

Quantifying Morphological Diversity in Bivalves Through Shell Sculpturedness

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Abstract

Morphological diversity can be analyzed for evolutionary patterns that can be overlooked by taxonomic diversity. The aim of the study was to see whether morphological diversity in bivalves was related to taxonomic diversity, latitude, evolutionary change over time as well as whether sculpturedness in bivalve species was influenced by ecology. The analysis was conducted on a dataset of over 45,000 modern bivalve images from all around the world in various environments, from which the amount of sculpture of the exterior shells were quantified, and is referred to as “sculpturedness” here, with the use of an edge detection algorithm. Additional comparisons were made with other bivalve data as well as a large set of over two million bivalve occurrences from the Global Biodiversity Information Facility. The results show a general increase in coefficients of variation within bivalve families with increasing species and genus richness while coefficients of variation between genera become more stable for genera rich in species. On a global scale, the dataset indicates that species with low mean sculpturedness are the most common, while their variation in sculpturedness within taxa show no clear pattern except that higher variation is much more common than stronger sculpture. Comparison of sculpturedness to ecological traits (mobility, fixation, feeding and substrate) of the bivalves show that the mean sculpturedness of species varies depending their specific traits, with epifaunal and semi-infaunal bivalves having higher means than infaunal bivalves. Sculpturedness was strongly correlated with ecologic traits with examples including immobile bivalves being more sculptured than swimming and mobile bivalves on average as well as byssate and cemented bivalves being more sculptured on average than unattached bivalves. Comparison with a dataset of fossil bivalves from the Pliocene to Miocene epochs hints toward a decrease in sculpturedness over time among bivalve families, though the difficulty of using the method to analyze their sculpturedness makes the accuracy of these hints uncertain.

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Introduction

The biological diversity we see in oceans today is the result of billions of years of evolution. A question that comes up here is what drives the shaping of these organisms. A well-documented pattern of extant species on Earth is the increase in species richness from higher to lower latitudes (Gaston 2007). While some studies seem to indicate that the marine latitudinal diversity gradient is unimodal, a more recent study indicates that it is instead bimodal (Gaston 2007; Yasuhara et al. 2020). In their article, Yasuhara et al. (2020) shows that the latitudinal diversity gradient has over glacial periods peaked in the tropics, while it today has two peaks and a lower diversity in the tropics. They show that it could be caused by an increase in temperature in the tropics, above that which marine organisms are adapted to. Although the surface of Earth has changed significantly over time through the process of plate tectonics, and the distribution of heat, dictating climate, this pattern of species richness is thought to have been present for a long period of time, with some groups of species trending towards a steepening latitudinal gradient over time (Gaston 2007). The latitudinal gradient in species richness is a pattern with a lack of consensus as to what the mechanisms shape this pattern. One study found that variation in body mass between different groups of organisms and its effect of energy use and dispersal ability could be a possible mechanism (Hillebrand 2004). In the same article, they describe another explanation, the effective time hypothesis, which bases the diversity in the tropics on higher energy availability, increasing mutation rates and generation times, larger area for speciation and higher climatic stability over geological time scales. Another study found that two processes shaped the latitudinal diversity gradient: those which drive origination rates in the tropics and those which drive geographic range limits of taxa (Jablonski et al. 2006). In general, the latitudinal diversity gradient can be used to explain how species spread across the globe and can be influenced by things like the shape of continents or basins, changes in environmental conditions as well as impactful events such as glaciations (Gaston 2007).

One of the methods of measuring diversity (number of included species) among taxonomic groups is by looking at morphological diversity, with morphology in the biological term referring to the form of organisms (Minelli 2016; Aronoff and Fudeman 2023). While taxonomic richness is one measure of biodiversity, morphological diversity is another, which can show evolutionary patterns that are otherwise overlooked if only looking for taxonomic richness. An example of the usefulness of morphological diversity is a study by Fortey and Owens (1990) looking at the morphotypes and diversity of families of trilobites showed that the emergence and disappearance blind trilobites may have been a contributing factor in trilobites morphological diversity changes throughout early periods of the Paleozoic Era (Foote 1997). Another study showed that certain species living in polar regions have a smaller shell to total body ratio than in equatorial regions, the reason for which are still unclear (Watson et al. 2017).

Evolving lineages of animal groups tend to change in size over time. This trend, called “Cope’s rule” after E. D. Cope, who first described the trend back in 1871, states that new lineages evolve at small sizes with an active trend towards larger sizes over time. The cause for this trend, Cope attributed to multiple advantages of having large body sizes like predator evasion, larger brain size and longevity. Much later, MacFadden and Alroy (1986, 1998) strengthened the evidence for the rule being an active trend by analyzing the evolution of horse body size (MacFadden) and 1500 mammal fossil species in North America (Alroy), finding the pattern toward larger body sizes being an active trend (Carroll 2001). If this rule also applies to the evolution of body sizes in groups of animals other than mammals remains to be seen.

Functional diversity, yet another method of measuring diversity, is often described (although not exactly defined) as “the value and the range of those species and organismal traits that influence ecosystem functioning”. Two main questions are usually important when studying the functional diversity of a group of species, how they influence the ecosystem and how they respond to changes in the environment. To measure the diversity, choosing relevant traits in the group is important to see how they affect the surroundings (Laureto et al. 2015). These traits can include, among other things, feeding habits, where they live, mobility and fixation in the case for Bivalves, a class of animals in the Mollusca phylum (Collins et al. 2019). Functional diversity, along with other sorts of diversity (taxonomic, latitudinal gradients, morphological) can be used to better understand drivers of global patterns of environmental changes (Berke et al. 2014).

Morphological disparity

While taxonomic and morphological diversity both provide information on taxonomic groups, their relationship between each other can also provide valuable information. In a study, Mike Foote (1993) compared taxonomic and morphological diversity between two extinct classes of fauna, Blastoidea (Echinoderm phylum) and Trilobita (Arthropod phylum). Early evolution of biological groups tends to increase in both morphological and taxonomic diversity as species occupy certain adaptive zones. Within Blastoidea and two of the clades within Trilobita, the morphology continues to increase even when taxonomic diversity decreases. Foote argues that this may point to taxonomic decreases that are unrelated to morphology and that they continue to radiate across the morphospace. Morphospace refers to a type of space in which one can categorize a group of organisms based on specific properties or traits. In the three other clades within Trilobita, the morphological diversity decreases with taxonomic diversity suggesting a link between them (Foote 1993; Budd 2021).

A question presents itself regarding whether morphological diversification early in evolutionary history of a clade can lead to an increased resistance to extinction. One might expect a greater variability of forms and sizes to also translate into one of the at

the very least being adequately equipped to survive extinction. There are studies which point in both directions. One study of Rostroconche molluscs evolving at the same time by P.J. Wagner (1997) showed no indication that early bursts of morphological diversification led to an increased resistance to extinction while another study of trilobite families by Foote found that those with a greater variability in sizes had better probabilities of surviving the end-Ordovician extinction event (Foote 1997).

Bivalves as a model group

What biological groups can be a suitable candidate to explore these topics on diversity? Bivalves (fig 0) are practically all benthic (bottom dwellers) whose types of life habits consist of three main groups: Life position (i.e. where it lives in relation to the substrate), mobility or attachment and feeding type. On a vertical scale, bivalves live from deeper in the substrate (infaunal) to above the substrate in the water column (epifaunal). In some species cases they are classified as semi-infaunal, meaning that it is partly below the substrate. For mobility and attachment, the type of substratum is of importance. They differ depending on whether the substratum is soft or hard. The bivalves can generally be divided into 7 categories based on this (Stanley 1970):

- Byssally attached bivalves (fig 0.5) attaches itself to the substrate with a structure made out of protein filaments called the byssus, a trait unique to bivalves (McCartney 2021).
- Cemented bivalves (fig 0.5) attach permanently to the substrate with secreted shell material.
- Reclining bivalves lie on or is partly submerged in the substrate due to inability to attach.
- Swimming bivalves (fig 0.5) as the name suggests move freely the water column on their own.
- Burrowing bivalves (fig 0.5) either partially or permanently live their lives dug into a soft substrate.
- Boring bivalves (fig 0.5) bore into hard substrate and lives in the space created.
- Nestling bivalves lack the ability to bore so they live instead in a pre-existing cavity in a hard substrate.



Figure 0. Examples of different bivalves that show their family, genus, species and the range in sculpture (as calculated by an edge detection algorithm).

These groups are defined as being as exclusive as possible, but there are instances where certain bivalve species employ more than one of these methods (e.g. many bivalves in the Pectinida order can swim but spend most of their time on the bottom using some of the other types listed). As for the feeding types, there are two general methods: suspension and deposit feeders. Suspension feeders are by far the most common method of feeding and is used by most epifaunal and hard substratum bivalves. The deposit feeding is done by some using specialized appendages called proboscides while others use a siphon, a kind of feeding tube (Stanley 1970). Bivalves are also suitable for examining the latitudinal diversity gradient and surrounding questions like the “out of the tropics model”, which suggests that taxa preferentially originate in the tropics, but radiates outward toward higher latitudes over time. This is in part due to the class being taxonomically stable with a large fossil record and their occurrence at all latitudes in the oceans (Jablonski et al. 2006).

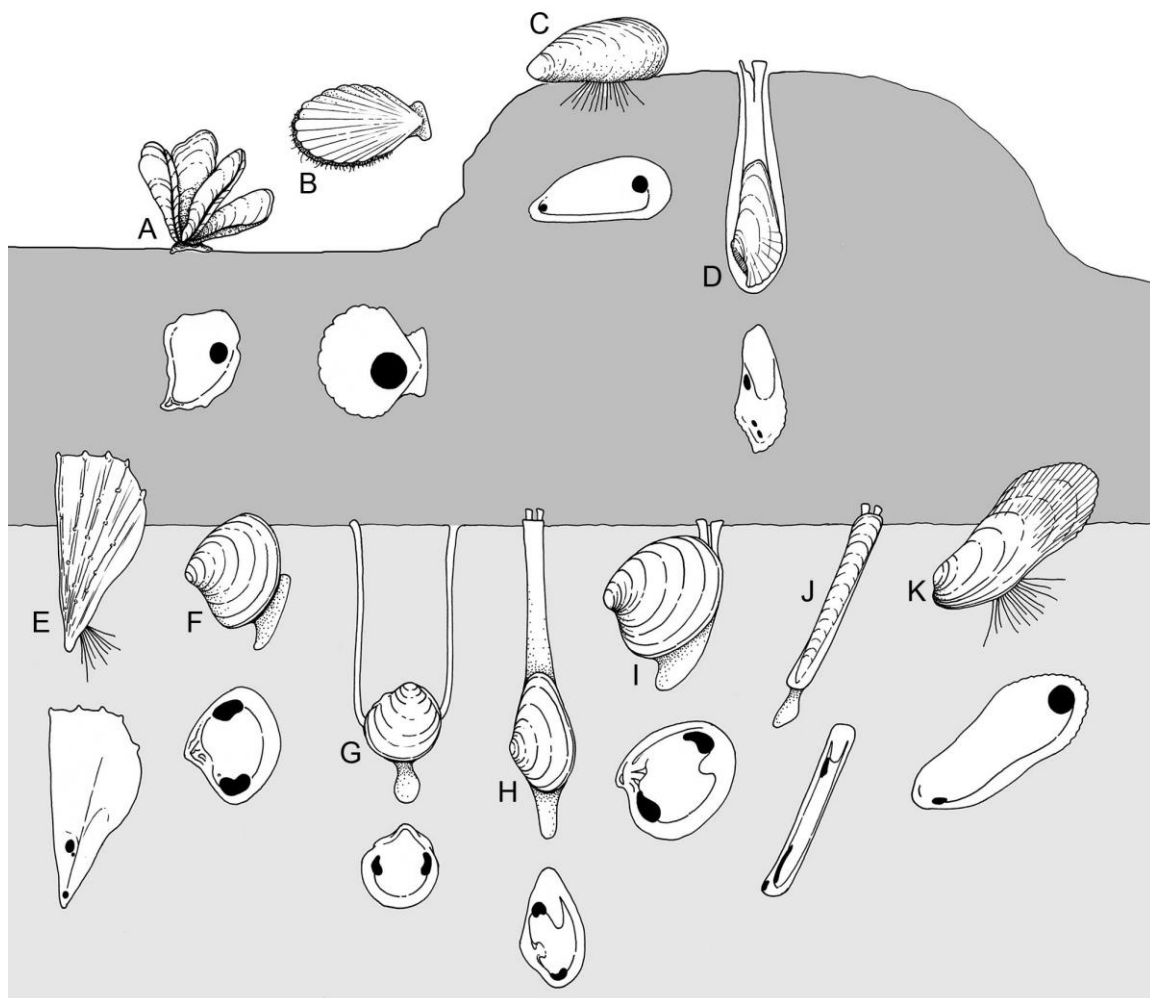


Figure 0.5. Illustration of some life modes of bivalves: (Light gray = soft substrate; dark gray = hard substrate) **A.** cemented. **B.** epibenthic swimmer. **C.** epibyssate. **D.** rock-borer. **E.** shallow burrower. **F.** shallow burrower. **G.** deep burrower with mucus siphons **H.** deep burrower with fused mantle siphons. **I.** shallow burrower. **J.** deep burrower with fused mantle siphons. **K.** endobyssate (Drawing by Christi Sobel; based on Stanley (1970), and other sources (Bivalve Ecology and Paleoecology)).

A study of the Veneridae family (fig 0) of bivalves, the diverse extant family by Edie et al. (2021) showed that they could be a comparative basis for examining different evolutionary patterns like deviations from the common body plan of bivalves. They argue that given the large phylogenetic and temporal range that their methods could be applied to study more bivalve families to gain further information of the relationship between modularity (described as the covariation of traits), integration (described as the partitioning of these traits into modules) as well as disparity and taxonomy (Edie et al. 2022). Bivalves also show a wide range of diversity even within singular functional groups. A study by Collins et al. (2023) showed that while specialization often leads to narrow morphological disparity, the endolithy (boring into hard substrata) utilizing bivalves has developed this trait separately at least 8 times. They found that this trait is accessible from many different branching evolutionary paths and that while endoliths seem to prefer a certain form, they are still morphologically diverse. However, the group is not very taxonomically diverse, a limitation which seem to stem from a lack of viable habitats rather than high extinction rates, low origination rates or both (Collins et al. 2023).

Each combination of bivalve life habits can be used to construct hypothetical ecospace (fig 1). Together the cubes form a sort of 3-dimensional space, a Bambachian cube, termed by Mondal & Harries (2016), which can be used to quantify the ecospace occupied by a clade (Bambach 1983).

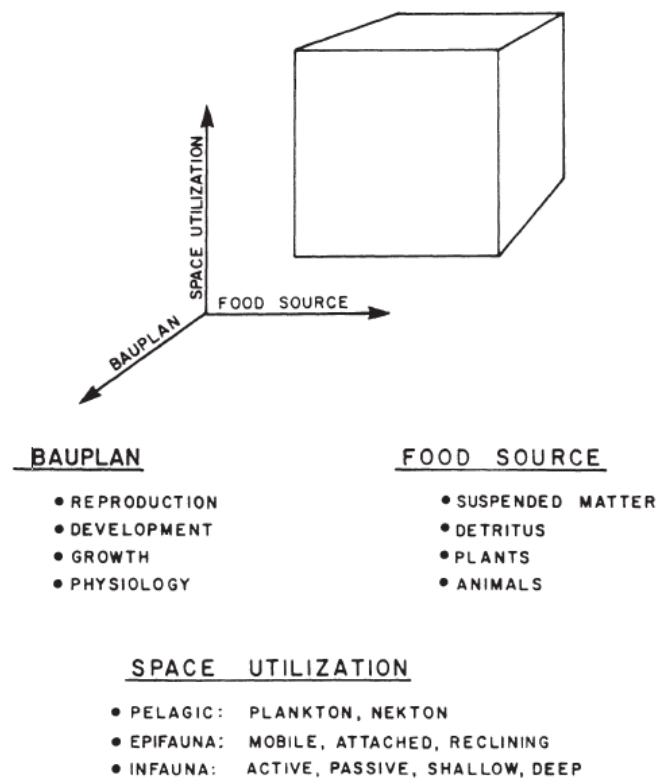


Figure 1: diagram representation of ecospace (Bambach 1983).

Based on these traits, Mondal & Harries (2016) constructed 140 total ecospace for bivalves, reflecting the theoretical maximum range of bivalve modes of life. They found

that the bivalves only occupy a mere 44 of the 140 total ecospace, finding the largest increase in ecospace occupation occurred during the Ordovician Period (486.85-443.1 Ma (Cohen et al. 2013)) due to various constraints (Mondal and Harries 2016). To better understand the morphological differences, Collins et al (2019) studied bivalves from two locations along the east coast of North America, the Florida Keys and the Gulf of Maine. The morphological differences between these two locations showed that the total variance in the shell ornamentation (how far from a hypothetically smooth shell, based on their calculations, the shell is) with the minimum value remaining unchanged across locations. In the Gulf of Maine, the bivalves occupied a wider range of morphospaces but the total variation in shell ornamentation was lower. They found that the differences across these two locations were mostly because of a loss of certain functional groups and clade at higher latitudes, meaning that these groups could either not survive in those environments or never spread that high to begin with (Collins et al. 2019).

So, what are some of the important features of bivalves and their shells? They can be defined by their bilaterally symmetrical, laterally compressed and external bivalved shells although there are exceptions, especially in those cemented to the substratum having a more asymmetrical shell form. These shells, made of aragonite, calcite or a mix of both protect the soft parts of the organism within the shell. The shells grow outwards from the Umbo, the name of the often-curved tip, which is the oldest part of the shell, originating from their larval stage. These shells can reach a wide variety of sizes, from a single millimeter to a meter in width as well as varying shell strengths and thickness. Some bivalves have radial, sometimes spiny ribs on their shells, radiating out from the beak of the shell while others have commarginal ridges as well as some which have both. Bivalves often have dull coloration, though some are more brightly colored, perhaps as an aid in camouflage. The exact reason for the colorization is unknown, some believe it to be a waste product from metabolism which is stored in the shell. The Bivalvia class can be further divided into five subclasses: Protobranchia, Pteriomorphia, Palaeoheterodonta, Heterodonta and Anomalodesmata (Beesley 1998).

The Protobranchia subclass is a group of primitive, mostly deposit-feeding infaunal bivalves. Some members of the subclass use suspension-feeding or sulphide-oxidizing symbiosis for sustenance instead. Common amongst this group are their ctenida (gills), which resembles that of some gastropods. They are ubiquitous in the marine realm and can be found everywhere from intertidal zones all the way to the hadal zone.

Pteriomorphia composes a group of mostly byssate epifaunal bivalves, both traits of which has been utilized from early in the history of the group. Because their byssate nature necessitates a viable feeding strategy when immobile, most Pteriomorphs are suspension-feeders. Among them are some of the best-known bivalves like mussels, oysters, scallops and arks, which also makes them one of if not the most economically essential bivalve group. They are either monomyarian or heteromyarian, meaning they

have either one or two muscles for opening and closing the two valves near the hinge and can be either equilateral or inequilateral, meaning their shells can be either symmetrical or asymmetrical along the hinge line. Attributing common morphological shell features to this group is rather difficult because although this subclass is monophyletic, it is very old, dating back to the early Ordovician, and have gone through multiple adaptive radiations and diversification since, particularly in the Late Devonian as well as the early and Late Mesozoic (Beesley 1998; Lemer et al. 2016; Lemer et al. 2019).

Palaeoheterodonta is a group composed of two distinct orders, the Trigonioidea and the Unionioidea, the first of which is a purely marine group and includes a single extant family (Trigoniidae) and genus (*Neotrigonia*) while the Unionioidea live in freshwater environments. The Unionioidea includes 7 families and the whole subclass includes over 1200 species. The common features of this group are their prismatic, equivalve (valves of equal size and form), inequilateral shells among others. The sculpture of the shells is a useful method of distinguishing the two orders apart. Trigoniids are usually quite small (≤ 40 mm in length) with radial ribs, scales or truncate ribs along the shell exterior. The Unioniids usually have elongate shells which reaches lengths of up to 15cm with varying thickness and radial sculpture structures along the shell exterior. All Palaeoheterodonts are infaunal, burying in soft sediment at a 45° angle, only exposing a part of the shell where their siphons stretch out of the substrate, allowing for filter-feeding.

The Heterodonta subclass are the most widely distributed of the bivalve subclasses and as such includes a wide variety of different traits amongst the different orders. Most are marine, siphonate filter-feeders. Other than this, the group has a wide variety of shell forms, sculpture, size and shell thickness.

Anomalodesmata is a ubiquitous subclass which contains a single order and some of the most peculiar and specialized bivalves. Members range from intertidal to abyssal zones and are either estuarine or marine, with small sizes and a nestling or burrowing lifestyle. The members are either filter-feeders, deposit-feeders or carnivorous. Their shell morphology is diverse and include some of the strangest bivalves, which belong to the Clavagellidae family, some of which stray far from the common bivalve form (Beesley 1998).

Since the Ordovician, the ratio of infaunal siphonate bivalves to endobyssate bivalves has increased. This change can be especially seen from the beginning of the Jurassic. Before this time, benthic fauna was dominated by epifaunal or semi-infaunal groups. A change in the shell structure can also be seen over time, especially during the Mesozoic, like the pectinoid bivalves, which developed a more foliated structure with folds. The cause of these changes in marine fauna, like some gastropods and bivalves, is referred to as the Mesozoic marine reorganization or revolution. The change to more sturdy shells may have been a response to the evolution of effective shell-destroying

(durophagous) fauna but not the only reason. The Mesozoic period also saw the development of efficient grazing methods among some marine groups, particularly teleostean fishes and echinoid echinoderms which may have favored an infaunal life habit instead of an epifaunal one (Vermeij 1977).

Hypotheses

Studying bivalve morphological diversity and what influences it is important because they, on top of being major contributors to the marine ecosystem, also provide sustenance for humans around the world (Collins et al. 2019). Therefore, it should be of interest to know how they are influenced by various factors. The purpose of this project is thus to examine the morphological and taxonomic diversity of extant members of the class Bivalvia with the following hypotheses:

- If taxonomic diversity drives morphological diversity, then we should observe higher morphological disparity in taxonomic groups with greater species richness
- If morphological diversity is influenced by latitude, then bivalve assemblages in certain latitudinal zones will exhibit greater morphological variation than those in others.
- If bivalve exterior shell sculpturedness (a quantified value of shell form) is influenced by ecology, then we should observe that bivalves with certain ecological traits are more sculptured than others.
- If morphological diversity is influenced time, then we should observe a difference in morphological disparity between fossil and modern bivalve shells

Method

To answer the hypotheses of this project a method of quantifying the sculpture of a bivalve shell was needed. This was done by automatically identifying edges on the outer surface of a bivalve shell, quantify the area they occupy and comparing it to the whole bivalve area to get a percentage value representing how sculptured the bivalve shell is. I used a dataset of over 50000 bivalve images on a black background, originally compiled and described by supervisor Steffen Kiel in another article (Hofmann et al. 2024). The images needed to only show the exterior shell, as the interior part of the shell does not interact much with the surrounding environment. The images also need to show only the bivalve and not anything else that might have accidentally been included in the image (instruments, rulers etc.) as the function used to calculate the edges (`image_canny`) will also detect these as edges and plot them out. These images were run through a script in R which quantified the sculpture of the shell, primarily with the help of the package called `magick`. `Magick` is a package which is used for various sorts of image processing (Ooms 2016). The dataset was first cleaned by removing all images of shell interiors which for the purposes of this project were irrelevant. After cleaning, the images were loaded into R (fig 2A), after which the images were normalized (fig 2B) and grayscaled (fig 2C) to allow `magick` to more easily detect the differences in brightness on the shell, a prerequisite to detecting the edges on the shell in the following steps. The images were then put through a threshold (2% in the script), which allowed `magick` to separate the shell from the background, painting the bivalve shell white (fig 2D).

To calculate the sculpture of the shell from this point, the shell was first flood-filled, which was used with `magick` to map out the entire area of the shell (fig 2E). The flood-fill function colors a pixel at a certain starting point (in this case the center of the image) as well as all connecting pixels that share color with this starting pixel. Since the bivalve was earlier painted white, this effectively makes the flood-filling add a color (blue in this case) to the exterior shell until it finds the shell boundary (Nisha and Varshney 2017).

The next step was to remove artifacts from the image which was done by using `image_split`, a function which divides the image into connected regions which could be one with the shell, dirt, a scale bar etc. (fig 2). The split image that needs to be kept was the image with the bivalve area (fig 2). After flood-filling, the image with the bivalve area is the flood-filled image, which will show as separate connected region of the divided image. The script then picks out the connected region which has the lowest number of white pixels, which will be the blue flood-filled image since it has none, effectively separating the bivalve shell from all artifacts. The last step of the sculpture calculation was using edge detection with the `image_canny` function on grayscaled image to calculate the edges (fig 2F). Edge detection works by identifying areas on the shell where there is a sharp change in color intensity (like changing from dark gray to white)

which is identified as an edge and marked as a pixel (fig 2C, 2F). The edge detection is simpler with a grayscale image rather than a regular image with color since it only processes one layer of color instead of three, a red, a green and a blue layer (Ad et al. 2017). The result was a pixel value of edges which was divided by the total number of pixels of the shell (the flood-filled image) and multiplied by 100, resulting in a percentage value for how sculptured the bivalve was. These steps were repeated for all images.

After all percentage values for sculpturedness were calculated, the means for each species, genus and family were calculated based on the sculpturedness values for each image per species and genus and the mean of the member species for each family. The next step was to clean the dataset. This was done by running a script which removed images whose sculpturedness values were significantly different at a 95% confidence level from the mean family sculpturedness, if the family had above 250 images. The number was chosen because families with low image numbers may have too few images for a meaningful representation of the family. This would mean that these families kept their quantity of images but would also keep their outliers. Species with fewer than 3 images were then removed from the dataset as I decided these had too few images to represent their entire species in any meaningful way, and their standard deviation values would also not be as useful. The last step of this was to recalculate the means for the members of each taxonomic rank respectively, as the number of images was now different, which meant the sculpturedness values would most likely yield different means. The method of calculating sculpturedness of bivalve shells were identical when calculating the sculpturedness in the fossil bivalve dataset. This fossil dataset was all Neogene to Pleistocene bivalves from Italy, Malta, Greece and Cyprus from the NRM Palaeobiology collection. They had all been digitized, meaning they were photographed and recorded with associated data on locality, age, etc. in the past years.

To analyze sculpturedness on a global scale, the package *rnaturalearth* was used, which can map out data provided it has coordinates. Since the images in the main dataset did not have coordinates, another dataset was downloaded from the Global Biodiversity Information Facility (GBIF). GBIF is “*an international network and data infrastructure funded by the world's governments and aimed at providing anyone, anywhere, open access to data about all types of life on Earth*” (GBIF info webpage), where a dataset of about 4.45 million bivalve occurrences (4,452,420 to be precise) was downloaded which was then cleaned, first removing families that were not in the main dataset, then genera, species and lastly bivalves with no depth data. Ideally, this would result in a large dataset which had the same number of unique families, genera and species as the main dataset. This would prevent mapping out bivalves with no calculated sculpturedness. The resulting dataset had around 445,000 occurrences of marine bivalves with coordinates.

To visualize the bivalve sculpturedness on a phylogenetic tree and add how old each genus was, the packages phytools and ape were used. These two can be used to make phylogenetic trees (Paradis et al. 2024; Revell 2025). The phylogenetic tree was plotted using a tre file from (Bieler et al. 2014) which was acquired from supervisor Steffen Kiel who got it from Rüdiger Bieler himself and contained the information regarding the shape of the phylogenetic tree and the length of each branch for some of the families in the main dataset. The tre file was based on figure 31 of the article which was made using molecular data along with “Bayesian inference analysis of nine genes + morphology”.

To analyze ecologic traits in relation to sculpturedness, and for comparison with a different measure of sculpture, a dataset by (Collins et al. 2019) was used, which had information of where bivalves lived in relation to the substrate, feeding strategies, mobility and fixation as well as maximum ornamentation (max deviation from a hypothetically smooth shell surface). This dataset had 408 unique species, 227 of which were also in the main dataset belonging to 159 genera and 48 families.

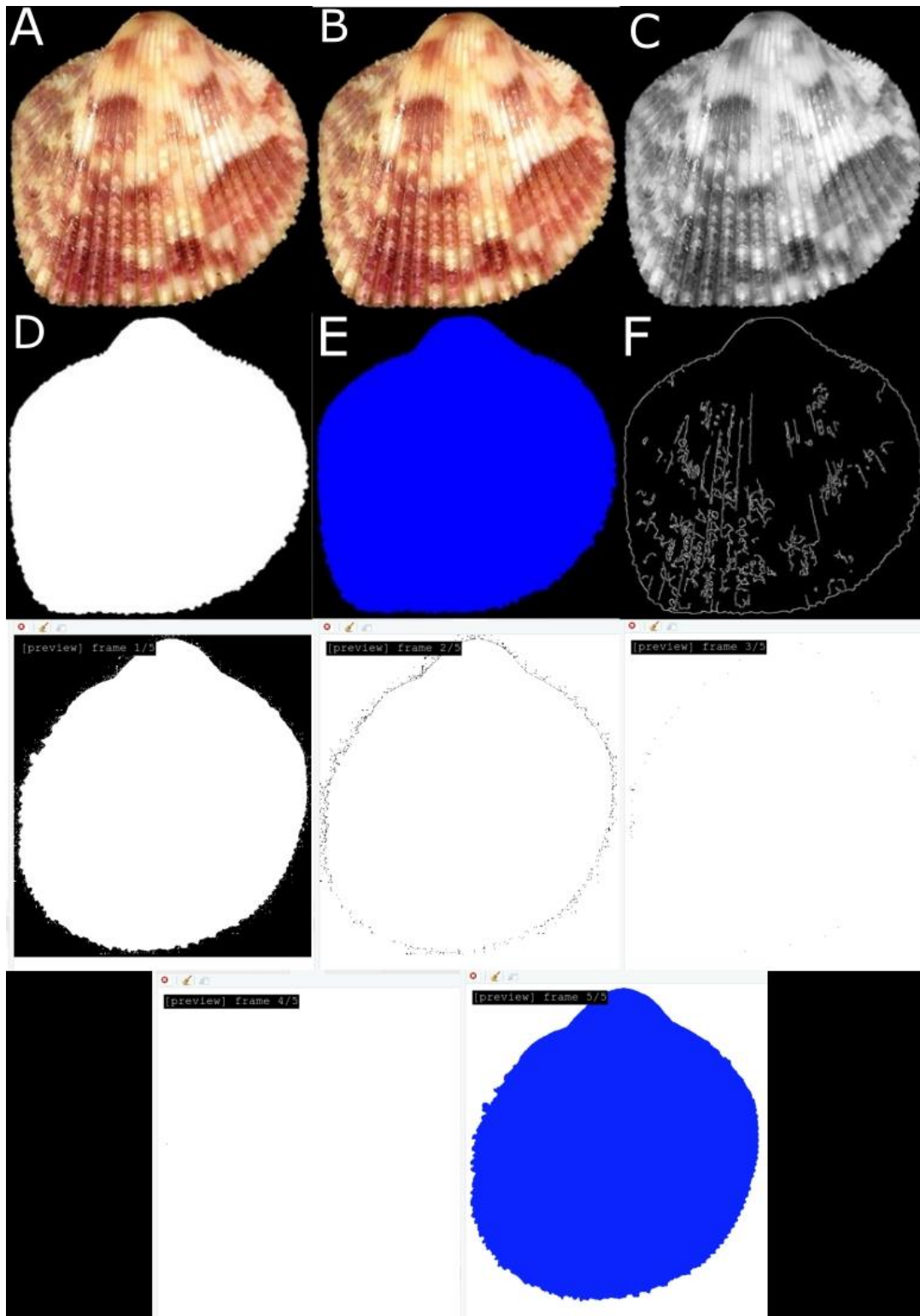


Figure 2. Example of the image processing in all the steps as well as the `image_split` process of choosing the correct image. A, image before processing, B, normalized image, C, grayscaled image, D, thresholding, E, flood-filling, F, edge detection. The lower half of the image shows each individual frame processed during `image_split` function. The frame with the least number of white pixels is then saved, which, in all cases is the blue flood-filled one.

Results

The cleaning and calculation of sculpturedness resulted in a dataset of 45,996 images. Among them, there were 91 families, 690 genera and 2301 species.

A first test was to see if sculpturedness was just a function of image numbers (more images = more strongly sculptured). The upper plots of figure 3 show that this is not the case. A second test was to check if the variation in sculpturedness was a function of image numbers (more images = higher standard deviation). As with mean sculpturedness, the lower plots of figure 3 show this is not the case.

Most families, genera and species had low image numbers (fig 3 top) but a large variation in means. Looking at a plot of mean genus sculpturedness summarized by families (fig 4), several of the families still have outliers, which can likely be attributed to the script omitting them from cleaning because of low image numbers (below 250). Plotting the variation in sculpturedness of a given taxon, measured as the standard deviation from the mean sculpturedness summarized by images per taxon shows a similar variation as mean sculpturedness (fig 3 bottom). The standard deviation varies among taxa with few images. Taxa with large numbers of images are few, but their sculpturedness and standard deviation can differ widely, showing some with high and some with low values.

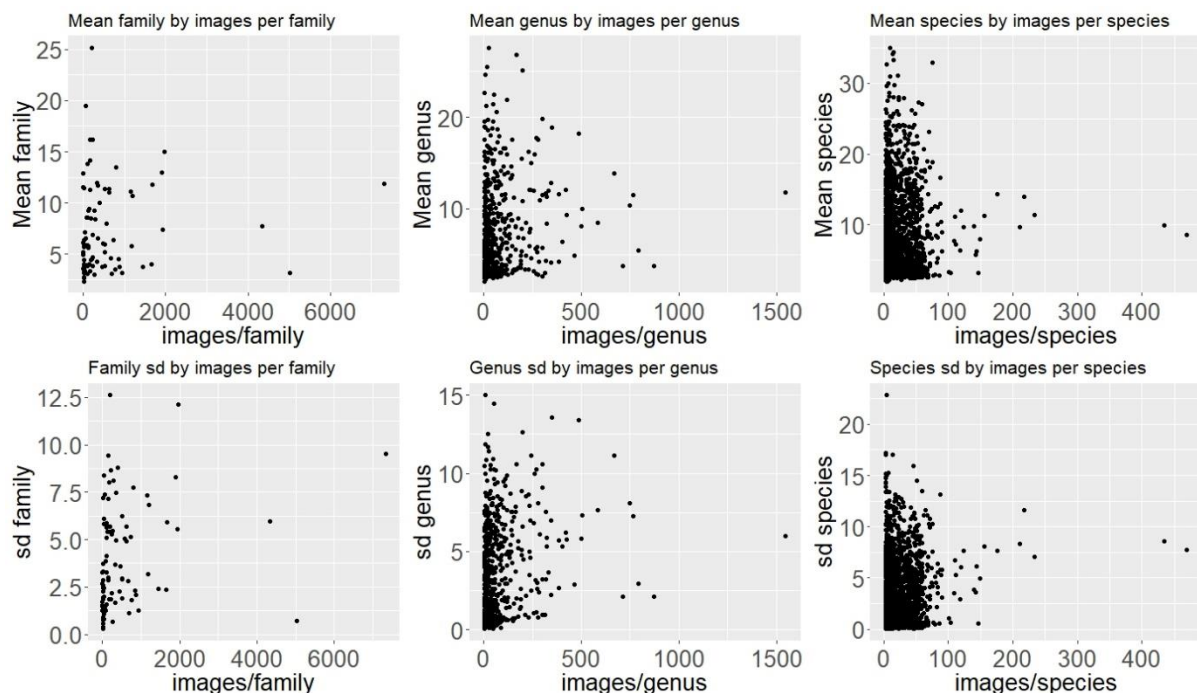


Figure 3. Measured mean sculpturedness and the respective standard deviations compared to the number of images. The top row shows mean taxon sculpturedness summarized by images per taxon. The bottom row shows taxon standard deviation summarized by images per taxon.

The next test was to see if there was a linear relationship between mean family and mean genus sculpturedness to see if their sculpturedness increased at similar rates. There seems to be a linear relationship, the only exception being some of the families with the highest means (fig 4, from left). Some of the families are also much more variable than others, although their median sculpturedness still follows this linear curve.

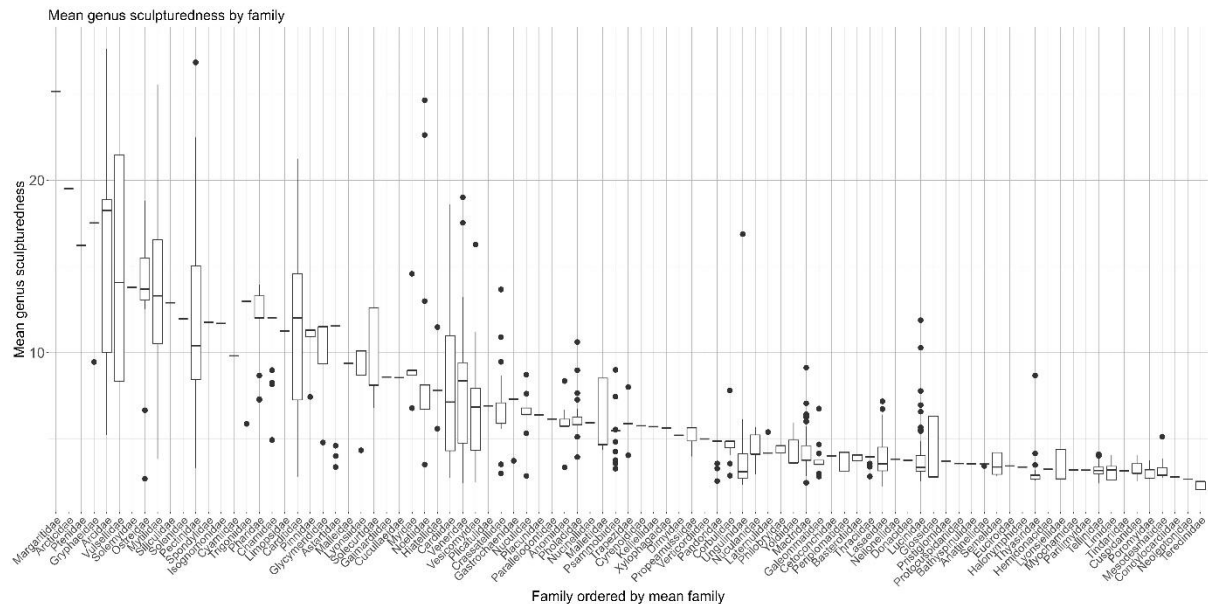


Figure 4. Box plots showing mean genus sculpturedness summed by family, and ordered by mean family sculpturedness.

Further analysis of the variation in sculpturedness required a new measure because standard deviation, a function of intensity of sculpture, would not be very informative in this regard because it shows the absolute spread of the means and not the relative variability. The new normalized measure, the coefficient of variation, is defined as the standard deviation divided by the mean sculpturedness. The result showed that all families except one had a coefficient of variation below 1.00 (fig 5 top), and when summarized by family standard deviation, it showed that most varied somewhere between 0.5 and 1, even as standard deviation increases (fig 5 bottom).

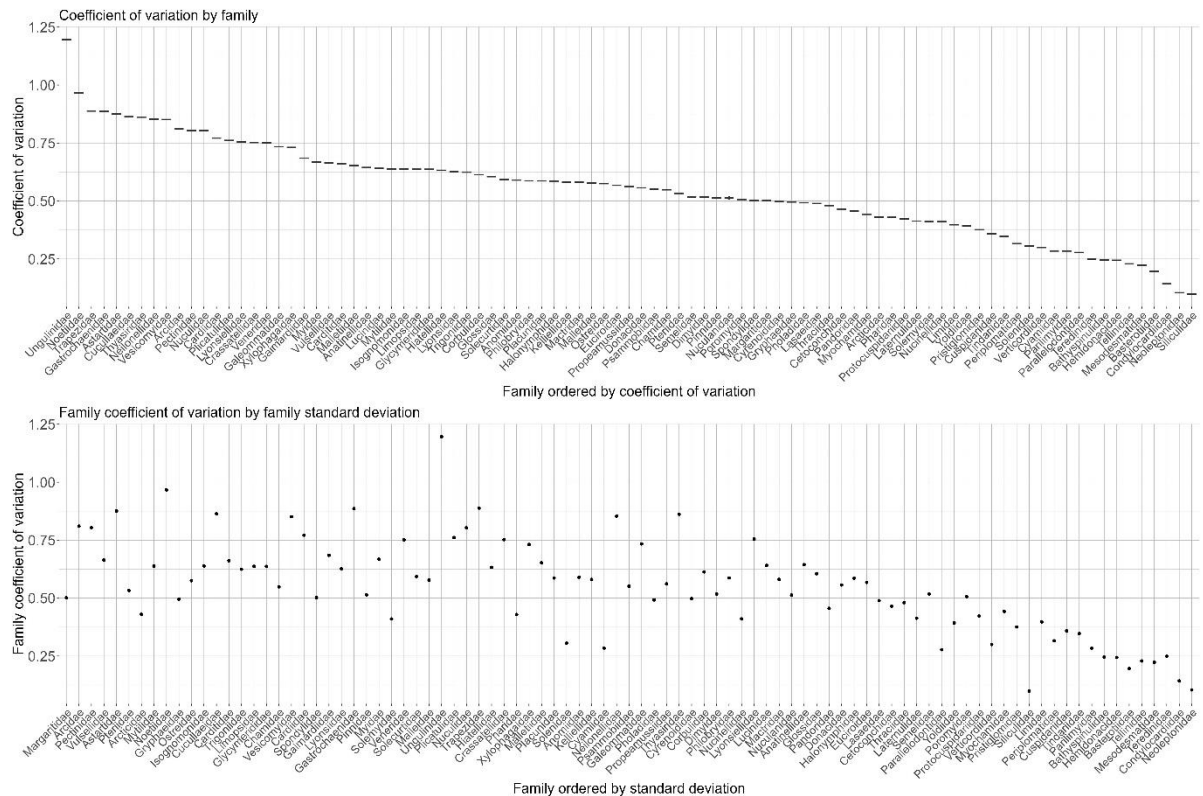


Figure 5. Shows the coefficient of variation of sculpturedness (cov) of the investigated families. Top panel: ordered from highest to lowest, bottom panel: ordered by the standard deviation of the respective families. Below a value of ~ 0.5 , cov and standard deviation are roughly correlated, but above ~ 0.5 , the relation is either random or not correlated.

The next test was to see if the means of genera as well as their coefficients of variation had linear relationships with higher taxonomic ranks than family. Figure 6 shows that this is the case for both means and coefficients of variation. Plotting mean genus sculpturedness summarized by orders (fig 6, top left), many of them have values below ten. The five highest mean genus orders, Ostreida, Mytilida, Solemyida, Arcida and Trigoniida all have median values above ten, although the Solemyida and Trigoniida only have two genera in the dataset, both with one genus being larger in quantity of images and mean genus sculpturedness. These two orders are also below the 250-image threshold, while the three others have image numbers much higher than that. The same can be seen when plotting mean genus summarized by subclasses, where there is a large difference between the two subclasses with the most images and the rest. Pteriomorphia, with the highest means and Imparidentia, with the third lowest means, make up 21,737 and 18,351 images of the 45,996 total, meaning the three other subclasses make up the remaining 5908 images. Of these three, Paleoheterodonta, with the fourth highest means, makes up only 24 of the total images.

Looking at the genus coefficients of variation summarized by orders (fig 6, bottom left), the ordering is not the same as mean genus summarized by orders. Nuculida, the 12th highest order in terms of mean sculpturedness has the highest coefficient of variation while the previous highest is now tenth. Plotting genus coefficients of variation summarized by subclasses (fig 6, bottom right), Pteriomorpha is still the highest and Anomalodesmata is still the lowest, but the four middle subclasses have changed places.

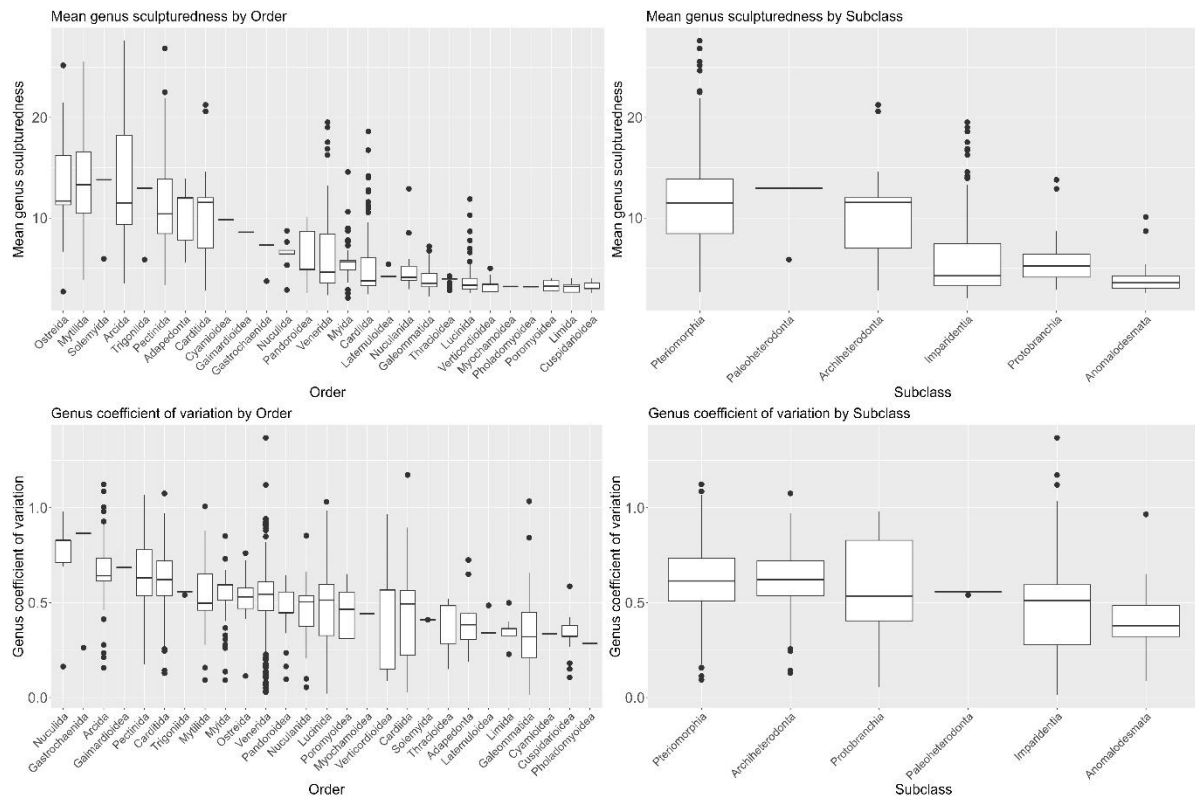


Figure 6. Box plots showing the mean genus sculpturedness and coefficient of variation when summed by order and subclass. Top left shows mean genus by order, top right, mean genus by subclass, bottom left, genus coefficient of variation (cov) by order, genus coefficient of variation by subclass.

Next for testing was to see if the mean family sculpturedness was normally distributed which required a way of comparing the actual data to a theoretical normal distribution. The mean family sculpturedness, plotted as probability density in blue on the plot, shows that there is a preference toward either high or low sculpture as well as a slight peak in density in the middle (fig 7). Attempting to overlay a normal distribution curve on top of it, the density distribution does not follow this normal curve in any way one would expect from a normally distributed dataset. A simple Anderson-Darling normality test (for a null hypothesis that the dataset is normally distributed) also results in a p-value of $< 2.2 \times 10^{-16}$, showing that the mean family sculpturedness is not normally distributed.

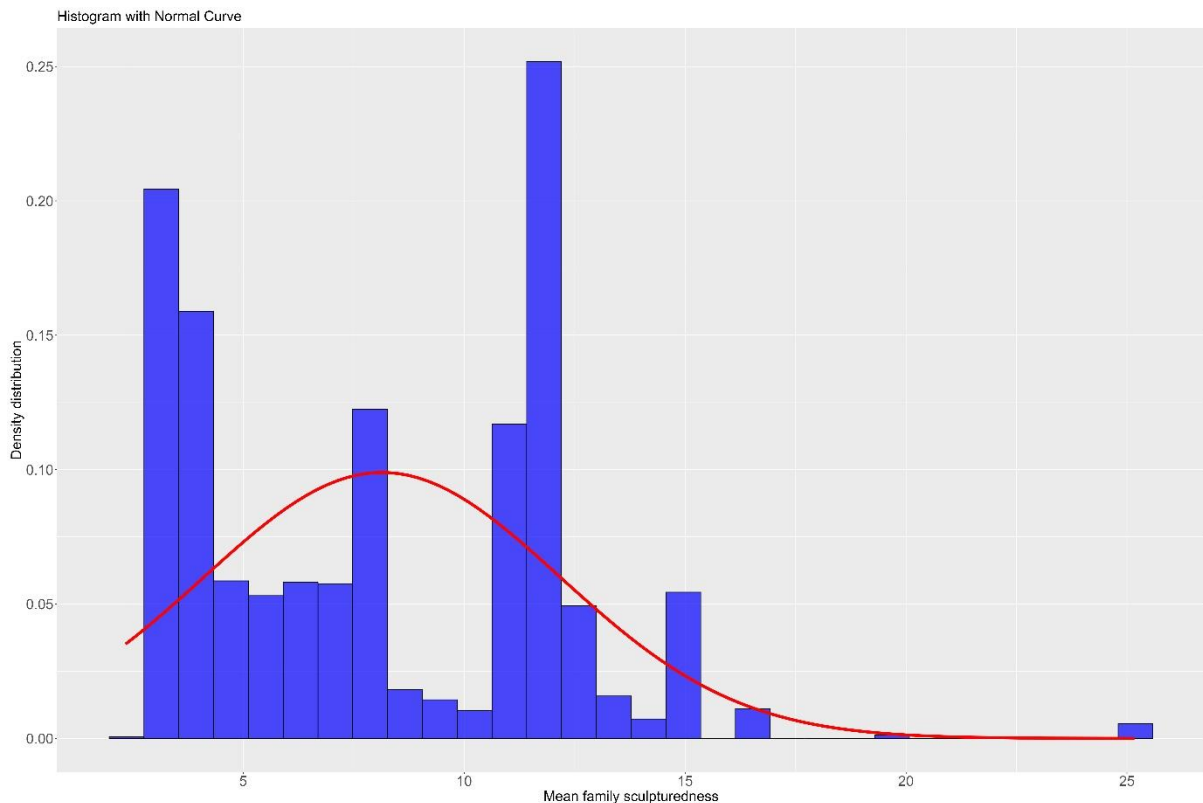


Figure 7. A histogram showing the density distribution of mean family sculpturedness with normal distribution curve (red line) overlaid on top. A normally distributed dataset would roughly plot out as a bell curve.

Another test was to see how the mean sculpturedness related to the standard deviation as well as the coefficients of variation (does a higher mean = higher standard deviation or coefficient of variation). Plotting mean taxon sculpturedness summarized by standard deviation shows a positive, slightly linear relationship (fig 8, top), with quite a large spread. This shows that variation is generally higher when mean family is higher. The plots of mean taxon summarized by coefficients of variation shows a large spread in mean values, especially so for the lower coefficient of variation values (fig 8, bottom). This shows that variation is greater amongst taxa with a lower mean value and that the higher the coefficient of variation, the lower the mean sculpturedness, which is especially clear for species and genus coefficient of variation (fig 8, bottom-left and middle).

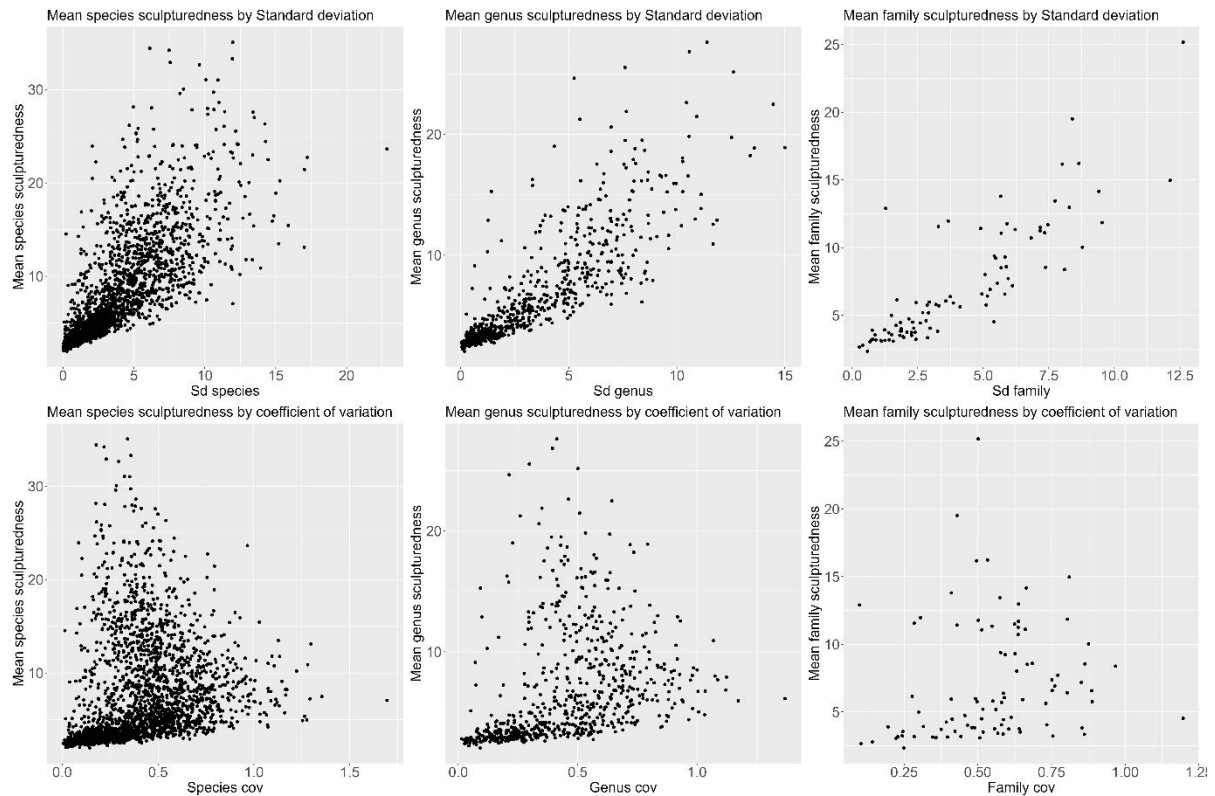


Figure 8. Scatter plots showing mean taxon sculpturedness as a function of standard deviation and coefficient of variation. Top row shows mean taxon by taxon standard deviation and bottom row shows mean taxon by taxon coefficient of variation.

Further tests with the coefficients of variation were to see if it related to the number of images per taxon, similar to means and standard deviation in figure 3. Additionally, a test was done to see how the same coefficients of variation was a function of the number of members of a taxon (species per genus/family and genera per family). When plotting taxon coefficients of variation summarized by images per taxon (fig 9, top), most taxa have low image numbers. Amongst species, most have fewer than 100 images, while the maximum number of images per species was above 400. For genera and families, most have under 500 and 2000 images, except few, with the largest having over 1500 and 6000 images in total. Comparing the genus coefficients of variation summarized by species per genus, species per family and genera per family (fig 9, bottom), most of the high and low coefficients of variation are among genera with few species, whilst genera with a larger number of species averages out toward a middle point of ~0.5.

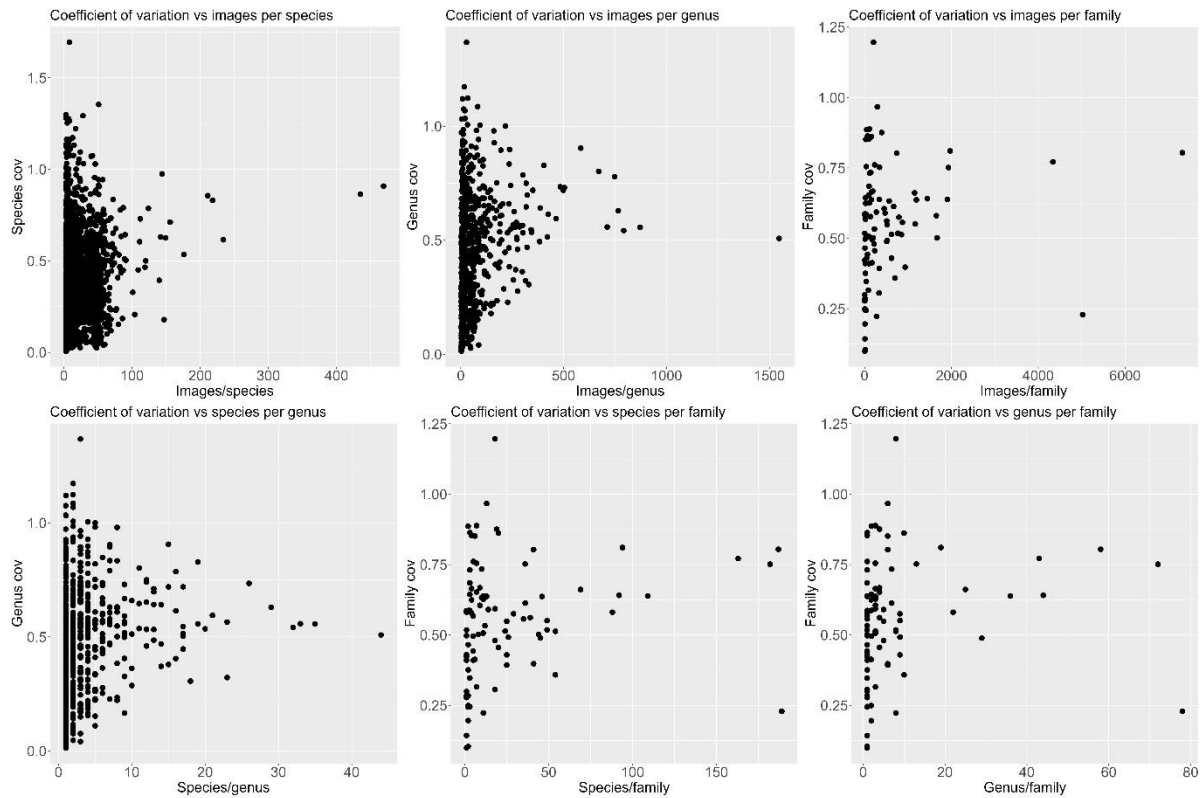


Figure 9. Scatter plots showing the coefficient of variation as a function of images and how many members taxa has. Top left shows coefficient of variation (cov) by images per species, top middle, cov by images per genus, top right, cov by images per family, bottom left, cov by species per genus, bottom middle, cov by species per family, bottom right, cov by genera per family.

To analyze the potential impact of ecological traits on sculpturedness, the dataset of 227 species with ecologic data from Collins et al. (2019) was added to the main dataset. Looking at the species with ecological traits, for mobility (fig 10, top left), the highest median mean family sculpturedness are among the immobile families, while the mobile families have both the lowest median and the highest mean family values overall. The swimming bivalves in the middle have mean family values all below 20% sculpturedness. Immobile bivalves made up ~35% of the 3590 images, swimming ~6% and mobile ~58%.

As for fixation, the byssate, making up ~33% of the images, had the highest median value, largest spread within the interquartile range, and the highest extreme values. Middle amongst them were the cemented (fig 10, top right), making up only ~8% of the images, but had a median value similar to the byssate, and all had mean species sculpturedness percentages higher than 7. Last in the fixation group, unattached bivalves made up ~58% of the images and had by far the lowest median value, but high extremes larger than the cemented bivalves. This means that half of the unattached bivalves had very low sculpturedness whilst the second half had a larger spread.

Feeding strategies among bivalves seem to largely lean toward suspension feeding (fig 10, lower left), making up ~73% of the images, with the second being mixed deposit/suspension making up ~11%. Suspension feeding bivalves also have the highest extremes as well as the highest median. The surface deposit bivalves have the largest interquartile range and highest upper quartile. The remaining groups make up only ~16% of the images. Sculpturedness in these groups (subsurface deposit, chemosymbiotic, mixed deposit/suspension, carnivore) are all very low (all are at least under 10), with carnivorous bivalves being the lowest apart from a few outliers higher than the second lowest.

Last among ecology data is where they live in relation to the substrate (fig 10, lower right). First among them, semi-infaunal (~4% of the images) have the highest median value and the largest spread in interquartile range as well as the highest extreme value of the images. None of these bivalves have below 8.2% sculpturedness, showing their preference toward more sculpturedness. Second comes epifaunal (34% of the images), which, being the richest group, have the second highest median and extreme values. This group shows a sculpturedness range from high to low, with the interquartile range being somewhere in the medium to high range from roughly 5-16% sculpturedness. Of note is the nestler group (5% of the images), which is dominated by a single species, with all other members showing up as outliers. The four groups with the lowest mean species sculpturedness all live below the substrate with three of them being infaunal and one being the borers. The shallow and deep infaunal siphonate bivalves both have large image numbers, making up roughly 25% and 21% respectively. Both also have very low median values, showing that at least half of them is very smooth. The shallow infaunal siphonate and the infaunal asiphonate both show similar interquartile ranges with the difference being the higher median in asiphonate bivalves.

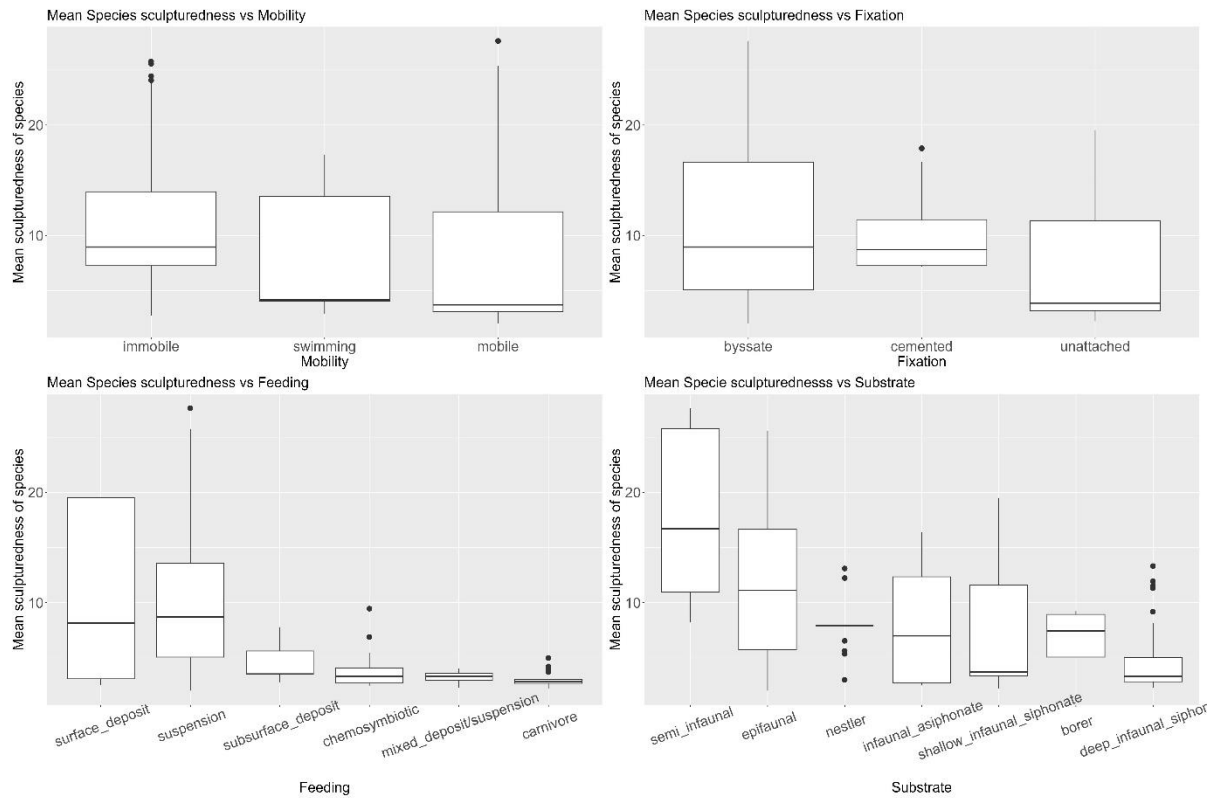


Figure 10. Mean species sculpturedness summarized by four ecological traits. From left to right, top to bottom, mean sculpturedness of species summarized by mobility, fixation, feeding and substrate. Because many of the species in the original dataset were not among the species in the dataset by Collins et al (2019), 42406 bivalve images had to be excluded from these plots.

The next step in testing was to check if the mean sculpturedness and coefficients of variation were related to the geographical distribution of the species. The GBIF dataset showed a wide global distribution of bivalve occurrences (fig 11). For clarity, the species were grouped by their mean sculpturedness into four tiers (0-10%, 11-20%, 21-30% and 31-40%), which were color-coded from dark blue (low values) to bright red (high values). It showed that the bivalves of the lower two tiers, the two blues, were by far the most common, being found across all latitudes. The second to highest tier (orange) contained far fewer records but still showed a wide distribution across latitudes, albeit with a large portion located at sub 30° latitudes. The highest group, the red, were even less common, with only a few points on the map, with all being located at sub 20° latitudes.

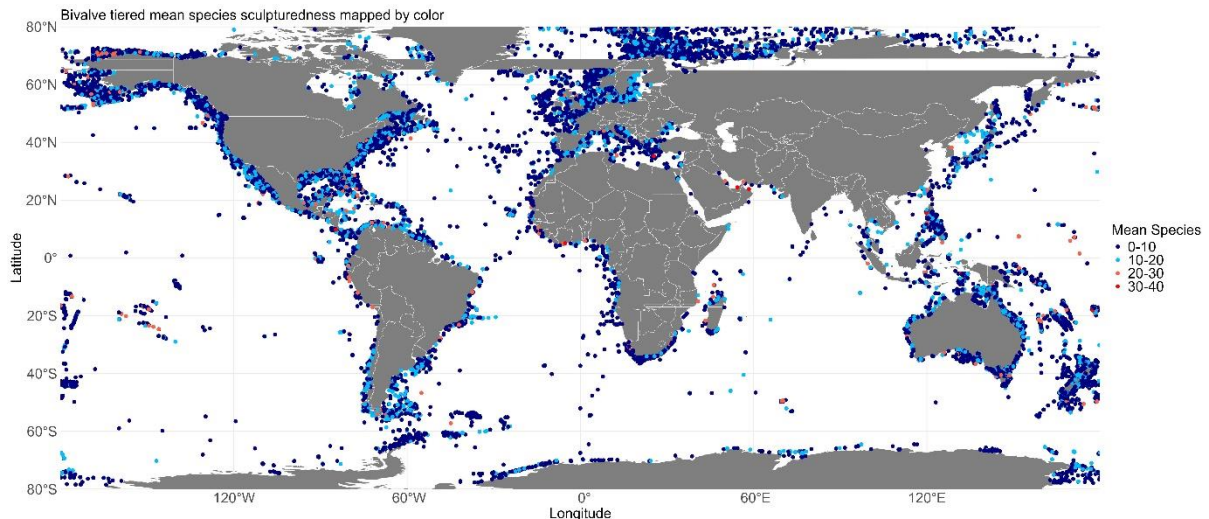


Figure 11. Geographic distribution of bivalves showing their mean species sculpturedness divided into tiers mapped by color. Blue is low sculpturedness, red is high.

Similar to the mean sculpturedness values, the species were grouped into five tiers by their coefficients of variation. Looking at the map with species coefficients of variation plotted out (fig 12), higher coefficients of variation are much more common than high mean species sculpturedness. The second highest coefficient of variation tier (0.75-1), can be found across all latitudes and was also the second richest group, making up ~40% of the bivalves in the dataset. The richest group were those with coefficients of variation values right in the middle (light blue), making up ~43% of the bivalves and could also be found across all latitudes. Second to lowest among the groups (~12%, dark blue) can still be found across all latitudes, albeit much more sparsely than the two largest groups. The two groups at the extremes, lowest (~4%, darkest blue) and highest (~0.15%, red), appear much less frequent than the three other groups. Bivalves around Antarctica showed low coefficients of variation in general, with the three lowermost coefficients of variation groups appearing to be the most common.

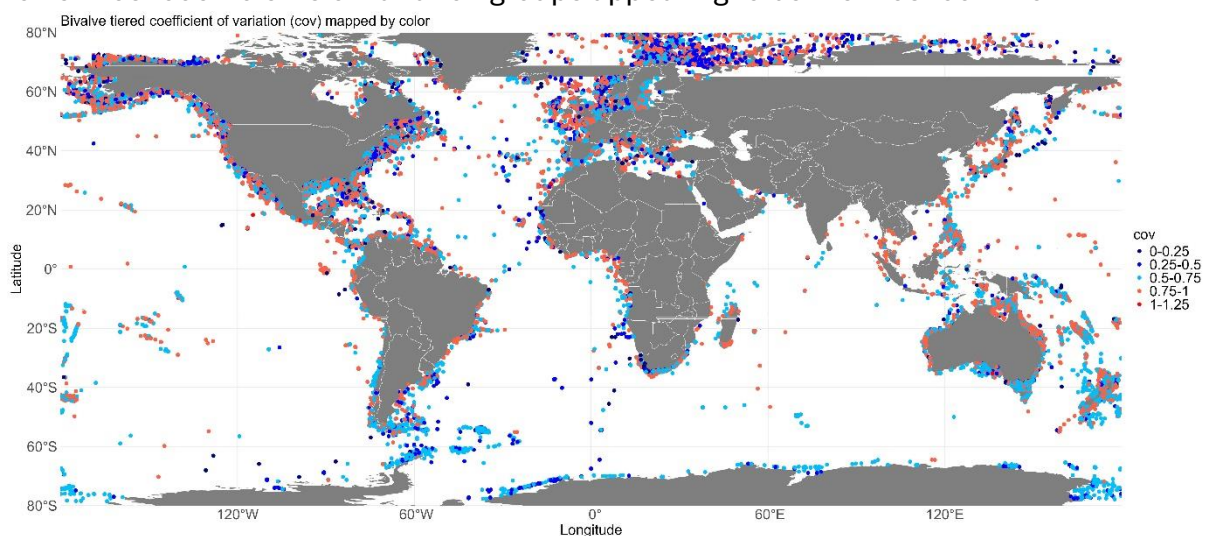


Figure 12. Geographic distribution of bivalves showing their coefficient of variation (cov) divided into tiers mapped by color. Blue is low cov, red is high.

Continuing from the coefficients of variation map (fig 12), a new map was made to see the geographic distribution of families with the highest values. To visualize the distribution of families with high coefficients of variation, the five with the highest were plotted on the map (fig 13) ranging in coefficient of variation from ~0.88-1.2 in the order from lowest to highest: Astartidae, Gastrochaenidae, Trapezidae, Noetiidae and Ungulinidae. The last-mentioned family was the sole family which made up the highest coefficient of variation tier and appeared to be mostly found around 20-40° latitude in both hemispheres. The Astartidae family (orange) appears to be exclusive to the northern hemisphere, being regionally abundant along the eastern coast of North America, the coastline of Scandinavia (including parts of the Baltic Sea), the North Sea and the Arctic Ocean. The Noetiidae family (light green) are regionally abundant around the Gulf of Mexico, the Caribbean Sea and the Mediterranean Sea as well as more scattered across the southern hemisphere. The remaining families appears less commonly (darker green, blue, pink), distributed across latitudes as well as smaller clusters for families like Ungulinidae (pink) around Australia, New Zealand and the western North American coast.

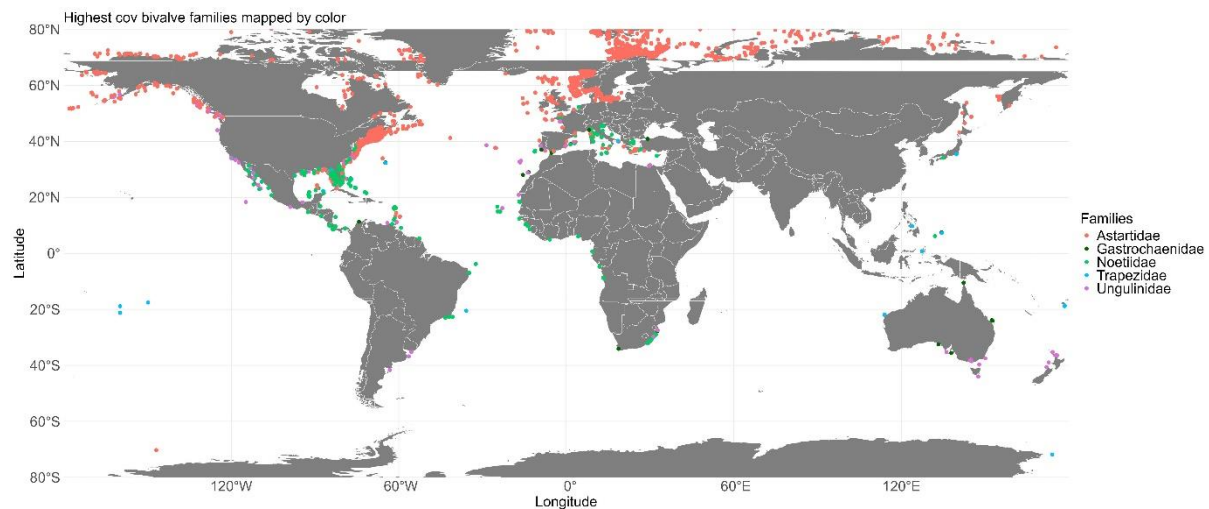


Figure 13. Geographic distribution of the 5 bivalve families with the highest coefficient of variation mapped by color. From highest to lowest: Astartidae (~0.88), Gastrochaenidae (~0.89), Trapezidae (~0.89), Noetiidae (~0.97), Ungulinidae (~1.2).

Continuing, a test was conducted to see whether the degree of sculpturedness showed trends on the phylogenetic tree. Adding the mean family sculpturedness of the families in the main dataset with the tre file results in a phylogenetic tree where some patterns can be seen in various clades (fig 14). The proportion of families with lower mean sculpturedness appears to be higher in the upper half of the tree. Many of the families in the two clades in the bottom half of the tree in contrast appear to have a bigger proportion of higher mean sculpture.

Lastly, a test was conducted to see how a dataset of fossil images, with exterior shell sculpturedness calculated with the same method, would compare to the main dataset of extant bivalve shell images. The bivalves in the dataset were dated somewhere from the Miocene to Pliocene epochs and had a total of 1308 images left after cleaning. They showed a wide range of sculpturedness values from 1.5 to 70%. Many of the bivalves in the images were quite fragmented so the cleaning removed around two thirds of the original images. Plotting the means of the genera summarized by families shows most families have only genus in the dataset, while others, like the Veneridae has more (fig 15, left). Plotting the difference in mean family sculpturedness from then to now (fossil sculpture – modern sculpture) show that around 15 of the 38 families with calculated sculpture has a negative difference, indicating an increase in sculpture over time while the 25 other families have a positive difference (fig 15, middle), indicating a reduction. In particular, the five families with the largest difference show large leaps in values with Noetiidae, the largest, showing a difference of 19.2 between the percentages, indicating that the family had a much more strongly sculptured shell in the Pliocene.

When comparing the coefficients of variation between the fossil and modern bivalves show that the modern ones have lower variation in average than the fossil ones, with most of the modern ones having a coefficient of ~0.5 to 0.75, while the modern values are mostly spread out between 0.1 and 1 (fig 15, right).

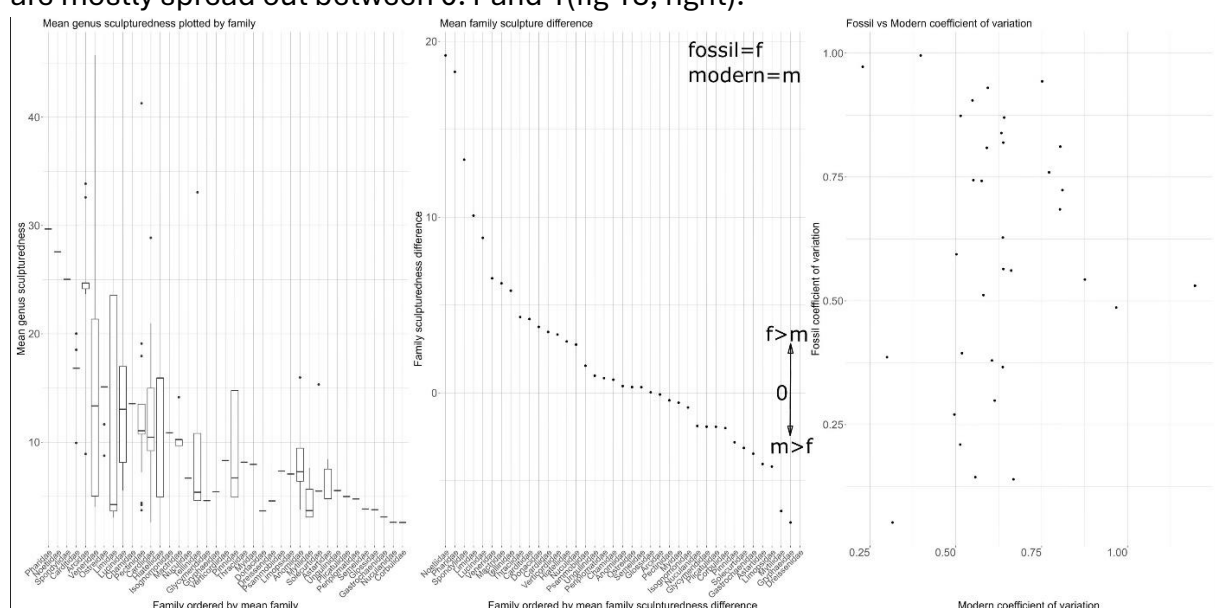


Figure 15. These plots show comparisons in sculpturedness between fossil (Miocene to Pliocene epochs) and modern bivalves. The first shows calculated sculpturedness of fossil bivalves summed by families ordered by sculpturedness more to less. The second shows the difference (fossil – modern) in mean sculpturedness of families. The right shows the coefficient of variation of fossil families summarized by modern family coefficients of variation.

Discussion

As seen from the figures plotting sculpturedness and cov summarized by images per taxon (fig 3, 9, upper), there is no relationship between them and image numbers. The question remains then what are the relationships which influence sculpturedness and coefficients of variation in bivalves, which is why this dataset is suitable for further investigating the hypotheses stated at the end of the introduction.

The bivalves in the dataset show a wide distribution in their degree of sculpturedness and has been shown to possibly have a relation to their variation in sculpturedness (fig 4, 8). As seen from figure 5, there is an initial increase in coefficients of variation with increasing standard deviation, but this growth seems to slow down above coefficient of variation values of 0.5 and above. Could this indicate that a correlation between the intensity of sculpture and variability only exists between species with low sculpture? The lower left plots of figure 8 could also argue for this, seeing as the coefficients of variation only seem to increase with mean species sculpturedness among those with low sculpturedness. The species with high sculpturedness seem to differ less and less in their variability in sculpture.

On the order rank, the mean genus sculpturedness (fig 6, top left) of the lower sculpturedness orders share quite similar median values, with the second half increasing more rapidly. On the subclass rank, the three subclasses with the lowest mean genus sculpturedness (fig 6, top right) all have similar median sculpturedness below 10%, while the three with the most sculpture have similar medians above 10%. Plotting coefficients of variation (fig 6, lower) in the same way shows a more gradual increase in values, but with a different order than the mean sculpturedness. This does seem to indicate, at least on the subclass level, that coefficients of variation are more similar to each other than their sculpturedness. Such a pattern is more difficult to see on the order rank. Coefficients of variation do seem to increase more steadily than sculpturedness, but both have quite a wide range in values and are not as similar to each other as on the subclass level. The reasons could be due to the larger sizes of individual subclasses as opposed to orders, including wide ranges of sculpturedness and coefficients of variation making them more stable. Interestingly, the density distribution of mean family sculpturedness (fig 7) shows that bivalve families have a higher likelihood of either having more or less sculpturedness than somewhere in the middle. This indicates that there may be some advantages in being strongly sculptured or smooth rather than being moderately sculptured. Figure 8 (lower) shows that the coefficients of variation in bivalve taxa varies more in taxa with lower mean sculpture.

The cause for this is uncertain, but it may have been because of a larger number of taxa with lower mean sculpture or that there is a larger variation in standard deviation across these taxa. Another possible cause for the larger differences in coefficients of variation among bivalve taxa with lower sculpture could be due to artifacts remaining on the

exterior shells. Periostracum for example is an outer protective protein, forming a dark layer on bivalve shells (Taylor and Kennedy 1969; Checa et al. 2014). If dark patches remain on otherwise light-colored shells, then the edge detection might pick these up as edges, when they are in fact not. The significance of these periostracum patches might also cause a more significant bias for smoother shells than for more sculptured shells.

Morphological diversity is a function of taxonomic diversity

The morphological diversity of the bivalves in the dataset, as shown by the coefficients of variation (fig 9, bottom), at a family level shows a slight trend toward higher coefficients of variation with increasing family richness, which could indicate a link between taxonomic and morphological diversity (higher taxonomic diversity = higher morphological diversity). For fewer species and genera per family, the families seem to differ much more from each other. The species per genus plot (fig 9, bottom left) shows this, with genera of similar taxonomic richness differing more in coefficients of variation as taxonomic richness gets lower. This indicates that there is a limit to the correlation between taxonomic and morphological diversity. This could mean that as the bivalve morphospace reaches its limit, the addition of more species would stay within these limits, not increasing variation any further. This may also indicate that the fewer species a genus has, the more individual bivalves can influence the coefficient of variation of genus mean sculpturedness. It could otherwise indicate that genera with greater richness in species are more likely to be evenly distributed in coefficients of variation. This seems to indicate that morphological diversity is indeed a function of taxonomic diversity. Within species morphological diversity may instead be influenced by environmental factors such as salinity and temperature (Morán et al. 2022).

Morphological diversity as a function of latitude

If morphological diversity were instead a function of latitude, one could expect a gradual increase or decrease in mean sculpturedness or coefficients of variation from the tropics toward the poles. The distribution of sculpturedness plotted on a map (Fig. 11) shows that all the points belonging to those species with the highest means are located close to the equator, which could indicate that the most strongly sculptured species prefer to live close to the equator, though their few numbers make it difficult to say conclusively. Higher latitudes, especially in the North Sea and Arctic Ocean, show regional abundance of the lower two tiers of sculpturedness, which could indicate that colder waters have advantages for bivalve species with low sculpture or that bivalves with high sculpture are at a disadvantage. This agrees with observations that ornamentation in bivalves generally decrease from the Florida Keys toward the Gulf of Maine (Collins et al. 2019). Their explanation for this, partly being due to a loss of topical clades also agrees with the out of the tropics model, that endemism (the percentage of

taxa which are restricted geographically) decreases with increasing latitude (Jablonski et al. 2006).

Collins et al (2019) show that both ornamentation and size of bivalves generally decreases toward the Gulf of Maine from the Florida Keys along the coast. The minimum and maximum values stay the same in most of the taxonomic groups, so the cause, they conclude, may be because of a loss of clades with high ornamentation (Collins et al. 2019). Looking at the map showing the coefficients of variation of bivalves (fig 12), there are few bivalves of the highest and lowest tiers along the same stretch of coastline, and a mix of the three middle tiers, which are more commonly associated with lower sculpture. At closer inspection of the five bivalve families with the highest coefficients of variation, there is a shift in families between the two locations. The Astartidae family is seemingly the only family of the five in the Gulf of Maine, while the around the Florida Keys have a mix of Noetiidae, Trapezidae and Ungulinidae, but no Gastrochaenidae. This indicates that certain families may prefer to live within certain latitudes. A potential problem could be the different methods used between this project and the one by (Collins et al. 2019). Since they measured the elevation of the shells above a hypothetical baseline and this project quantified the sculpture without any regard to elevation, the map is likely to show different results. Another study shows that this change in taxonomic richness not only occurs in other locations but has occurred in different epochs as well. This study showed that fossil gastropods and bivalves in Chile dated to the lower Miocene, along the coast of the Southeast Pacific Ocean decreased in functional richness from low to high latitudes (Grossmann et al. 2023).

Figure 12 shows no overall relation between latitude and coefficients of variation. Bivalves seem to be abundant in northern latitudes, but this is likely simply because of more shelf area and is likely unrelated to shell sculpture.

The general coefficient of variation around Antarctica is low, with most belonging to the 0.25-0.5 and 0.5-0.75 tiers as well as a few, which belongs to the 0-0.25 and 0.75-1 tiers (fig 12). Similarly, the general mean sculpturedness of species around Antarctica (fig 11) is dominated by the lowest tier (0-10%). Some of the higher coefficients of variation in these parts may also be there by mistake. Looking at figure 13 shows that all except one single bivalve in the Astartidae family live in the northern hemisphere (1 out of 34251 occurrences), which may indicate that the latitude has been flipped. This is because the only thing separating northern latitudes from southern in R is a minus before the latitude at southern coordinates. The low coefficients of variation around Antarctica indicates that the families around these parts are quite uniform in sculpture, differing little from their mean family sculpturedness. The cause for the low sculpturedness may be due to a relative abundance of bivalve species with ecological traits associated with low sculpture (fig 10) like subsurface deposit feeders, deep infaunal siphonate bivalves to name a few. Another cause could also be, as Collins et al. (2019) described, to be a lower predation intensity at higher latitudes compared to tropical regions. Another

cause for these low coefficients of variation could also be the low taxonomic diversity among fauna in the Antarctic (Krug et al. 2010). Comparing mean family sculpturedness of the locally extinct taxa with the extant taxa (fig. 1 in Krug et al. (2010)) shows that the extinct ones had on average a higher sculpture than the extant ones (9.2% compared to 6.8%) hinting at a preferential extinction of more sculptured families. As they explain, could be due to a combination of four different drivers: Antarctic glaciation, geographic isolation (and onset of the Antarctic Circumpolar Current), extinction of durophagous predators and changes in primary productivity throughout the Cenozoic. A lack of these predators could then lead to a disadvantageous position for certain bivalves due to a combination of costs for skeletal defenses, high metabolic rates and temperature adaptations. This could have led to a decrease both in sculpturedness of bivalve shells as lack of predators made it unnecessary and taxonomic diversity lowering morphological diversity. From this it seems unlikely that there is an overall relation between latitude and morphological diversity but rather that the change is an effect of decrease in taxonomic richness with increasing latitude.

Sculpturedness is dictated by ecology

A comparison of sculpturedness and ecologic parameters suggests that bivalves that do not or rarely move have on average a higher mean sculpturedness (fig 10, top). Data also show that bivalve species which lives, at least partly, above the substrate (semi-infaunal, epifaunal) are much more strongly sculptured than those which lives in the substrate (fig 10, bottom right). Two potential reasons, the first being protection against predators, the second being easier burrowing with smooth shells. This makes sense if strong sculpture is a way for bivalves to protect against predators. If this were the case, then they would be expected to be more commonly found in locations where there are more predators. In their article, Collins et al. (2019) show that the ornamentation of bivalves is higher in the Florida Keys than the Gulf of Maine. Ornamentation in this case is thought to be an effective countermeasure against crushing forces applied by predators like certain fish and crustaceans. They are also hypothesized to be connected to higher predation rates in tropical regions (Collins et al. 2019), which does seem to agree with the sculpturedness map (fig 11), where the highest tier sculpturedness are most commonly found close to the equator. From this it seems likely that sculpturedness in bivalves is strongly influenced by their ecology.

Morphological diversity has increased over time

Over time, the plot (fig 15, middle) indicates that a majority bivalve families present in both the main and the fossil datasets has reduced in sculpture over time. If sculpturedness of the shells had a similar relation to predation as ornamentation, this could indicate a reduction in predation over time, but, when checking which genera are present in the fossil dataset and absent in the main dataset, 27 genera are missing. Part of the reason for this could be the uncertain labeling of some genera in the fossil

dataset (e.g. *Acrosterigma?*, *Neopycnodonte?*). The reduction in sculpturedness may then also be the effect of some genera either having become extinct or that their genera are simply not in the main dataset. Change in the sculpture of these bivalves may also be a result of a change in the proportion of infaunal bivalves. The plot shows that infaunal bivalves as well as borers have the lowest mean sculpturedness (fig 10), so a larger proportion of them among families could result in a lowering of the mean sculpturedness. In his article, Vermeij (1977) describes that since Ordovician, there has been a relative decrease in the diversity of endobysate bivalves and an increase in infaunal siphonate bivalves, which he describes, may have been a response to an increase in predation in the region above the substrate (Vermeij 1977). This agrees with the ecology data, where epifaunal bivalves make up ~34% of the total, while the infaunal as well as boring bivalves make up ~57%, the rest belonging to semi-infaunal and nestling bivalves. The differences between coefficients of variation between the fossil bivalves and the modern (fig 15, right), indicate that bivalve families of today have a greater variation than fossil bivalves. This could also reflect the difference in quantity of bivalves in both datasets. Yet another explanation could be how the edge detection algorithm produces different results on images of fossil shells compared to modern shells, the main reason being that modern shells are shinier and can be colorful, which might blur the sculpture. Another article, studying the relation between concentric ribs in bivalves and predation by gastropod drilling showed that the degree of successful drilling increased with increasing rib strength (Klomp maker and Kelley 2015). They found that moderately sized concentric ribs were the most effective in protecting against drilling. From this, while there are hints that point toward a reduction in sculpture over time, the relatively smaller fossil dataset makes it difficult to say if morphological diversity has decreased over time or if some other method is needed.

Limitations

There are still some unresolved issues with the method. As can be seen by the comparison between fossil and modern bivalves, differences in color may have a significant influence on the resulting sculpturedness. More detailed cleaning of both datasets might also improve the accuracy of the sculpturedness of families, genera and species by removing things like bivalve images with periostracum. Further investigation on how the edge detection algorithm identifies edges on bivalve shells could aid in increasing the accuracy of the method. There is also an uncertainty as to whether it was a correct decision to exclude the cleaning of bivalve families with less than 250 images. There may very well be a better way of cleaning the dataset than was done with this method.

Conclusions

- The results obtained in this study point towards morphological diversity in bivalves being a function of taxonomic diversity on a family level, but on the genus level points toward the stability of coefficients of variation in a genus increasing with taxonomic richness, resulting in genera with larger taxonomic richness being more similar in variation than genera with lower taxonomic richness.
- Morphological diversity in bivalves is unlikely to be a function of latitude, though many families show a strong preference for certain latitudes.
- It is likely that morphological diversity in bivalves is strongly influenced by their ecological traits.
- While there are certain hints toward a reduction in sculpturedness over time, the fossil dataset is not enough to say so with any certainty. A larger fossil image record of bivalves would aid in making more certain comparisons. A more thorough cleaning of the fossil dataset (like removing specimens with periostracum) would also aid in making it more accurate.

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