, 77785, 77800, 79821, 81244, 82076, 82077, 82176, 82236, 82247, 82360, 83176, 83177, 89005, 89337, 89682, 89831, 89835, 90753, 91236, 91240, 93475, 93513, 93532, 93567, 94429, 95970, 96000, 96234, 96241, 96247, 96719, 97351, 97409, 97813, 98850, 102862, 105718, 106159, 106488, 108020, 109091, 110153, 111525, 111753, 112147, 113200, 113201, 113302, 115487, 115748, 115813, 116430, 118681, 118806, 119319, 119323, 119324, 124112, 124962, 125397, 129637, 129722, 129788, 129832, 129853, 133473, 133493, 133601, 133606, 133684, 134535, 134902, 135558, 137681, 137682, 137719, 139052, 139053, 139415, 139432, 142166, 142598, 143133, 143150, 143185, 144445, 144477, 144845, 144850, 145664, 145675, 146459, 148573, 148585, 150288, 151300, 153407, 153408, 153409, 153412, 153414, 153417, 153418, 153420, 153425, 153427, 153431, 153435, 153436, 153438, 153441, 153442, 153443, 153448, 153449, 153453, 153454, 155193, 155194, 156210, 156304, 156502, 156506, 159163, 160867, 164833, 165290, 165293, 165296, 168561, 171978, 173191, 174408, 174437, 175512, 179659, 182578, 182652, 182703, 183855, 185274, 185275, 195806, 196097, 196109, 197002, 197064, 197174, 197431, 198462, 198585, 198692, 198711, 199024, 200459, 206286, 208206, 208207, 208209, 208211, 208213, 208219, 208220, 208222, 208223, 208224, 208226, 208227, 208229, 208231, 208241, 208249, 208253, 208254, 208272, 208278, 208279, 208280, 208282, 208287, 208289, 208290, 208291, 208304, 208305, 208306, 208310, 208311, 208317, 208319, 208321, 208323, 208325, 208327, 210016, 211353, 211630, 211840, 211874, 211876, 212227, 212425, 212603, 212734, 212913, 212938, 212952, 213434, 215134, 215191, 215216, 215320, 215321, 215863, 215966, 216415, 216416, 216442, 216443, 216497, 216763, 217202, 218548, 218655, 219546, 219553, 219595, 219837, 221027, 222146, 224388, 224662, 225078, 229085, 229086, 229087, 230655, 233298, 233311, 233324, 236859, 237744, 237763, 238524, 238592, 238639, 238712, 238747, 238919, 240983, 240986, 242363, 242413, 243184, 244063, 246165, 246713, 247966, 250422, 250447, 251597, 251848, 252466, 252648, 252666, 253012, 253034, 254087, 254143, 254826, 254832, 255648, 255666, 255667, 255708, 261368, 261554, 261555, 261556, 261559, 261561, 261563, 261788, 261803, 262269, 262502, 262503, 263122, 263123, 263185, 263215, 263367, 265163, 265588, 265629, 265683, 265840, 266131, 266196, 266404, 266614, 267403, 267923, 273035, 275531, 275532, 277709, 280687, 280688, 280690, 280691, 281482, 281825, 281842, 281843, 282179, 282184, 282931, 282933, 282936, 289581, 289582, 289585, 289586, 289590, 289592, 289593, 291825, 291832, 291834, 291837, 291838, 291839, 291841, 292073, 293884, 293885, 293886, 294579, 298592, 298610, 298633, 298640, 298655, 298657, 298662, 298663, 301974, 302178, 302527, 302826, 302909, 316919, 325302, 325303, 325304, 325309, 325311, 325313, 325314, 325315, 325317, 325318, 325324, 325328, 325334, 325337, 325431, 325436, 325440, 325452, 325453, 328380, 328385, 328394, 328395, 328397, 328401, 328402, 328403, 329605, 329866, 329868, 329870, 339831, 360126, 360135, 360136, 360138, 360139, 360140, 362708, 362729, 362758, 363197, 363468, 363569, 363630, 366142, 369998, 370656, 371814, 373577, 373581, 373628, 374963, 374967, 376871, 376873, 376878, 376893, 376903, 378291, 378778, 378779, 383850, 383852, 383853, 383855, 383856, 383857, 383863, 383865, 383869, 383870, 383875, 383876, 383881, 383884, 383889, 383890, 383895, 383899, 383906, 383909, 383910, 386107, 386135, 386136, 386164, 386236; **SBMNH** 95823, 138145, 151948, 158203, 158208, 158549, 158565, 158571, 158702, 237112, 237219, 358391, 358435, 367167, 367922, 454285, 454484, 470936, 470999, 471515, 471517, 615064.

Capítulo II

Distributional patterns of Vetigastropoda (Mollusca) all over the world: a track analysis

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Distributional patterns of Vetigastropoda (Mollusca) all over the world: a track analysis

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The distributional patterns of the species of the mollusc subclass Vetigastropoda were analysed using the panbiogeographical method of track analysis. We analysed distributional data of 434 species and 72 genera of the world obtained from specialized literature and records in 12 malacological collections. We constructed the individual tracks for the species analysed and superimposed them, applying a parsimony analysis of endemicity with progressive character elimination. We identified 26 generalized tracks, extending in the Pacific Ocean (14), Indian Ocean (six), Atlantic Ocean (four), Mediterranean Sea (one) and Atlantic–Pacific Oceans (one). The generalized tracks show the complex relationships of the mollusc biota, representing geographical and phylogenetic boundaries of taxa with diverse geographical affinities. Five panbiogeographical nodes were identified by the intersection of two or more generalized tracks. Our analysis offers an approximation for understanding the distributional patterns of vetigastropod species worldwide from the perspective of evolutionary or historical biogeography. The results obtained for the Vetigastropoda coincide completely or in part with those previously presented for other taxa. The generalized tracks support hypotheses of primary biogeographical homology that might be corroborated by evidence from other different, phylogenetically unrelated taxa.

ADDITIONAL KEYWORDS: biogeography – Gastropoda – geographical distribution – historical biogeography – marine – systematics.

INTRODUCTION

With ~100 000 living species, Mollusca are a phylum with the second largest number of animal species (Ponder & Lindberg, 2008; Sigwart *et al.*, 2021). This group is ancient, with a fossil record dating back to the Cambrian period, 541 Mya (Valentine *et al.*, 1999; Cohen *et al.*, 2013). Molluscs inhabit all types of environments and have varied feeding habits (Hickman *et al.*, 2001). The class Gastropoda is the most abundant and diverse of the phylum (Ponder & Lindberg, 2008; Rosenberg *et al.*, 2009). The current phylogenetic classification of gastropods is based on morphological and molecular characters (Bouchet *et al.*, 2017).

Vetigastropoda are a group of molluscs distributed worldwide (Williams *et al.*, 2007). They were formerly classified in Prosobranchia and later proposed as an independent subclass based on phylogenetic criteria (Bouchet *et al.*, 2017). Numerous faunistic lists have been published detailing the species that inhabit various countries (Agudo-Padrón *et al.*, 2009; Ojeda *et al.*, 2014), but little attention has been paid to their distributional patterns at a global scale and to the processes that might have shaped these distributions. Vetigastropods extend back several million years in geological time (Wanninger & Wollesen, 2019) and, owing to their global distribution, they might have been influenced by global climatic changes and geological events shaping the structure and distribution of marine ecosystems worldwide (Díaz-Merlano & Puyana-Hegedus, 1994; Ávila & Malaquias, 2003; Linse *et al.*, 2006). Several authors have associated various biotic and abiotic factors with the expansion of the

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*Corresponding author. E-mail: juanmorrone2001@yahoo.com.mx distribution of some taxa of Vetigastropoda (Crothers, 1994; Wares *et al*., 2001; Walther *et al*., 2002; Yee & Murray, 2004; Mieszkowska *et al*., 2007; Benkendorfer & Soares, 2009; Mieszkowska & Lundquist, 2011; Wernberg *et al*., 2011; Haupt *et al*., 2013; Petuch, 2013; Saleky *et al*., 2016; Yamazaki *et al*., 2017; Bañón *et al*., 2019; López-Márquez *et al*., 2019; Son *et al*., 2020).

Panbiogeography is an approach that emphasizes the spatial dimension of biodiversity (Craw *et al*., 1999) and assumes that vicariance is the process shaping the general patterns of biotic distribution (Escalante *et al*., 2018). It is applied through a track analysis, which allows primary biogeographical homology to be hypothesized based on the comparison of individual tracks of different taxa and the identification of generalized tracks and nodes (Morrone, 2004). The generalized tracks can be arranged hierarchically in a biogeographical classification system (Morrone & Escalante, 2016), which can be contrasted with systems previously developed with other methods (Escalante, 2009). Track analyses have been applied to freshwater taxa, such as fish, crustaceans and plants (Huidobro *et al*., 2006; Herrera-Vázquez *et al*., 2008; Echeverry & Gallo, 2015; Cavalcanti *et al*., 2019), whereas studies on marine taxa are few and have dealt with macroalgae, crustaceans, hagfishes, mammals, reef fish, sharks and flatworms (Aguilar-Aguilar & Contreras-Medina, 2001; Heads, 2005; Cavalcanti & Gallo, 2008; Celis-Villalba, 2009; Espinosa-Pérez *et al*., 2009; Gallo *et al*., 2010; Martínez-Castro, 2014). Track analyses for other groups, such as molluscs, are non-existent. Several quantitative methods have been proposed to perform track analyses (Escalante *et al*., 2018), but the most widely used is parsimony analysis of endemicity (PAE; Echeverry & Morrone, 2010; Morrone, 2015). Our main objective was to analyse the distributional patterns of vetigastropod species worldwide through a track analysis to contribute to a preliminary assessment of their biotic evolution.

MATERIAL AND METHODS

The track analysis was performed using 8700 distributional records (occurrence points) of the subclass Vetigastropoda obtained from specialized literature and malacological collections with records of species available in online databases (Table 1). Georeferenced data available in the literature or in the query databases were used, and for those where this information was not available, the name of the locality was searched in Google Earth (2021) to obtain the georeference.

Individual tracks were constructed for each species by a script in R software using Prim's algorithm to connect them by minimum spanning trees (Page, 1987). To build the data matrix of 506 species and 642 cells (Supporting Information, Table S1), individual tracks were mapped onto a grid of 6° × 6° of latitude and longitude (Vargas *et al*., 2008) on a world map, and their presence or absence in each grid cell was coded with 1 or 0, respectively. This analysis applies a parsimony algorithm to the data matrix from supraspecific and specific taxa (Rosen & Smith, 1988; Escalante, 2009), where clades supported by two or more species represent

Table 1. Mexican and international collections (USA) consulted in the present study

Collection	Acronym
Colección Nacional de Moluscos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico	CNMO
Colección Malacológica 'Dr Antonio García-Cubas', Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico City, Mexico	COMA
Colección Regional de Invertebrados Marinos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico City, Mexico	CRIM
The Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA	ANSP
Invertebrate Zoology Collection, California Academy of Sciences, San Francisco, CA, USA	CAS
Mollusk Collection, Field Museum of Natural History, Chicago, IL, USA	FMNH
Invertebrate Zoology Collection, Florida Museum of Natural History, Gainesville, FL, USA	FLMNH
Malacology Collection, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA	MCZ
Malacology Collection, Natural History Museum of Los Angeles County, Los Angeles, CA, USA	NHM
Invertebrate Zoology, National Museum of Natural History, Washington, DC, USA	NMNH
Invertebrate Zoology, Santa Barbara Museum of Natural History, Santa Barbara, CA, USA	SBMNH
Benthic Invertebrate Collection, Scripps Institution of Oceanography, University of California, San Diego, CA, USA	BIC

generalized tracks (Escalante *et al*., 2018). Data from the genera with more than one species were added to this matrix to increase the evidence analysed. Data matrices were analysed with TNT v.1.5 (Goloboff & Catalano, 2016) with a traditional heuristic search (TBR, maximum of 1000 trees and 100 replications). We applied a parsimony analysis of endemicity with progressive character elimination, also named PAE-PCE (Echeverry & Morrone, 2010), with WINCLADA (Nixon, 1999). This program was used to visualize the most parsimonious cladograms, when there were two or more equally parsimonious cladograms, to obtain the strict consensus cladogram. Clades supported by two or more taxa were considered as a generalized track (GT), and then taxa supporting the clades (synapomophies) were eliminated from the data matrix, repeating the parsimony analysis until no more synapomorphies were found. Clades obtained in different analyses identify generalized tracks, and the areas where different generalized tracks overlap are considered to represent panbiogeographical nodes.

RESULTS

The PAE was applied to the data matrix (Supporting Information, Table S1) and a strict consensus cladogram obtained (2469 steps, consistency index of 0.20 and retention index of 0.70). After removal of synapomorphies supporting clades from this first cladogram, a second run led to another consensus cladogram (2524 steps, consistency index of 0.20 and retention index of 0.69). Subsequently, a third analysis did not show more synapomorphies in the cladograms obtained. Based on the clades in the cladograms, we identified 26 generalized tracks (Fig. 1). The number of synapomorphies supporting the generalized tracks in the cladogram ranged from two to 19 species. The generalized tracks are as follows:

(a) Japan GT: from Tosa Bay to Sagami Bay in Japan. It is supported by two species: *Haliotis gigantea* Gmelin, 1791 and *Tristichotrochus aculeatus* (G. B. Sowerby III, 1912).

(b) Philippines GT: from east of the island of Taiwan, through the Philippine Archipelago to the Celebes Sea. It is supported by two

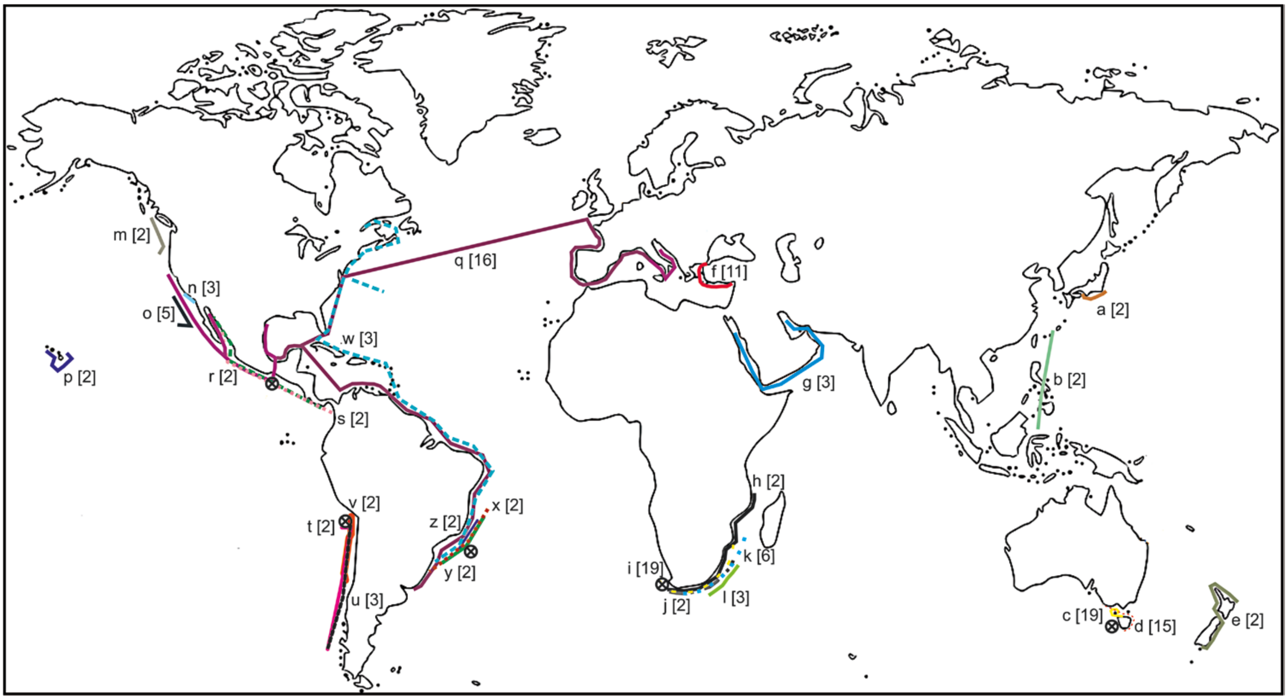

Figure 1. Generalized tracks obtained in the analysis: (a) Japan; (b) Philippines; (c) Tasmania; (d) South-eastern Australia; (e) New Zealand; (f) Mediterranean Sea; (g) Arabian Peninsula; (h) South Africa–Mozambique; (i) Eastern South Africa; (j) South Africa; (k) Western South Africa; (l) Port Alfred–Kosi Bay; (m) North Pacific; (n) Northern Archipelago; (o) North-west Coast of California; (p) Hawaiian Archipelago; (q) Pacific–Atlantic; (r) Gulf of California–Colombia; (s) Gulf of California–Panama; (t) Peru–Chile; (u) South American; (v) Chile; (w) Western Atlantic; (x) Espiritu Santo–Rio Grande; (y) South Brazil; and (z) South-eastern Brazil. The nodes are labelled with a cross inside a circle. Numbers in square brackets indicate the number of species supporting each generalized track.

species: *Anatoma equatorial* (Hedley, 1899) and *Anatoma finlayi* (Powell, 1937).

(c) Tasmania GT: South Pacific Ocean, ranging from Yellow Rock Beach on King Island, running along the west coast of this island to the south until it reaches Surprise Bay, passing through Tasmania from Hunter Island until it reaches Storm Bay. It is supported by two genera, *Argalista* Iredale, 1915 and *Austroliotia* Cotton, 1948, and 19 species: *Amblychilepas oblonga* (Menke, 1843), *Argalista rosea* (Tenison Woods, 1876), *Argalista kingensis* May, 1923, *Astele armillata* (Wood, 1828), *Astele subcarinata* Swainson, 1855, *Austroliotia australis* (Kiener, 1838), *Austroliotia botanica* (Hedley, 1915), *Calliostoma allporti* (Tenison Woods, 1876), *Chlorodiloma adelaidae* (Philippi, 1851), *Emarginula candida* A. Adams, 1852, *Emarginula dilecta* A. Adams, 1852, *Fissurellidea megatrema* d'Orbigny, 1839, *Herpetopoma scabriusculum* (A. Adams & Angas, 1867), *Liotella annulata* (Tenison Woods, 1878), *Phasianotrochus irisodontes* (Quoy & Gaimard, 1834), *Scutus antipodes* Montfort, 1810, *Sukashitrochus pulcher* (Petterd, 1884), *Tricolia rosea* (Angas, 1867) and *Zalipais inscripta* (Tate, 1899).

(d) South-eastern Australia GT: South Pacific Ocean; it ranges from Portland in Victoria, Australia, passing through King Island to the Saltwater River in Tasmania. It is supported by four genera, *Amblychilepas* Pilsbry, 1890, *Chlorodiloma* Pilsbry, 1889, *Fossarina* A. Adams & Angas, 1864 and *Phasianotrochus* P. Fischer, 1885, and 15 species: *Amblychilepas javanicensis* (Lamarck, 1822), *Amblychilepas nigrita* (G. B. Sowerby I, 1835), *Calliostoma hedleyi* Pritchard & Gatliff, 1902, *Chlorodiloma odontis* (W. Wood, 1828), *Cirsonella weldii* (Tenison Woods, 1877), *Clanculus aloysii* Tenison Woods, 1876, *Clanculus flagellates* (Philippi, 1849), *Clanculus limbatus* (Quoy & Gaimard, 1834), *Clanculus plebejus* (Philippi, 1851), *Clanculus undatus* (Lamarck, 1816), *Diloma concameratum* (W. Wood, 1828), *Fossarina legrandi* Petterd, 1879, *Lodderena minima* (Tenison Woods, 1878), *Macrochisma tasmaniae* G. B. Sowerby II, 1862 and *Phasianotrochus irisodontes* (Quoy & Gaimard, 1834).

(e) New Zealand GT: south-eastern part of the Pacific Ocean, at the western end of the North and South Islands; the line covers the east coast of both islands. It is supported by two subspecies: *Haliotis virginea virginea* Gmelin, 1791 and *Haliotis virginea crispata* A. Gould, 1847.

(f) Mediterranean Sea GT: within the Mediterranean Sea, it ranges from the Sea of Mamara in Turkey, passing through the Aegean Sea to the Syrian coast. It is supported by 11 species: *Clanculus corallinus* (Gmelin, 1791), *Clanculus cruciatus* (Linnaeus, 1758), *Clelandella miliaris* (Brocchi, 1814), *Emarginula rosea* Bell, 1824, *Gibbula guttadauri* (Philippi, 1836), *Gibbula magus* (Linnaeus, 1758), *Jujubinus exasperatus* (Pennant, 1777), *Jujubinus striatus* (Linnaeus, 1758), *Phorcus mutabilis* (Philippi, 1851), *Steromphala adansonii* (Payraudeau, 1826) and *Steromphala albida* (Gmelin, 1791).

(g) Arabian Peninsula GT: northern Indian Ocean; it ranges from the Red Sea, passing through the Gulf of Aden and the Arabian Sea to the Persian Gulf. It is supported by the genus *Priotrochus* P. Fischer, 1879 and three species: *Ethminolia degregorii* (Caramagna, 1888), *Monodonta nebulosa* (Forsskål in Niebuhr, 1775) and *Priotrochus obscurus* (W. Wood, 1828).

(h) South Africa–Mozambique GT: this track is located from the south-eastern Atlantic Ocean to the western Indian Ocean. It runs from St. Helena Bay, Jeffreys Bay to Durban, following the west coast of Africa north to the Mozambique Channel and Pemba. It is supported by the genus *Oxystele* Philippi, 1847 and two species: *Ethalia striolata* (A. Adams, 1855) and *Trochus cariniferus* Reeve, 1842.

(i) Eastern South Africa GT: this track is located in the south-eastern Atlantic Ocean towards the western Indian Ocean. It runs from Saldanha Bay, Cape Town, through the south coast to Kosi Bay. It is supported by 19 species: *Calliostoma ornatum* (Lamarck, 1822), *Cinysca spuria* (Gould, 1861), *Clanculus miniatus* (Anton, 1838), *Diodora elevata* (Dunker, 1846), *Diodora elizabethae* (E. A. Smith, 1901), *Fissurella mutabilis* G. B. Sowerby I, 1835, *Gibbula benzi* (F. Krauss, 1848), *Gibbula zonata* (W. Wood, 1828), *Haliotis alfredensis* Bartsch, 1915, *Oxystele sinensis* (Gmelin, 1791), *Oxystele tabularis* (F. Krauss, 1848), *Oxystele tigrina* (Dillwyn, 1817), *Pseudominolia articulate* (Gould, 1861), *Puncturella capensis* Thiele, 1919, *Tricolia bicarinata* (Dunker, 1846), *Tricolia capensis* (Dunker, 1846), *Tugali barnardi* (Tomlin, 1932), *Turbo cidaris* Gmelin, 1791 and *Turbo cidaris cidaris* Gmelin, 1791.

(j) South Africa GT: this track is located in the south-eastern Atlantic Ocean. It runs from Cape Town Bay to Durban. It is supported by two species: *Gibbula cicer* (Philippi, 1844) and *Tricolia kochii* (Philippi, 1848).

(k) Western South Africa GT: this track is located in the south-eastern Atlantic Ocean towards the western Indian Ocean. It runs from Cave Agulhas, through the south coast to Kosi Bay. It is supported by six species: *Cosmetalepas africana* (Tomlin, 1926), *Emarginula thorektes* Kilburn, 1978, *Profundisepta voraginosa* (Herbert & Kilburn, 1986), *Pseudotorinia kraussi* J. E. Gray in M. E. Gray, 1850, *Sinezona doliolum* Herbert, 1986 and *Tristichotrochus multiliratus* (G. B. Sowerby III, 1875).

(l) Port Alfred–Kosi Bay GT: this track is located in the south-eastern Atlantic Ocean towards the western Indian Ocean. It run from Port Alfred to Kosi Bay in South Africa. It is supported by three species: *Diodora kraussi* Herbert & Warén, 1999, *Emarginula macclurgi* Kilburn, 1978 and *Emarginula viridicana* Herbert & Kilburn, 1986.

(m) Eastern North Pacific GT: this track is located in the north-eastern Pacific Ocean. It runs from the south of Vancouver Island, Canada to front Yachats, OR, USA. It is supported by two species: *Clypeosectus curvus* McLean, 1989 and *Temnocinclis euripes* McLean, 1989.

(n) Northern Archipelago GT: this track is located in the eastern Central Pacific. It runs from Guadalupe beach, CA, USA, passing through the Californian Channel Islands to Vista Hermosa at southern Ensenada, Baja California, Mexico. It is supported by three species: *Calliostoma gemmulatum* Carpenter, 1864, *Calliostoma tricolor* Gabb, 1865 and *Calliostoma turbinum* Dall, 1896.

(o) North-west coast of California GT: this track is located in the eastern Central Pacific. It runs from Point Fermin, CA, USA, through Guadalupe Island, Mexico, off the Baja California Peninsula to the south at Tortugas Bay. It is supported by five species: *Haliotis cracherodii* Leach, 1814, *Megastraea turbanica* (Dall, 1910), *Tegula eiseni* E. K. Jordan, 1936, *Tegula gallina* (Forbes, 1852) and *Tegula regina* (Stearns, 1892).

(p) Hawaiian Archipelago GT: this track is located in the central Pacific. It runs from Waialua Beach on the island of Oahu to Hilo Bay on the Big Island, Hawaii. It is supported by two species: *Leptothyra candida* (Pease, 1861) and *Sinezona kayae* Geiger & McLean, 2010.

(q) Pacific–Atlantic GT: widely distributed across the Pacific and Atlantic Oceans. It is supported by 16 species: *Calliostoma gordanum* McLean, 1970, *Calliostoma nepheloide* Dall, 1913, *Cittarium pica* (Linnaeus, 1758), *Diodora inaequalis* (G. B. Sowerby I, 1835), *Diodora listeri* (d'Orbigny, 1847), *Fissurella barbadensis* (Gmelin, 1791), *Fissurella nodosa* (Born, 1778), *Fissurella oriens* G. B. Sowerby I, 1834, *Fissurella spongiosa* Carpenter, 1857, *Fissurella volcano* Reeve, 1849, *Fissurellidea bimaculata* Dall, 1871, *Lucapina suffuse* (Reeve, 1850), *Lucapinella limatula* (Reeve, 1850), *Montfortia Hermosa* (H. N. Lowe, 1935), *Tegula rubroflammulata* (Koch in Philippi, 1843) and *Turbo funiculosus* Kiener, 1848.

(r) Gulf of California–Colombia: This track is located in the eastern central Pacific towards the south-eastern Pacific. It runs from south of Coronado Island in the Gulf of California through the Mexican and Mesoamerican Pacific and south to Bahía Solano, Chocó, Colombia. It is supported by two species: *Octomarginula natlandi* (Durham, 1950) and *Uvanilla olivacea* (W. Wood, 1828).

(s) Gulf of California–Panama: this track is located in the eastern Central Pacific towards the south-eastern Pacific. It runs from south of Kino Bay in Los Choyudos, Sonora, Mexico in the Gulf of California through the Mexican and Mesoamerican Pacific and south to the Gulf of Chiriquí, Panama. It is supported by two species: *Calliostoma aequisculptum* Carpenter, 1865 and *Calliostoma rema* A. M. Strong, Hanna & Hertlein, 1933.

(t) Peru–Chile GT: this track is located in the south-eastern Pacific; it runs from Bahía de la Independencia, Peru, south to Chiloe Island, Chile. It is supported by two species: *Fissurella costata* Lesson, 1831 and *Fissurella crassa* Lamarck, 1822.

(u) South American GT: this track is located in the south-eastern Pacific; it runs from Caleta Camarones, south to Chiloe Island, Chile. It is supported by three species: *Fissurella cumingi* Reeve, 1849, *Fissurella latimarginata* G. B. Sowerby I, 1835 and *Fissurella limbata* G. B. Sowerby I, 1835.

(v) Chile GT: this track is located in the south-eastern Pacific; it runs from Punta Camarones to Concepción, Chile. It is supported by two species: *Tegula tridentata* (Potiez & Michaud, 1838) and *Tegula luctuosa* (d'Orbigny, 1841).

(w) Western Atlantic GT: this track is located on the western coast of the Atlantic Ocean. It runs from Quebec, Canada, through Bermuda and southwards through the West Indies to Santa Catarina, Brazil. It is supported by three species: *Astralium latispina* (Philippi, 1844), *Diodora meta* (Ihering, 1927) and *Puncturella granulata* (Seguenza, 1863).

(x) Espírito Santo–Rio Grande GT: this track is located in the south-western Atlantic. It runs from San Mateo, Espírito Santo to Porto Alegre, Rio Grande do Sul, Brazil. It is supported by two species: *Anatoma copiosa* Pimenta & Geiger, 2015 and *Solariella carvalhoi* Lopes & Cardoso, 1958.

(y) South Brazil GT: this track is located in the south-western Atlantic. It runs from San Mateo, Espíritu Santo to Santa Catarina, Brazil. It is supported by two species: *Arene microforis* (Dall, 1889) and *Falsimargarita imperialis* (Simone & Birman, 2006).

(z) South-eastern Brazil GT: this track is located in the south-western Atlantic. It runs from San Mateo, Espírito Santo to Ilha Grande, Rio de Janeiro, Brazil. It is supported by two species: *Haliotis pourtalesii aurantium* Simone, 1998 and *Halystina umberlee* Salvador, Cavallari & Simone, 2014.

Fourteen generalized tracks were identified extending in the Pacific Ocean, six in the Indian Ocean, four in the Atlantic Ocean, one in the Mediterranean Sea and one spanning the Atlantic and Pacific Oceans. Five panbiogeographical nodes were identified by the intersection of two or more generalized tracks: (1) Tasmania (c) and South-eastern Australia (d); (2) South Africa–Mozambique (h), Eastern South Africa (i), South Africa (j) and Western South Africa (k); (3) Pacific–Atlantic (q), Gulf of California–Colombia (r) and Gulf of California–Panama (s); (4) Peru–Chile (t), South American (u) and Chile (v); and (5) Pacific–Atlantic (q), Western Atlantic (w), Espírito Santo–Rio Grande (x), South Brazil (y) and South-eastern Brazil (z) (Fig. 1).

DISCUSSION

Most of the generalized tracks are located within the warm and warm temperate provinces proposed by Briggs & Bowen (2012), except for the Tasmanian, South Australian, New Zealand and North Pacific. Although the present work is framed in an evolutionary biogeographical framework, there are some coincidences between our generalized tracks and 64 ecoregions, 23 provinces and ten realms recognized by Spalding *et al*. (2007) (Table 2).

Glasby (2006) analysed the relationships between 24 areas of endemism of polychaetes by applying a Brooks Parsimony Analysis. Our generalized tracks correspond to 19 of his areas of endemism, which are included in three realms proposed by the author: 11 of them in the Boreal Realm, five in the Pantropical Realm and three in the Austral Realm. Van Soest & Hajdu (1997) analysed the relationships between 31 areas of endemism of sponges. Our generalized tracks correspond to 18 of these areas of endemism, which are included in four of the 'wide' areas of endemism. This allows us to hypothesize that groups of marine invertebrates share similar environmental requirements and respond in a similar way to habitat changes (Colman, 1940; Ellingsen, 2002; Xie *et al*., 2016; Van der Linden *et al*., 2017; Holman *et al*., 2021). This helps us to recognize the co-evolution of marine areas and organisms; such a pattern can be extended to other groups of benthic marine invertebrates and even fish (van Soest & Hajdu, 1997).

Some of our generalized tracks coincide, in part, with those indicated by other authors working with different marine species. Three generalized tracks proposed by Cavalcanti & Gallo (2008) for hagfishes are similar to those found in the present work. Their Western Pacific track is similar to our Philippines GT, except that this track extends further to the south. Their North Eastern Pacific track is similar to our Eastern North Pacific GT and like the section that crosses the Pacific Ocean of the Atlantic–Pacific GT, except that the track of Cavalcanti & Gallo (2008) is continuous from the peninsula of Baja California to Canada. In the same way, their Southern Eastern Pacific track is similar to our Chile GT, except that it is more extensive towards the north.

Two of the generalized tracks for marine mammals found by Aguilar-Aguilar & Contreras-Medina (2001) are similar to those of the present study. Their American Pacific generalized track is like a section of our Atlantic–Pacific GT, but Aguilar-Aguilar & Contreras-Medina's (2001) track is more extensive because it covers the entire Pacific coast of the USA, Canada and Alaska. A coincidence was also found with regard to a section of the Pacific–Atlantic GT that runs through the Gulf of Mexico, the Caribbean Sea and the coasts of Venezuela, Suriname, Guyana, French Guyana and Brazil, but the Atlantic generalized track of these authors crosses the Atlantic Ocean from the coast of America to Africa, whereas our GT crosses towards Europe instead of Africa. Our Western Atlantic GT is more similar to the track of Aguilar-Aguilar & Contreras-Medina (2001) than the Atlantic–Pacific track, except that the Western Atlantic GT is broader to the north, because it reaches the Atlantic coast of Canada, and to the south in Santa Catarina, Brazil, but does not cross to Africa.

The Gulf of California–Colombia and Gulf of California–Panama GT resemble a section of the Pacific track of Vargas *et al*. (2008) obtained with coral species of the genus *Pacifigorgia* Bayer, 1951; this track runs from the Gulf of California, Mexico southwards through the Gulf of Panama to Rio Grande do Sul, Brazil. Our Atlantic–Pacific GT is similar, except that it crosses the isthmus of Tehuantepec and extends further south to Santa Catarina, Brazil.

Espinosa-Pérez *et al*. (2009) found three generalized tracks for the isopods distributed in the Eastern Pacific; these tracks coincide, in part, with our analysis, in the area that corresponds to the North Pacific, North-west Coast of California and Northern Archipelago GT, in addition to the three GT that include South America off the coasts of Peru and Chile. In contrast, our Pacific tracks coincided, in part, with a temperate–cold north-eastern Pacific track from the work on Cirripedia by Celis-Villalba (2009). Our Gulf of California–Colombia and Gulf of

Table 2. Comparison between the generalized tracks and marine regionalization system by Spalding *et al.* (2007)

Generalized track	Ecoregions	Provinces	Realms
a	[51] Central Kuroshio Current	Warm Temperate North-west Pacific	Temperate Northern Pacific
b	[121] South Kuroshio [127] Eastern Philippines [128] Sulawesi Sea/Makassar Strait	South Kuroshio Western Coral Triangle	Central Pacific
c	[204] Cape Howe	South-east Australian Shelf	Temperate Australasia
d	[205] Bassian [206] Western Bassian		
e	[196] North-eastern New Zealand [199] Central New Zealand [200] South New Zealand	Northern New Zealand	Temperate Australasia
f	[31] Aegean Sea [32] Levantine Sea	Mediterranean Sea	Temperate Northern Atlantic
g	[87] Northern and Central Red Sea [88] Southern Red Sea [89] Gulf of Aden [90] Arabian Persian Gulf [91] Gulf of Oman	Red Sea and Gulf of Aden Somali/Arabian	Western Indo-Pacific
h	[95] East African Coral Coast	Western Indian Ocean	Western Indo-Pacific
i	[101] Bright of Sofala/Swamp Coast	Benguela	Temperate Southern Africa
j	[191] Namaqua	Agulhas	
k	[192] Agulhas Bank		
l	[193] Natal		
m	[57] Oregon, Washington, Vancouver Coast and Shelf	Cold Temperate North-east Pacific	Temperate Northern Pacific
n	[57] Oregon, Washington, Vancouver Coast and Shelf	Cold Temperate North-east Pacific	Temperate Northern Pacific
o	[58] Northern California		
p	[152] Hawaii	Hawaii	Eastern Indo-Pacific
q	[26] Celtic Seas [27] South European Atlantic Shelf [30] Adriatic Sea [34] Ionian Sea [35] Western Mediterrean [36] Alboran Sea [41] Virginian [42] Carolinian [43] Northern Gulf of Mexico [58] Northern California [59] Southern California Bight [60] Cortezian [61] Magdalena Transition [65] Greater Antilles [66] Southern Caribbean [67] Southwestern Caribbean [68] Western Caribbean [69] Southern Gulf of Mexico [70] Floridian [71] Guianan [72] Amazonia	Northern European Seas, Lusitanian, Mediterranean Sea, Cold Temperate North-west Atlantic, Warm Temperate North-west Atlantic, Cold Temperate North-east Pacific, Warm Temperate North-east Pacific, Tropical North-western Atlantic, North Brazil Shelf, Tropical South-western Atlantic, Tropical East Pacific, Warm Temperate South-western Atlantic	Temperate Northern Atlantic, Temperate Northern Pacific, Tropical Atlantic, Tropical Eastern Pacific, Temperate South America

Table 2. Continued

Generalized track	Ecoregions	Provinces	Realms
	[75] North-eastern Brazil [76] Eastern Brazil [166] Mexican Tropical Pacific [167] Chiapas–Nicaragua [180] South-eastern Brazil [181] Rio Grande [183] Uruguay–Buenos Aires Shelf		
r s	[60] Cortezian [166] Mexican Tropical Pacific [167] Chiapas–Nicaragua [168] Nicoya [170] Panama Bright	Warm Temperate North-east Pacific Tropical East	Temperate Northern Pacific, Tropical Eastern Pacific
t u v	[176] Humboldtian [177] Central Chile [178] Araucanian [188] Chiloense	Warm Temperate South-eastern Pacific Magallanic	Temperate South America
w	[37] Gulf of St. Lawrence–Eastern Scotian Shelf [39] Scotian Shelf [40] Gulf of Maine/Bay of Fundy [41] Virginian [42] Carolinian [62] Bermuda [64] Eastern Caribbean [65] Greater Antilles [66] Southern Caribbean [70] Floridian [71] Guianan [72] Amazonia [75] North-eastern Brazil [76] Eastern Brazil [180] South-eastern Brazil	Cold Temperate North-west Atlantic, Warm Temperate North-west Atlantic, Tropical North-western Atlantic, North Brazil Shelf, Tropical South-western Atlantic, Warm Temperate South-western Atlantic	Temperate Northern Atlantic, Tropical Atlantic, Temperate South America
x y z	[76] Eastern Brazil [180] South-eastern Brazil [181] Rio Grande	Tropical South-western Atlantic Warm Temperate Atlantic	Tropical Atlantic, Temperate South America

The [ ] indicate the ecoregion number from Spalding *et al.* (2007).

California–Panama GT coincide, in part, with the tropical Eastern Pacific track of that study. In turn, our Western Atlantic GT coincides broadly with the tropical western Atlantic track of that work, but it is wider to the north and south.

Gallo *et al.* (2010) found two generalized tracks on the east coast of the Atlantic (Caribbean and eastern coast of South America), which are similar to a section of our Atlantic–Pacific GT and to our Western Atlantic GT in the Atlantic Ocean. However, our tracks are wider northwards along the coast of the USA and Canada. Regarding the track analysis carried out by Martínez-Castro (2014) for sharks, a generalized track was found that connects the Atlantic coast of America with the Mediterranean Sea in a similar way to our Atlantic–Pacific GT. The latter includes a connection through the Panama Canal, which was also pointed out by Ortigosa-Gutiérrez (2009), who found a great affinity between the heterobranch molluscs of the Pacific and the Atlantic. The Indo-Pacific generalized track resembles, in part, our Philippine GT, but the generalized track of sharks is wider towards the south of Australia.

When considering other biogeographical analyses based on molluscs, Geiger's (1999) analysis of the family Haliotidae worldwide recognized a group that corresponds to the South African GT. Cunha *et al*. (2019) presented a distribution similar to that of the present work for the Fisurellidae, with seven described regions: the Eastern Pacific and Western Atlantic regions correspond to the Atlantic–Pacific and North-west Coast of California GT; the Eastern Atlantic and Mediterranean regions correspond to the rest of the Atlantic–Pacific GT and the Mediterranean Sea GT; the South African region includes the South Africa GT; and the Indo-West Pacific region includes our Philippine, Tasmania and South-eastern Australia GT. Cunha *et al*. (2019) hypothesized that the Fissurellidae originally evolved in the Tethys Sea (175 Mya), in what today constitutes the Western Indo-Pacific region. For several million years they continued to diversify, and with the opening of the new oceans they dispersed to the western coast of Africa, the western Atlantic and the eastern Pacific. Given that some of our generalized tracks are supported by species of Fisurellidae, either totally or in part, this hypothesis can be extended to other Vetigastropoda.

The convergence of the generalized tracks allowed the identification of five panbiogeographical nodes in Australia, Brazil, Chile, Mexico and South Africa. Heads (2005) proposed that nodes might have one or more of the following characteristics: (1) presence of endemic organisms; (2) absence of organisms that are widely distributed in other areas; (3) diverse geographical and phylogenetic affinities; and (4) represent geographical and phylogenetic limits of taxa. These characteristics are present in our nodes, as pointed out by Cunha *et al*. (2019) in their biogeographical analysis of Fissurellidae.

Our analysis offers an approximation for understanding the distribution patterns of vetigastropod species worldwide from the perspective of evolutionary biogeography. The generalized tracks obtained support hypotheses of primary biogeographical homology, which might be falsified by undertaking a cladistic biogeographical analysis based on the phylogenetic analyses available.

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DATA AVAILABILITY

No additional online data sources referred to; only the data in Table S1.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Data matrix of the species and genera of Vetigastropoda analysed.

Capítulo III

Evolutionary biogeography of Vetigastropoda (Mollusca): a cladistic biogeographic analysis

Luis Gabriel Aguilar-Estrada & Juan J. Morrone

enviado a *Organism Diversity and Evolution*

Evolutionary biogeography of Vetigastropoda (Mollusca): A cladistic biogeographic analysis

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Abstract

Cladistic biogeography is an evolutionary biogeographic approach that infers area relationships by comparing area cladograms based on the phylogenies available of the taxa under study. Vetigastropod molluscs, with about 4000 species, are distributed in coastal areas or deep sea waters of all the oceans. A cladistic biogeographic analysis was carried out based on the phylogenies of 16 families of Vetigastropoda to infer the relationships between the areas they inhabit around the world, using areas previously recognized for marine polychaetes. We found two major areas that we consider kingdoms, each divided in two regions: Pantropical kingdom, including Southwestern Africa and Red Sea (Western Indian Ocean region) and New Zealand, the Central Indian Ocean, Australia, Japan and China Sea (Indo-West Pacific region); and Cold-Temperate kingdom, including Southern Ocean (Magellan-Antarctic region) and Northern Hemisphere (Boreal region). The high degree of congruence between the area cladograms of different groups of animals shows that these organisms have most likely evolved together in similar habitats. We found coincidences when comparing our results with the distributional patterns of marine mollusks at worldwide, as well as with studies on biogeographical regionalization and areas of endemism proposed for other marine groups, as fish, polychaetes and sponges.

Keywords: Area cladograms; Gastropoda; Historical biogeography; Mollusca; Vicariance.

Introduction

Species are not equally distributed across the marine environment (Guzmán et al., 1998). It has been proposed that marine organisms are more widely distributed than terrestrial species because they experience fewer physical barriers to their dispersal (Linse et al., 2006); however, the extent of continents and oceans currents may represent barriers, which generate environmental gradients that are made up of sets of different species (Briggs, 1974, 1995; Longhurst, 1998). The distribution of mollusks in the oceans depends on several factors, namely, temperature, salinity, depth, currents, turbulence, larval development, dispersal capacity (Díaz-Merlano & Puyana-Hegedus 1994), and anthropogenic influence, which have variations in evolutionary time (Ávila & Malaquias, 2003; Linse et al., 2006). Each species occupies a geographical area with particular conditions where it survives; like most marine organisms, mollusks are restricted by their osmoregulation capabilities and their enzymatic assemblages, which are susceptible to changes in environmental factors shaping their distribution (Camus, 2001; Petuch, 2013). Several authors have postulated that distributions of different taxa are historically linked and present similar patterns related to geological and ecological events (Corral-Rosas & Morrone, 2017). Recently, global distribution patterns have been recognized for species of marine gastropods (Aguilar-Estrada & Morrone, 2022) and appear to be largely in line with the patterns formulated by van Soest and Hadju (1997), Glasby (2006) and Spalding et al. (2007) for other marine taxa. Nevertheless, there are no studies that used marine mollusks distributions to find out whether their phylogenetic relationships can be correlated with present-day distributions.

Evolutionary biogeographic studies have two distinct stages, a first stage is a conjecture on a common history, that means that different taxa are integrated in space and time (primary biogeographic homology), and a second one refers to the cladistic testing of the previously hypothesized homology or secondary biogeographic homology (Morrone, 2004). One of the approaches that attempts to identify primary homology hypotheses is panbiogeography, while cladistic biogeography deals with secondary hypotheses (Senna-Garraffoni et al., 2006; Morrone & Escalante, 2016). Cladistic biogeography elucidates common historical patterns of different taxa by using phylogenetic and distributional data, assuming a correspondence between taxon and area relationships (Parenti & Ebach, 2009; Corral-Rosas & Morrone, 2017; López-García & Morrone, 2022). This approach infers area relationships by comparing area cladograms derived from different phylogenetic hypotheses (Frota et al., 2020). Biogeographic cladistic analyses have been implemented mostly for terrestrial organisms (López-García & Morrone, 2022) such as plants (Crisp et al., 1995; Contreras-Medina & Luna-Vega, 2002), vertebrates (Ron, 2000; Chakrabarty, 2004), insects (Choi, 2000) and land mollusks (Scott, 1997; Craw, 2001). Studies on marine taxa are scarce and have dealt with macroalgae (Cheshire et al., 1995), corals (Wallace et al., 1991; Pandolfi, 1992; Santini & Winterbottom, 2002), arthropods (Watling & Thurston, 1989; Moller, 1991; De Grave, 2001; Fransen, 2002), fishes (Mooi & Gill, 2002; Parenti, 2008; Frota et al., 2020), sponges (van Soest & Hajdu, 1997; Fernández et al., 2012), echinoderms (Ghiold & Hoffman, 1986,1989), polychaetes (Glasby, 1999; Glasby & Álvarez, 1999; Garraffoni et al., 2006) and nemerteans (Härlin, 1996). Cladistic biogeographic analyses for other groups, such as marine mollusks, do not exist although if there are such studies in the terrestrial environment (Scott, 1997; Craw, 2001). Our main objective was to infer the relationships between the Vetigastropod taxa and the areas they inhabit by means of a cladistic biogeographic analysis around the world.

Material and methods

Taxa

We used the phylogenetic hypotheses available in the literature for the subclass Vetigastropoda worldwide. Data on the geographical distribution of Vetigastropoda species are available in Aguilar-Estrada and Morrone (in prep.). Sixteen cladograms of mollusk taxa were analyzed, including genera and species. Although there are other potential taxa with published phylogenetic analyses that could be considered, some of them lack information on the geographic distribution of the species analyzed and others include only a limited sample of the terminal taxa, as occurs in most molecular analyses, so they could not be considered in the analysis.

Analysis

A cladistic biogeographic analysis is based on a correspondence between phylogenetic relationships and area relationships (Morrone, 2005, 2009; Parenti & Ebach, 2009). It comprises three basic steps: construction of taxon–area cladograms from taxon cladograms, by replacing the terminal taxa by the area(s) inhabited by them; resolution of the problems due to widespread taxa, redundant distributions, and missing areas; and derivation of general area cladogram(s) representing the most logical solution for all the taxa analysed (Morrone & Carpenter, 1994). General area cladograms represent hypotheses on the biogeographical history of the taxa analysed and the areas where they are distributed (Morrone, 2009).

The cladistic biogeographic analysis was carried out based on the correspondence between phylogenetic hypotheses and area relationships (Morrone, 2005, 2009; Parenti & Ebach, 2009). This analysis consisted of the following steps: (1) construction of taxon-area cladograms for each taxonomic cladogram, where the terminals were replaced by the area(s) inhabited by them using Glasby's (2006) area for polychaetes (Fig. 1); (2) parenthetic texts were elaborated for the taxon-area cladograms, which were compiled in a word processor (Table 1); (3) a file with the parenthetic cladograms was uploaded to BuM 2.0 software (http://nuvem.ufabc.edu.br/bum; Santos et al., 2021); (4) a presence/absence data matrix was obtained after the software resolved the problems due to widespread taxa, redundant distributions and missing areas; and (5) a parsimony analysis of the data matrix (Table 2) was undertaken using TNT (Goloboff et al., 2008), performing searches of the most parsimonious general area cladograms with the heuristic "traditional search" algorithm of TNT, with 1000 replications, and tree-bisection-reconnection branch-swapping (TBR), holding ten trees during each replication (Goloboff, 1993).

Results

The parsimony analysis of the data matrix produced 40 most parsimonious general area cladograms (Fig. 2). The strict consensus general area cladogram consists of two basic clades considered kingdoms, each with two subordinated subclades or regions:

(1) Pantropical kingdom: It includes subclades A) including three areas of the Red Sea, which is separated into a smaller group consisting of the Western Indian Ocean and South & Southwest Africa (Western Indian Ocean region); and B) including New Zealand, the Central Indian Ocean, northern and southern Australia, the Western Indo-Pacific areas and Japan and the China Sea (Indo-West Pacific region).

(2) Cold-temperate kingdom: It includes subclades C) including two areas West Antarctica and South Georgia and Magellan (Magellan-Antarctic region); and D) the Northern Hemisphere areas, including the Arctic, Atlantic and Pacific, as well as two smaller clades first one formed by the areas of the Boreal Pacific and California, and the second formed by three areas Brazil, Caribbean and Western Atlantic Boreal (Boreal region).

The largest areas recognized in the general area cladogram are shown on a map (Fig. 3) based on the areas of endemism of Glasby (2006). The areas recognized are compared to those of previous analyses (Table 3).

Discussion

Our hypothesis suggests that the phylogenetic relationships between the taxa and the areas they inhabit are largely congruent (Santini & Winterbottom, 2002). The high degree of congruence between the area cladograms of different groups of animals and their areas shows that these organisms have most likely evolved together in similar habitats (Colman, 1940; Moller, 1991; Ellingsen, 2002; Xie et al., 2016; Van der Linden et al., 2017; Holman et al., 2021), so they may have responded (speciated) to the same vicariance events.

It has been hypothesized that the marine currents of Kuroshio and Tsushima have had great influence on the distribution of vetigastropod species *Monodonta australis* Lamarck, 1822 and *Turbo sazae* H. Fukuda, 2017, functioning as genetic differentiators, since they can transport planktonic larvae to distant places, that can lead to speciation processes (Yamasaki et al., 2017; Son et al., 2020). Other marine invertebrates (crustaceans and mollusks,) show important levels of genetic differences between Southern Ocean provinces supporting the vicariant speciation hypothesis (González-Webar et al., 2010). However, these differences do not always correspond to vicariance processes in the strict sense but are related to the presence of oceanographic barriers and the dispersion strategies of each species, which may act differently e. g.

marine organisms are capable of colonizing distant environments (Scheltema, 1971), these unexpectedly wide geographical distributions are the result of alternative dispersal mechanisms (Johnson et al., 2001) such as teleplanic larvae, adults that survive in plankton, transport of individuals in substrates of passive movement, "rafting" and colonization in trampoline "stepping stones" (Santini & Winterbottom, 2002). In the case of benthic molluscs, this is typically the ability of a planktonic larva to traverse areas of ocean unsuitable for adult establishment, usually passively via currents (Kohn, 1990). It has been proposed that planctotrophic larval development favors rapid dispersal and wide geographical distribution due to the high capacity of larvae to disperse by ocean currents to distant locations (Shuto, 1974), e. g., *Diodora cayenensis* (Lamarck, 1822) and *Lucapinella limatula* (Reeve, 1850) have managed to disperse from the Canary Islands to the Atlantic on American coasts (Vermeij & Rosenberg, 1993).

When comparing our results with Aguilar-Estrada and Morrone’s (2022) study, in which a track analysis was carried out for Vetigastropoda worldwide, we found coincidences with respect to the regionalization obtained in the present study. The tracks Arabian Peninsula, South Africa-Mozambique; Eastern South Africa, South Africa; and Western South Africa and Port Alfred-Kosi Bay represent the Western Indian Ocean region. The tracks that these authors found in the western hemisphere: Japan, Philippines, Hawaiian Archipelago, Tasmania; and South-eastern Australia and New Zealand make up the Indo-West Pacific region. The tracks for the Southern Ocean: Peru-Chile, South American and Chile make up the Magellan-Antarctic region for the present work. The rest of the tracks (e. g., North Pacific, Mediterranean Sea, Northwest California Coast) are located within the Boreal region in this study.

Very few cladistic biogeographic analyses have been conducted with marine invertebrates. We found coincidences when comparing our results with biogeographical regionalizations and areas of endemism proposed for various groups of organisms such as anphipods, fish, polychaetes and sponges (van Soest & Hadju, 1997; Glasby, 2006; Spalding et al., 2007; Briggs and Bowen, 2012; Arfianti & Costello, 2020). One study that found a regionalization similar to the one presented here is that of Wallace et al. (1991), with the coral genus *Acropora*, presented four areas based on their cladistic biogeographic analysis: Red Sea, Western to central Indian Ocean, Eastern Indian Ocean and western to central Pacific Ocean, this work has many similarities with our clades A and B in the Indo-West Pacific area. Santini and Winterbottom (2002) conducted a biogeographic cladistic analysis based on fish, corals and mollusks, providing an explanation of the geological events that led these groups to spread throughout the Indo-West Pacific, such patterns are similar to those shown by Cunha et al. (2019) with

Fissurellidae, which originally evolved in the Tethys Sea (175 Ma), and whose species were subsequently able to disperse over several million years to the west coast of Africa, the Western Atlantic and the Eastern Pacific. Taking into account the similarities in the general area cladogram of the present work with the study by Santini and Winterbottom (2002), and that several species of Vetigastropoda are frequent inhabitants of coral reefs (Nangammbi & Herbert, 2008; Sawayama et al., 2022), this hypothesis can be extended to other mollusk groups such as Vetigastropoda, where subduction processes form island chains, which provide "steps" for the dispersal of marine species. This has been observed in regions with active tectonic activity such as southeast Asia, with *Lunella* spreading across the Pacific through these island assemblages (Williams et al., 2011).

The low definition in the cladogram that form a polytomy for the Northern Hemisphre subclade (Boreal region) could be explained due to lack of phylogenetic hypotheses for most families of Vetigastropoda. Recent studies have shown changes in the classification of this subclass with respect to the proposal of Bouchet et al. (2017), where eight superfamilies and 38 families of vetigastropods are currently accepted (Cunha et al., 2021) based on morphological, molecular (Uribe et al., 2022) and recently mitogenome data (Uribe et al., 2017). For example, family relationships within Trochoidea have recently been redefined (Guo et al., 2021), pending the inclusion of several unsampled families (Cunha et al., 2021). This same lack in distributional data has been observed in other invertebrates such as amphipods in the regionalization of Arfianti & Costello (2020), who mentioned that this information is needed for America, central East Pacific, Africa, Red Sea, and the Mediterranean.

Conclusion

Our analysis provides a preliminary inference on the relationships between Vetigastropoda taxa and the areas they inhabit by means of a cladistic biogeographic analysis. The general area cladogram obtained provides a test related to a secondary biogeographic homology hypothesis that matches the distributional patterns found above for marine mollusks worldwide. The development of studies such as the present depends on the existence of phylogenies for particular taxonomic groups, without these data, it is impossible to carry out them. In this work only cladograms of vetigastropod molluscs were used, but at least theoretically, the coevolution of areas and organisms extends to many other marine organisms and can serve as a working hypothesis in which more data can be incorporated. Future studies could include cladograms of other taxa, such as algae, corals, fishes, polychaetes or even other mollusk taxa that could provide different phylogenetic hypotheses and thus allow a more robust analysis.

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Figure captions

Fig. 1 Map with the areas analyzed in the cladistic biogeographical analysis, taken from Glasby (2006). 1, Arctic; 2, Boreal East Atlantic; 3, Boreal West Atlantic; 4, Northeast Atlantic; 5, Mediterranean-Black Sea; 6, West Africa; 7, Caribbean; 8, Brazil; 9, Southwest Atlantic; 10, South & Southwest Africa; 11, Western Indian Ocean; 12, Red Sea; 13, Central Indian Ocean; 14, Indo-West Pacific; 15, Northern Australia; 16, Southern Australia; 17, Greater New Zealand; 18, Japan & China Sea; 19, Boreal Pacific; 20, California; 21, East Pacific; 22, Peruvian; 23, Magellan; 24, West Antarctic & South Georgia.

Fig. 2 Strict consensus of the general area cladograms obtained. Pantropical: Clade A (green), clade B (yellow), Cold-Temperate: clade C (purple) and clade D (blue).

Fig. 3 Areas recognized in the analysis. Pantropical: Clade A (green), clade B (yellow), Cold-Temperate: clade C (purple) and clade D (blue).

Tables

Table 1. Taxon-area cladograms analysed for the families of Vetigastropoda. 1, Arctic; 2, Boreal East Atlantic; 3, Boreal West Atlantic; 4, Northeast Atlantic; 5, Mediterranean-Black Sea; 6, West Africa; 7, Caribbean; 8, Brazil; 9, Southwest Atlantic; 10, South & Southwest Africa; 11, Western Indian Ocean; 12, Red Sea; 13, Central Indian Ocean; 14, Indo-West Pacific; 15, Northern Australia; 16, Southern Australia; 17, Greater New Zealand; 18, Japan & China Sea; 19, Boreal Pacific; 20, California; 21, East Pacific; 22, Peruvian; 23, Magellan; 24, West Antarctic & South Georgia.

Family	Parenthetical taxon-area cladograms	References
Anatomidae	(((((((((((10, 23, 24, 14#15#16, 15#16), 14#15#18), 17), 14#17#18, 1#2#3#4#5#6#7#19#20), (10#11#12, 3#7#8)), 10#11), 3#7#8), 16), 24), 14#15#18), 17)	Geiger (2003)
Calliostomatidae	((((18#19,18),19#20),(11#18,18)),17,((3#7#8,7),21),(24,17),5)	Williams et al. (2010)
Collonidae	((14#18#19,23#24,11#14#18),(18,10),11#12#13#18)	Williams et al. (2008)
Eucyclidae	((((((18,14#18),19#20),14#18),7),((14,14#15#17),(18,24))),14)	Zhang & Zhang (2018)
Fissurellidae	(8#9#10, (20,19#20)); ((3#7#8#9#20#21, 3#7#8),(7, 3#7),(8,7)) (4#5#6, (10, 2#4#5), (10#11, 11), (13,14), (14#18,(18, 14)), (14#15#16#17,14, 14#15#16#18), (11#13#14#15#16, 13#14#15, 14, (11#13#14#15#16, 13#14#15#18))) (18#20, (18, (18,14#18), (14, (13,14) (14, 14#18), (14, 13#14#15, (2#4#5, 2#3#4#5#6#7#8) (14#15#16#18, (14#15#16, 15#16#17, 16, (14#18, 14, 18, 11) (15#16#17, 17), (18, (15#16#17, 15#16)) (3#4#5#7#8#9#20#21, 7), (3#4#5#6, 4), (8, 3#4#5#7#8#9#20#21), (11#13, (11, (14, (14#16)))), (15#16, 10), (6#10#11, 11)	Cunha et al. (2019)
Haliotidae	(((15,16),16),(15#16),((11#12#14),4,5),((4#5#6),17),(13#14#15#16#17#18),(10(19,20),20),(18#20)	Geiger (1999)
Lepetodrilidae	((14,(20#21,(11,(24,4#6))))) ((14,18),(20#21,19#20))	Linse et al. (2019)
Margaritidae	((((19#20,(1#2,19)),(18,14)),(19,(18,(1#17,1))),(1#8,(1,14))),(24,14#18))	Zhang & Zhang (2017)
Phasianellidae	((((((10#11,10),(10#11,10)),5),11#12#14#15#16#18),21),11#12#13#14#15#16#18)	Nangammbi et al. 2016
Pleurotomariidae	(((((3#7,(14#18,14)),18),14),((3#7#8,7)))	Zhang et al. (2016)
Pseudococculinidae	((18,2#14#18),(7#18,14))	Kano et al. (2016)
Scissurellidae	((((((5#6#10#11#12, 3#4#5#7#8#11), 17), 15#16#17, (3#7, (14#15#16,11#14#15#18)), 3#4#5#7#8#11,10, 16#17), 16, 14#18) (((17,19#20), 16,15#17), 4) (((17,14#15#16#18), 7), 14#15#18)	Geiger (2003)
Skeneidae	((14,24),((14,18),(14,(11#18,(14,18))),(14,(11,24))))	Chen & Linse (2019)

Tegulidae	((((((((((20#21,20),((3#7#8,20),21)),20),3#7),22),21),22#23),(20,19#2),(14#18,20)),20)	Hellberg (1998)
Turbinidae	(16,((14,15#16),(16,(14#18,(14#15#18,(14#15,16)))))) (16,(4#5,(14,(14#18)))) ((20,18),(3#7#8,3#7)),((14#15#20,16),(17,(14#15,(10#11#12#14#18,14#18)))) (10#11, (15,14,(14#15, 14))), (3#11#12#14#15#17#18, (3#5#7#9#20#21, 20#21#22), (7#8#9, 11#12), (3#7#8#14#20#21)) (18,15),(14#18,14),(11,(14,(3#18,14#15,(14#18,(14,(15,(16, (18#14)))))))))	Williams et al. (2010)
Trochidae	((((14, 11#12#14#18),14#18),((17#18, 14#15#18), 12#13#14)), 16) ((17,16#17),15#16,17),((17,17#18#22#23), 16#17), 18) ((16,15#16), 13#14#15#18) (15#16,14#15#16#17,14#16,(14#18,14#15)) ((13#14#15#16#17#18,14#18),(10#11#13#14#16#18)) (((17,16#17),15#16,17),(17,17#18#22#23)) ((17,14#15#17),((4#5#12,4#5),2#4#5#6,5)) (((14#18, 16), 11#12#13#14#15#16#18),(14#15#18)) (((13#14#15#18, 17#18), (14#15#16#18, 14#15#16)), (11#14#18, (15#16, 13#14#15#16#18))) (((17#18, 14#18), (14#17#18)),((18, 14#15#18), 17, 15#16)) ((((((14#15#18,16), 14#18), 14#15#18), 13#14#15#18), 17), 14#17)	Williams et al. (2010)

Table 2. Data matrix analyzed. OUT (root), ARC (Arctic), BEA (Boreal East Atlantic), BOP (Boreal Pacific), BRA (Brazil), BWA (Boreal West Atlantic), CAL (California), CAR (Caribbean), CIO (Central Indian Ocean), EAP (East Pacific), GNZ (Greater New Zealand), IWP (Indo-West Pacific), JCS (Japan & China Sea), MAG (Magellan), MBS (Mediterranean-Black Sea), NEA (Northeast Atlantic), NOA (Northern Australia), PER (Peruvian), RES (Red Sea), SOA (Southern Australia), SSW (South & Southwest Africa), SWA (Southwest Atlantic), WAG (West Antarctic & South Georgia), WEA (West Africa), WIO (Western Indian Ocean).

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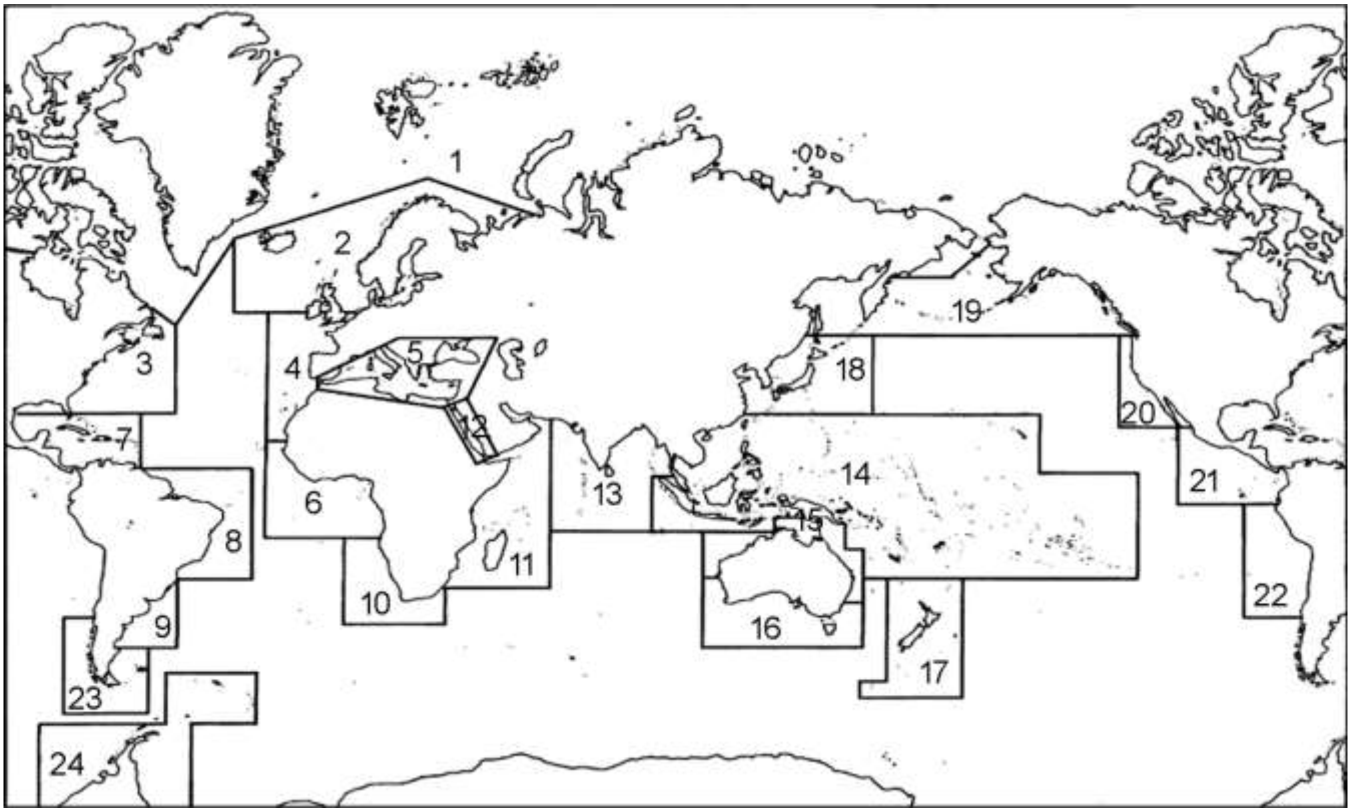
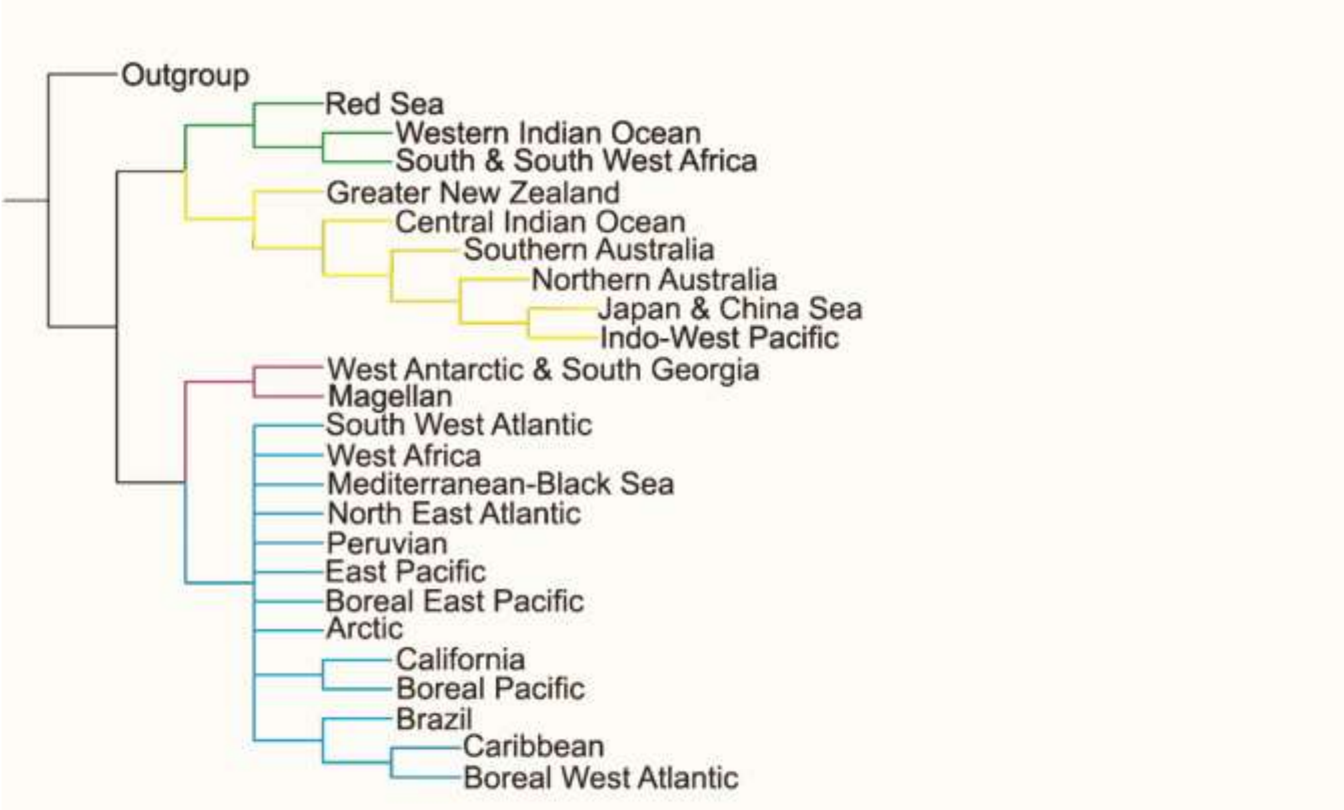
Table 3. Comparison with the different regionalization proposals with other taxa: sponges (Van Soest & Hadju, 1997), polychaetes (Glasby, 2006), benthic and pelagic biotas (Spalding et al., 2007), fishes (Briggs & Bowen, 2012), and amphipods (Arfianti & Costello, 2020).

Kingdoms	Regions	“Wide” areas of endemism (Van Soest & Hajdu, 1997)	Realms (Glasby, 2006)	Kingdoms (Spalding et al. 2007)	Regions (Briggs & Bowen, 2012)	Biogeographic regions (Arfianti & Costello, 2020)	Localization in world oceans
Pantropical	Western Indian Ocean region	Indo-West Pacific	Pantropical Austral	Temperate Southern Africa Western Indo-Pacific	Warm regions	South Africa	Southeast Atlantic and Western Indian Ocean
	Indo-West Pacific region	Indo-West Pacific, Antiboreal-Antarctic	Pantropical	Western Indo-Pacific Central Indo-Pacific Temperate Australasia Temperate North Pacific	Warm regions	Tasman Sea, Coral Sea, S Australia & Indo-Pacific seas & Indian Ocean (In part), South & East China Sea Hawaii, Indo-Pacific seas & Indian Ocean, New Zealand, Laccadive Sea & Bay of Bengal	Western and Eastern Indian Ocean, North-Western Pacific, Central West Pacific and Southwest Pacific
Cold-temperate	Magellan-Antarctic region	Antiboreal-Antarctic	Austral	Temperate South America Southern Ocean	Cold regions Cold-temperate regions	Southern Ocean	Southeast Pacific and Antarctic

	Boreal region	Boreal-Arctic, Mediterranean-Atlantic, Central West Atlantic	Boreal	Temperate Northern Pacific, Temperate Northern Atlantic Tropical Atlantic	Cold regions	Black Sea, NE Atlantic, Mediterranean Sea, Offshore & NW North Atlantic, Caribbean, Gulf of Mexico & Offshore S Atlantic Ocean, Inner Baltic Sea, Norwegian Sea, Arctic seas, N Pacific, N American Boreal, N Pacific	Central Eastern Pacific, Central West Atlantic and the South-West Atlantic




Outgroup
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Central Indian Ocean
Southern Australia
Northern Australia
Japan & China Sea
Indo-West Pacific
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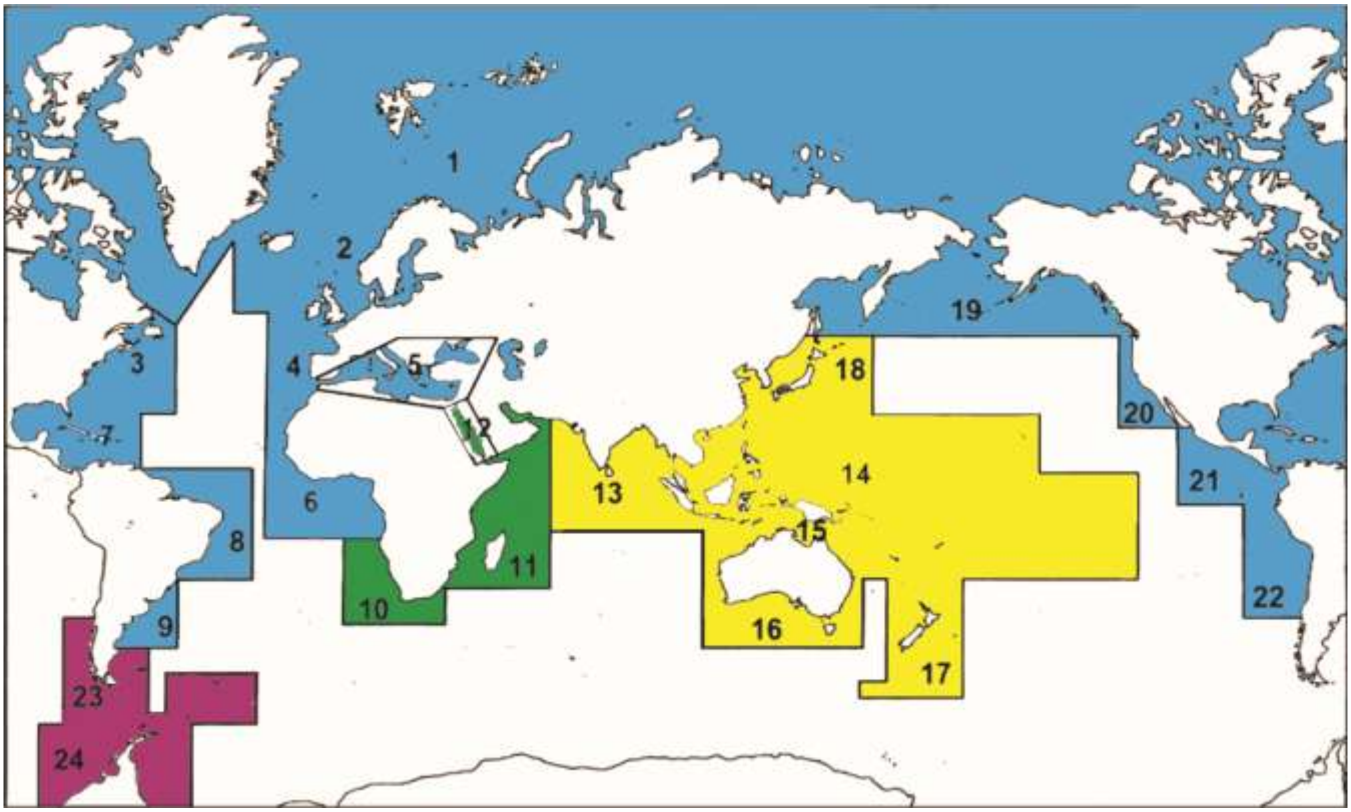
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Author contributions

Both authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by LGAE and JJM. The first draft of the manuscript was written by LGAE and JJM. Both authors read and approved the final manuscript.

Declarations

Conflict of interest The authors declare no competing interests.

VI. DISCUSIÓN GENERAL

El presente trabajo representa un primer intento de compilar la información disponible para la subclase Vetigastropoda a nivel mundial. Con base en el trabajo de Cunha et al. (2021), el número total de especies registradas en el presente trabajo representa aproximadamente el 20% de las 4,000 especies de esta subclase. Hasta el momento, no hay estudios similares realizados con moluscos marinos, con la excepción del trabajo de Geiger (1999) de la familia Haliotidae y Cunha et al. (2019) sobre la familia Fissurellidae, en conjunto dichos trabajos solo tienen información para dos de las 38 familias que componen esta subclase.

Se encontró que el 80% de las familias diferentes de Fissurellide están distribuidas en ambos lados del Océano Pacífico. Existe evidencia geológica que proporciona una explicación sobre los eventos que llevaron a los moluscos a distribuirse a través del Pacífico Indo-Oriental (Santini y Winterbottom, 2002). Estas distribuciones geográficas inesperadamente amplias también pueden ser el resultado de mecanismos de dispersión alternativos tales como larvas teleplánicas, adultos que sobreviven en plancton, transporte de individuos en sustratos que se mueven pasivamente, colonización por "rafting" y colonización en "trampolín" (Johnson et al., 2001). Las larvas teleplánicas tienen un desarrollo a largo plazo y sirven como un medio de dispersión a largas distancias, flotando durante dos a cuatro meses, por lo que pueden colonizan nuevos ambientes (Scheltema, 1971).

Cabe señalar que hay áreas importantes que pueden funcionar como centros de biodiversidad, específicamente el Pacífico Indo-Occidental; esto se ha visto en otros grupos de organismos marinos como peces y equinodermos (Carpenter y Springer, 2005; Hubert et al., 2017; Saulsbury y Baumiller, 2022). Los moluscos son un taxón muy diverso, ya que cuentan con al menos 200,000 especies (Ponder et al., 2019), son uno de los grupos más importantes en los ambientes marinos, y se sabe que su existencia en los distintos hábitats, hace posible la existencia de otros grupos de organismo marinos, por esta razón se deben continuar con los estudios ecológicos y biogeográficos sobre moluscos marinos, ya que se consideran ingenieros de los ecosistemas (Gutiérrez et al., 2003; Burgos et al., 2019).

Las características abióticas del medio ambiente son el factor fundamental que determina la distribución geográfica; sin embargo, se sabe poco sobre la influencia de los factores bióticos en los patrones de distribución de los moluscos (Vermeij, 1972). Hay pocos datos sobre el tipo de interacciones bióticas que pueden ejercer un efecto sobre la distribución geográfica de los moluscos marinos; sin embargo, se han observado cambios latitudinales en respuesta a los depredadores (Fawcett, 1984), así como cambios en la distribución de especies asociadas a hábitats específicos como los arrecifes coralinos (Rex et al., 2005). De esta manera, la presencia de una especie en un área determinada está dada por la disponibilidad del hábitat, que a su vez se define por las condiciones ambientales, adaptaciones, fisiología e interacciones bióticas (Guzmán et al., 1998).

La distribución diferencial de las familias de Vetigastropoda a nivel mundial puede estar relacionada con varios factores ambientales, en el caso de las especies de aguas profundas sus distribuciones pueden estar relacionadas con los nutrientes, características del sustrato, circulación oceánica, fenómenos tectónicos y surgencias. En las especies de aguas someras esto se relacionado principalmente con la disponibilidad de alimento, ya que este factor limita la exploración de otros hábitats (Williams et al., 2013; Kiel, 2016; Lee et al., 2019).

La mayoría de las trazos generalizados coinciden con los estudios de regionalización de van Soest y Hadju (1997) con esponjas, Glasby (2006) con poliquetos, Spalding et al. (2007) con biota pelágica y bentónica y Briggs y Bowen (2012) con peces. Esto nos permite suponer que los grupos de invertebrados marinos comparten un ambiente similar y responder de manera parecida al hábitat en el que se encuentran (Colman, 1940; Ellingsen, 2002; Xie et al., 2016; Van der Linden et al., 2017; Holman et al., 2021). Lo que nos ayuda a reconocer la coevolución de las áreas marinas y los organismos; tal patrón puede extenderse a otros grupos de invertebrados marinos bentónicos e incluso peces (van Soest y Hajdu, 1997). También se encontraron coincidencias parciales de los trazos generalizados con respecto a otros organismos marinos como: cirripedios, corales, isópodos, mamíferos marinos, peces bruja y tiburones (Aguilar-Aguilar y Contreras-Medina, 2001; Cavalcanti y Gallo, 2008; Vargas et al., 2008; Celis-Villalba, 2009; Espinosa-Pérez et al., 2009; Gallo et al., 2010; Martínez-Castro, 2014). Al considerar otros análisis biogeográficos basados en moluscos marinos como el de Geiger (1999) quien analizó la familia Haliotidae y Cunha et al. (2019) con miembros de Fissurellidae se encontraron coincidencias con respecto a lo registrado anteriormente por dichos autores. La coincidencia de resultados entre diversos estudios, muestra que algunas de las especies de moluscos estudiadas en el presente trabajo, eran parte de biotas ancestrales que por eventos tectónicos e incluso paleoclimáticos, se han fragmentado y a consecuencia de ello, han seguido historias evolutivas particulares (Contreras-Medina y Eliosa-León, 2001).

Con base en el análisis biogeográfico cladístico aplicado a las familias de Vetigastropoda, la hipótesis propuesta sugiere que las relaciones filogenéticas entre los taxones y las áreas que habitan son en gran parte son congruentes (Santini y Winterbottom, 2002). El alto grado de congruencia entre los cladogramas de áreas de diferentes grupos de animales y las áreas que habitan muestran que estos organismos probablemente han evolucionado juntos en hábitats similares (Colman, 1940; Moller, 1991; Ellingsen, 2002; Xie et al., 2016; Van der Linden et al., 2017; Holman et al., 2021), por lo que pueden haber respondido (especiado) a los mismos eventos de vicariancia. Uno de los mecanismos propuestos para explicar la diferenciación genética entre las poblaciones de Vetigastropoda son las corrientes marinas, ya que pueden transportar larvas planctónicas a lugares distantes, que pueden conducir a procesos de especiación (Yamasaki et al., 2017; Son et al., 2020). Otros invertebrados marinos (crustáceos y moluscos) muestran niveles importantes de diferenciación genética entre las provincias del Océano Austral que apoyan la hipótesis especiación por vicarianza (González-Webar et al., 2010). Sin embargo, estas diferencias no siempre se corresponden con los procesos de vicarianza en el sentido estricto, pero están relacionadas con la presencia de barreras oceanográficas y las estrategias de dispersión de cada especie, que pueden actuar de manera diferente (Scheltema, 1971).

Se han realizado muy pocos análisis biogeográficos cladísticos con invertebrados marinos. Sin embargo, encontramos coincidencias al comparar nuestros resultados con las regionalizaciones biogeográficas propuestas con este enfoque para varios grupos de organismos como: anfípodos, esponjas, peces y poliquetos (van Soest y Hadju, 1997; Glasby, 2006; Spalding et al., 2007; Briggs y Bowen, 2012; Arfianti y Costello, 2020). Teniendo en cuenta las similitudes en el cladograma general de áreas del presente trabajo con el estudio de Santini y Winterbottom (2002), y que varias especies de moluscos son habitantes frecuentes de arrecifes de coral (Nangammbi y Herbert, 2008; Sawayama et al., 2022), esta hipótesis puede extenderse a los miembros de Vetigastropoda. La baja definición en el cladograma que forma una politomía para la subclado del hemisferio norte (región boreal) podría explicarse debido a la falta de hipótesis filogenéticas para la mayoría de las familias de Vetigastropoda. Estudios recientes han demostrado cambios en la clasificación de esta subclase con respecto a la propuesta de Bouchet et al. (2017). Vetigastropoda se compone de 38 familias con base en datos morfológicos y moleculares. Recientemente datos mitogenómicos han proporcionado información nueva para poder redefinir las relaciones filogenéticas al interior de la subclase a la espera de la inclusión de varias familias no consideradas en los análisis (Cunha et al., 2021; Guo et al., 2021; Uribe et al., 2017; 2022). Esta misma carencia en los datos de distribución ha sido observada en otros invertebrados como anfípodos en la regionalización de Arfianti y Costello (2020), quienes mencionaron que esta información es necesaria para América, el Pacífico Central, África, el Mar Rojo y el Mar Mediterráneo.

VII. CONCLUSIONES

El análisis de trazos implementado a la subclase Vetigastropoda proporcionó una aproximación general para comprender los patrones de distribución de las especies de dicha subclase en todo el mundo desde la perspectiva de la biogeografía evolutiva. Los trazos generalizados obtenidos ofrecieron soporte para hipótesis de homología biogeográfica primaria, que fue comprobada mediante un análisis biogeográfico cladístico con base en los análisis filogenéticos disponibles para 16 familias de Vetigastropoda. Este análisis proporcionó una inferencia preliminar sobre las relaciones entre los taxones de Vetigastropoda y las áreas que habitan. Se obtuvieron 40 cladogramas de áreas, de los cuales se generó un cladograma general de áreas, el cual proporcionó una evidencia relacionada con una hipótesis de biogeografía secundaria. El desarrollo de estudios como el presente depende de la existencia de filogenias para un grupo taxonómico específico. En este trabajo solo se utilizaron cladogramas de moluscos vetigastrópodos, pero al menos teóricamente, la coevolución de áreas y entidades biológicas se extiende a muchos otros organismos marinos y puede servir como hipótesis de trabajo en aquellas que logren incorporar más datos. Los estudios futuros podrían recabar la información disponible para otras especies marinas, con las cuales se podría implementar el enfoque panbiogeográfico y posteriormente emprender la búsqueda de las filogenias para cada grupo y así incluir los cladogramas para otros taxones marinos como algas, corales, anfípodos, poliquetos o incluso peces y de esta forma generar un estudio más robusto que lleve a entender la relación de las distribuciones actuales con respecto a las filogenias existentes y confirmar las conclusiones formuladas con este trabajo.

Los estudios biogeográficos son necesarios para conocer los patrones de distribución a los que pertenecen distintos taxones tanto terrestres como marinos. Este trabajo trata de promover la investigación en biogeografía marina, una rama de la biogeografía que ha sido poco estudiada con respecto a los invertebrados marinos. Las investigaciones centradas en el inventario y la recopilación de datos de distribución geográfica son la base de cualquier estudio con un enfoque biogeográfico; la información recogida puede ayudarnos a identificar lugares donde es necesario realizar trabajo de campo o simplemente saber cuáles son las áreas de distribución de las especies y de esta manera tener un panorama general sobre la biodiversidad marina del planeta. Los resultados de estos estudios pueden generar información relevante para la evaluación sobre el estado de conservación de diferentes áreas prioritarias para el conocimiento biológico, ya que en algunos casos estas áreas experimentan diferentes repercusiones por las actividades antropogénicas. Con la información disponible será posible crear programas e implementar acciones que conduzcan a la conservación de las especies marinas, planes de manejo que contribuyan al mantenimiento de los recursos naturales a nivel mundial frente a escenarios de cambio climático.

VIII. CONSIDERACIONES FINALES

La implementación de cualquier metodología de estudio que se utilice para resolver una hipótesis de trabajo como es el caso de los patrones de distribución de moluscos marinos (utilizados en esta investigación), dependen de las distintas técnicas y programas disponibles para el análisis, en cuyo caso pueden ser determinantes para generar los resultados esperados y así establecer los alcances de la investigación.

El caso de la panbiogeografía constituye un método que requiere de pocos elementos para llevarse a cabo, se necesitan los puntos de distribución de los taxones, con coordenadas geográficas o la localidad. Si se tienen pocos datos, las localidades pueden buscarse en algún sistema de información geográfico. Sin embargo, al tratarse de un trabajo que utiliza otras fuentes de información para llevarse a cabo, se pueden encontrar errores en la geoposición o datos incompletos para la localidad, errores de identificación taxonómica, por lo que al generarse el trazo individual y los trazos generalizados, es posible que uno o más taxones no correspondan al área de distribución, ya sea por error en los datos de las etiquetas de museo o colecciones biológicas, errores de escritura al cargar las bases de datos en las plataformas digitales y de esta forma estemos tratando con un grupo distinto (de hecho puede ser algo que no existe). La elaboración de las bases de datos es un paso fundamental para empezar cualquier estudio biogeográfico, se debe hacer lo posible por trabajar con datos de calidad que reflejen la distribución para cada taxón supraespecífico de interés. Estas bases de datos, deben ser depuradas y estandarizadas, para tener información confiable. Para el caso de los vetigastrópodos, en algunas ocasiones no se contó con el número mínimo de datos de geoposición (al menos tres) para poder generar un trazo individual, esto debido a la poca información existente para algunas especies, por lo que esta información fue descartada del análisis.

No obstante las limitaciones del trabajo, se logró generar una inventario sobre las especies que se utilizaron en esta investigación, con lo que se cuenta con cerca de una cuarta parte de las 4000 especies de la subclase Vetigastropoda. Este trabajo es una primera aproximación acerca de los patrones de distribución de este taxón a nivel global, se generaron los trazos individuales y generalizados que son la base de las hipótesis de homología biogeográfica primaria. Estos datos son importantes, ya que hasta el momento no existía un trabajo parecido elaborado con moluscos marinos.

En el caso de la biogeografía cladística, requiere suficiente cantidad de taxones y cladogramas taxonómicos del grupo de interés para llevar a cabo la investigación y así elaborar los cladogramas taxonómicos de áreas, para poder incluirlos en el trabajo y ser analizados y de esta forma obtener un cladograma general de áreas. Cuando esos elementos son insuficientes los resultados pueden llegar a ser limitados y siempre estarán en función de los cladogramas taxonómicos disponibles. Una de las ventajas de implementar este enfoque es que se pueden generar filogenias nuevas con secuencias de ADN provenientes de distintos taxones con uno o varios marcadores moleculares; si no se cuenta con los recursos para elaborar una filogenia del grupo de interés, se pueden utilizar las filogenias que estén disponibles en el momento de llevar a cabo la investigación. Es importante decir que los estudios filogenéticos son una parte importante de los análisis de biogeografía cladística, por lo que se debe promover y continuar con el desarrollo de dichos trabajos para diferentes taxones de invertebrados marinos distintos a los moluscos y así los resultados de los futuros estudios con este mismo enfoque sean lo más robustos posibles, ya que son la base de las hipótesis de homología secundaria.

IX. REFERENCIAS BIBLIOGRÁFICAS

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X. ANEXO

Línea de comandos escrita en el software R para generar los trazos individuales.

```
########################### Uvanilla costata
library (fossil)
library (readr)
library (maptools)
read.csv(file="Uvanilla_costata.csv",sep=",",header=T)->Uvancost
Uvancost[1:7,2:3]->Uvancost2
earth.dist(Uvancost2)->ek
fdata.mst<-dino.mst(ek,random.search = TRUE)
plot(coordinates(Uvancost2))
mstlines(fdata.mst,coordinates(Uvancost2))
shape.mst<-msn2Shape(fdata.mst,Uvancost2)
write.shapefile(shape.mst, "Uvancost", arcgis="TRUE")
data(wrld_simpl)
plot(wrld_simpl, xlim=c(-180,180), ylim=c(-90,90), axes=TRUE,col="light yellow")
points(coordinates(Uvancost2), col="orange", pch=20, cex=0.75)
mstlines(fdata.mst, coordinates(Uvancost2),col="red")
```