ABSTRACT

Exploring the Morphospace of Cidaroid Echinoid Spines

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Crown group cidaroids (Echinodermata: Echinoidea: Cidaroida) display a variety of spine morphologies thought to be adapted in response to selective pressures around them. Echinoid spines directly interact with their surroundings and morphologies should reflect environmental conditions changing through time. To quantify trends in morphology through time, 2D geometric morphometrics were applied to cidaroid spines to track changes in morphospace. This was completed through four anatomical landmarks and 250 semi-landmarks to grasp the entirety of the spine shape. Once plotted into multivariate space, trends related to time and morphology were found within one family of cidaroids, Psychocidaridae. These trends coincided with major geologic events, such as the Marine Mesozoic Revolution and Cretaceous-Paleogene extinction. Contractions and shifts in morphospace could then be related to predation and changes in marine community structure. Additionally, modern cidaroids display an expansive morphological diversity, while not being taxonomically diverse.

Exploring the Morphospace of Cidaroid Echinoid Spines

by

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A Thesis

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I would like to acknowledge and thank Dr. Petsios for the guidance through this degree and wonderful mentorship.

# DEDICATION

To my parents and family who supported me in my endeavors. I would also like to thank the Missouri paleontologist who helped spark my interest in paleontology, and the professors of FHSU and Baylor for their wonderful support. Thank you to those at the Sternberg Museum of Natural History for supplying me with experiences I needed. Thank you to everyone who has helped and inspired me.

# CHAPTER ONE

## Background

Cidaroid urchins have unique spines within the realm of echinoids. Mature spines of cidaroid echinoids lack an epidermis (Märkel & Röser, 1983). An epidermis allows for an efficient immune response among echinoderms (Dupont & Thorndyke, 2012). A lack of epidermis allows cidaroids to be populated by epibionts to act as camouflage and protection (Wahl et al., 1997; Smith, 1984). Epibionts have been found to increase the resistance of the spines against acidified water, as well as not reducing the mechanical strength of the spine to a severe degree (Dery et al., 2014; Dery et al., 2017). This resistance to epibionts may be due to the concentric rings of stereom, or growth rings, deposited as the spine matures (Ebert, 1986). Spines are typically a means to protect the individual, yet brooding cidaroids, like members of the genus *Goniocidaris* in Antarctica, hold juveniles among the apical spines to protect the young (Baker, 1985). Cidaroid spines are crucial for locomotion. Spines act as levers and stilts to propel the echinoid forward. Cidaroid have a preference toward hard grounds, but species with long, thin spines will traverse soft, muddy environments (Prouho & Lawrence, 1888; Fell, 1966). Cidaroid echinoid spines play many crucial roles in their survival.

The most recently published phylogenetic analyses place the family Psychocidaridae as the most basal of the three crown groups (Koch & Thompson, 2021). The earliest member of this family was dated to the Late Triassic in Italy (Kier, 1977b). This family is continued through a single living member, *Tylocidaris ohshimai* (previously *Psychocidaris ohshimai)* which inhabits waters around Southeast Asia. It was

noted that the animal's spines were unique among cidaroids (Ikeda, 1935a; Ikeda, 1935b; Ikeda, 1939a; Ikeda, 1939b). The bulb- and club-shaped spines from Psychocidaridae are commonly found throughout the Cretaceous and Paleogene (Shulz et al., 1984; Rosenkrantz, 1970). Others have recognized these spines as diagnostic characters for the family, and have used them as index fossils throughout the Danian (Brotzen, 1959). These index fossils detail the shift between different psychocidarid taxa through the occurrence of different spine morphologies, mainly *Tylocidaris* (Gravesen, 1993). This family holds value as an index fossil, and the single surviving taxon may give a glimpse into this once prolific clade.

Cidaridae is the most diverse of the crown group families. The earliest specimens date back to the Triassic (Smith, 1984). This family diversified at a constant rate through the Cretaceous until today, when there are over 30 genera within the family. Most of the early fossil record for Cidaridae is based on spines, whether that be isolated spines or partially articulated specimens (Greenstein, 1992). Spines of this clade are quite recognizable, with modern specimens boasting a variety of colors and morphologies, with fossil specimens still being unique enough to identify. Cidaridae spines are usually quite stout, just not to the degree of members of Psychocidaridae (Clark, 1907). The abundance of Cidaridae allows for a diverse sample to be collected and analyzed.

The last family, Histocidaridae, is known to live in deeper waters. As this clade dwells in deeper waters, the spines of these individuals are adapted to such, being long and thin compared to the thicker spines found in the other crown group cidaroids (Garcia-Guillen et al., 2022). These thin spines allow for movement through soft sediment (Fell, 1966). They also display distinct ornamentation on said spines, such as serrations running

along the spines (Garcia-Guillen et al., 2022). As the spines and thinner in comparison with other cidaroids, this leads to more damaged and broken spines. The environment being deeper sea can also lead to fewer specimens as there have been few recorded deep-sea outcrops with echinoid material (Smith & Stockley, 2005).

Spines were chosen as the structure of choice for morphological analysis for several reasons, such as inherent preservation potential and availability. Echinoids are prone to disarticulation after death due to minimal suturing of plates with sedimentation rates lower than the rate of decay, leading to lone spines and test plates being common fossil finds. Spines can be easily recognizable and identified fairly accurately if preservation allows (Kier, 1977a; Kier, 1958). Spines preserve so well that a study found that 77% of type descriptions of fragmented Cidaridae were isolated spines (Greenstein, 1992). Echinoids will additionally shed injured spines and regenerate new spines with may aid in the prevalence of echinoid spines in the fossil record (Prouho & Lawrence, 1888). As spines preserve well and are easily accessible, they create a perfect sample pool for a typically difficult group to study.

# CHAPTER TWO

## Methods

The main methods for this project involved generating outlines to capture the morphology of cidaroid spines. The urchins in question span across 11 genera of crown group cidaroids. A complete list of targeted taxa is shown in Table 1. Similar studies have been done with other invertebrates, such as ostracods, and produced results as such specimens are symmetric and eliminate much of the need for 3D morphometrics (Wan et al., 2021). It is more common to see 2D and 3D morphometrics together, using 2D landmarking on slices of a 3D structure (Stohr et al., 2019). Others have compared the differences between the 2D and 3D methods, showing that 2D morphometrics gives a general understanding of a complex shape, while 3D morphometrics shows better precision overall (Buser et al., 2018). With echinoid spines, the shape is axially symmetric along the length of the spine in a majority of cases, leading to the spine looking identical if spun along the longest axis. A benefit of the 2D method is that partially exposed fossils in matrix may be analyzed without the requirement of X-ray imaging, which was crucial for some specimens used. The outline dataset included only complete spines, as the analyses could not be performed on spines lacking a base, tip, or ornamentation. The images used were sourced from online databases, including GBIF (gbif.org), iNaturalist (inaturalist.org), and the Paleobiology Database (paleobiodb.org; PBDB), and collections (such as the Sam Noble and online collections: Florida Museum of Natural History, National Museum of Natural History inParis, and Natural History Museum in London). The initial outlines were captured using the software ImageJ

(Rasbrand, 2018). The final outlines comprised four landmarks, homologous morphological locations across echinoid spines (Fig. 2.1), and 250 resampled semi-landmarks to approximate the rest of the spine shape. Resampling is performed using the *Morpho* package in R statistical software environment and then combined with the homologous landmarks to form the complete outline (Schlager, 2017). The anatomical landmarks were placed across the collar and ring and the spine tip (Fig. 2.1). The semi-landmarks capture the diverse ornamentation across cidaroids and resampled to 250 to ensure each specimen has an equal number of points. Procrustes superimposition was used to correct for non-shape variability between specimens, such as size and orientation (Gower, 1975). These outlines were then plotted in multivariate space using principal component analysis (PCA) in R software using the package *geomorph* (Baken et al., 2021). Groupings were delineated by geologic time bins, taxonomy, and morphological categories.

Ornamentation can add to the complexity of the spine outline and was analyzed as well. The ornamentations of the spines were categorized and adapted from Kroh & Smith (2010). Eight ornamentation types were used in this study (Fig. 3.1). The ornamentation of each spine was then overlaid across the PCA to elucidate any correlation between multivariate shape, ornamentation, and time.

Table 2.1. List of Cidaroid Genera

| Family | Genera | Species |
|---|---|---|
| Psychocidaridae | *Balanocidaris* | *B. besairiee* |
| | | *B. glandifera* |
| | | *B. gibberula* |
| | | *B. julii* |
| | *Caenocidaris* | *C. cucumifera* |
| | *Tylocidaris* | *T. abildgaardi* |
| | | *T. clavigera* |
| | | *T. honorinae* |
| | | *T. herupensis* |
| | | *T. odumi* |
| | | *T. ohshimai* |
| | | *T. rosenkrantzi* |
| | | *T. salina* |
| | | *T. walcotti* |
| Cidaridae | *Acanthocidaris* | *A. hastigera* |
| | *Goniocidaris* | *G. impressa* |
| | | *G. noetlingi* |
| | | *G. tubaria* |
| | *Phyllacanthus* | *P. hemigranosus* |
| | | *P. imperialis* |
| | | *P. dubius* |
| | | *P. parvispinus* |
| | *Prionocidaris* | *P. baculosa* |
| | | *P. bispinosa* |
| | *Stereocidaris* | *S. ingolfiana* |
| | | *S. sceptrifera* |
| | *Stylocidaris* | *S. affinis* |
| | | *S. calacantha* |
| | | *S. cingulata* |
| | | *S. conferta* |
| | *Typocidaris* | *T. marginta* |
| Histocidaridae | *Histocidaris* | *H. cobosi* |
| | | *H. purpurata* |

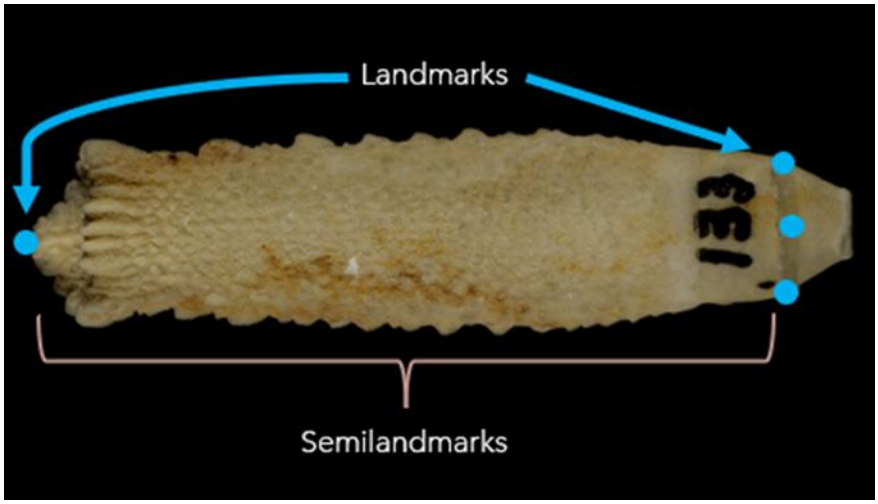


Figure 2.1. *Goniocidaris noetlingi* (MNHN R05835) specimen with model of landmark placement. Landmarks were placed with one at the tip and three around the collar and milled ring. Semilandmarks were placed along the shaft of the spine and around ornamentation to capture the complete outline for analysis.

# CHAPTER THREE

## Results

Spine morphology was measured and compared for this project to capture variability seen in cidaroid spines through a PCA. Currently, 147 spine specimens are included in the data covering 11 genera. These 11 genera belong to the three crown group cidaroid families (Koch & Thompson, 2021). Much of this project has been focused on Psychocidaridae, with 65 specimens and the best spread across time. The other two families, Histocidaridae and Cidaridae, have two and 80 specimens, respectively.

Psychocidaridae morphospace was compared across geologic time through several means in an attempt to elucidate trends across time. Figures 3.2 and 3.3 shows Psychocidaridae morphospace through time at the epoch level. Stage-level comparisons were not possible due to the scarcity of specimens for several stages across the studied interval. The morphospace through the Mesozoic shifts across epochs with a distinct expansion across the Cretaceous Paleogene extinction event (K-Pg), where we see an expansion of morphospace and into a severe contraction to Psychocidaroids today. Another view of this family through time was done using time bins. Figure 3.4 presents the family in three bins of time, specifically around the K-Pg, as pre-Danian, Danian, and post-Danian, to look at this interval in more detail. The shift in morphospace is once again visible around the K-Pg, and another shift after the Danian. To grasp the differences in the spines, Mesozoic spines are observed to be thick and bulbous from near the base to tip, while Danian spines have a thin spine shaft and a bulb as the end. Post-Danian is broken into two distinct groupings in morphospace. The group nearest the

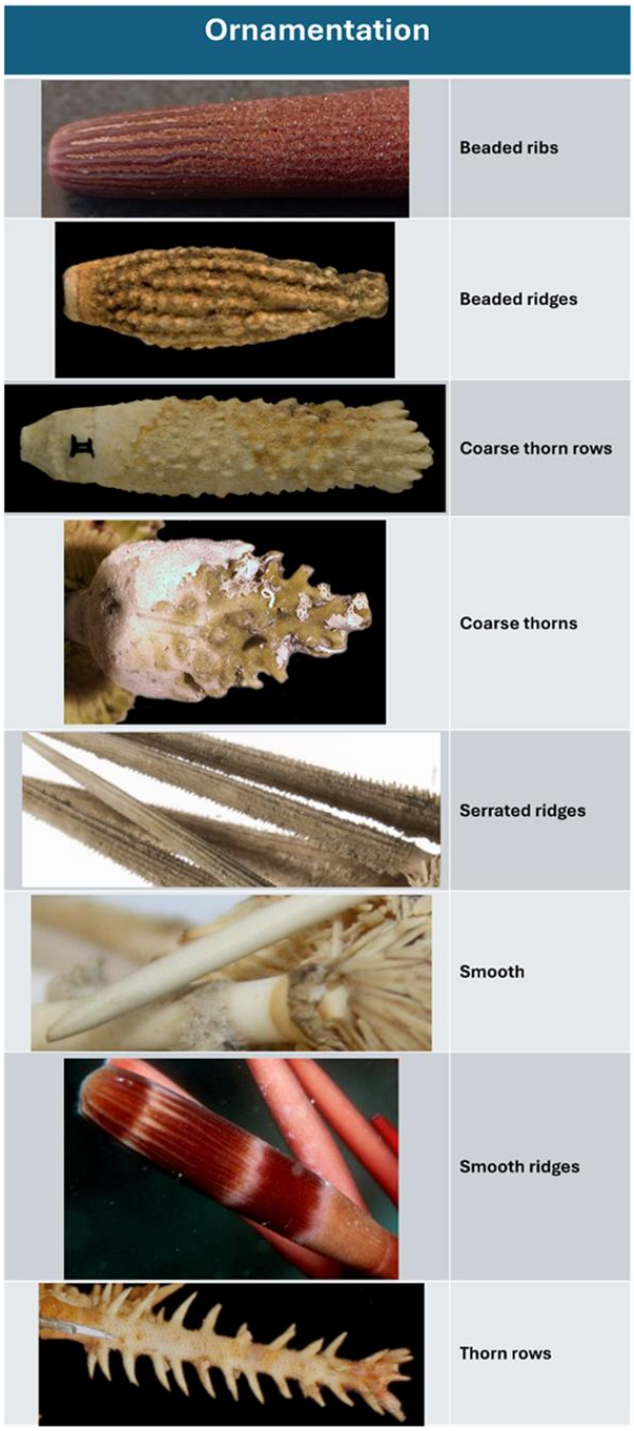


Figure 3.1. Ornamentation categories adapted from Kroh & Smith (2010). Beaded ribs: *Phyllacanthus parvispinus*, Harper, iNaturalist. Beaded ridges: *Typocidaris marginata*, MNHN J06029. Coarse thorn rows: *Goniocidaris noetlingia*, MNHN R05835. Coarse thorns: *Tylocidaris ohshimai*, USNM 9043. Serrated ridges: *Stylocidaris ingolfiana*, NHMD 89937. Smooth: *Stylocidaris conferta*, MCZ, Harvard ECH-4240. Smooth ridges: *Phyllacanthus imperialis*, uwkwaj, iNaturalist. Thorn rows: *Prionocidaris bispinosa*.

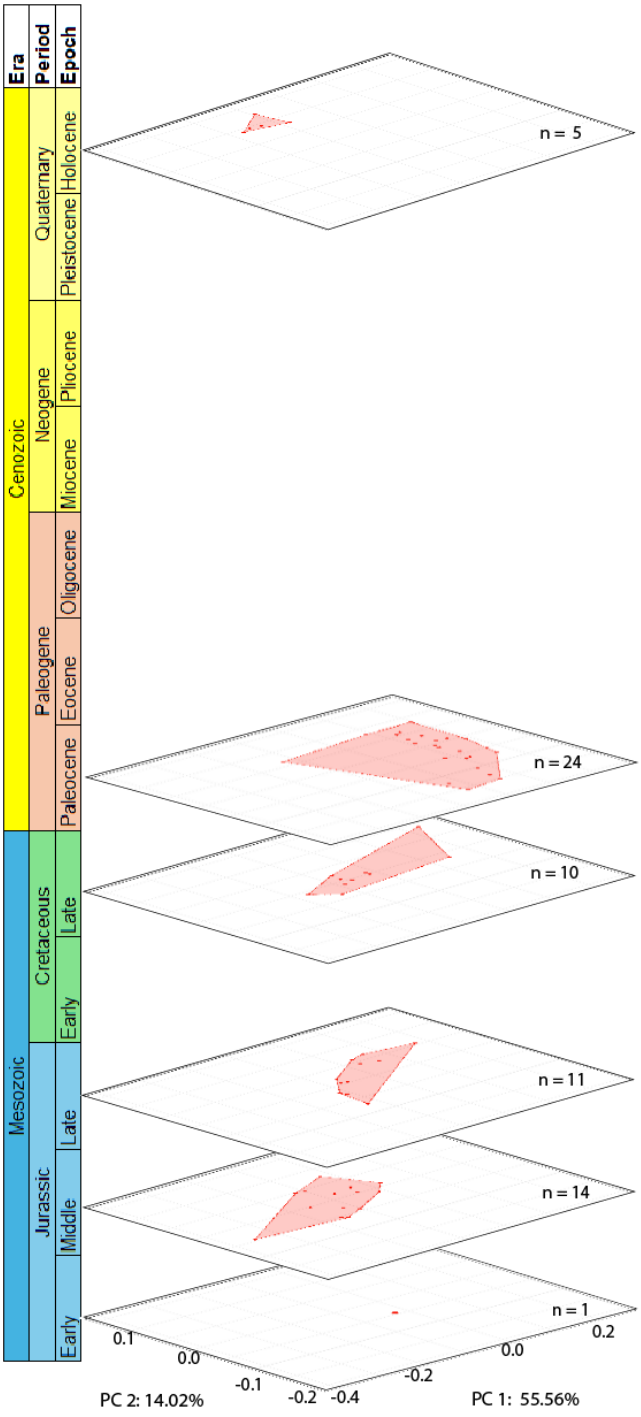


Figure 3.2. Psychocidaridae morphospace through time plotted in multivariate space. The number of specimens per epoch is given on the right edge of each PCA. Total variance: 69.58%. Specimen count: 65.

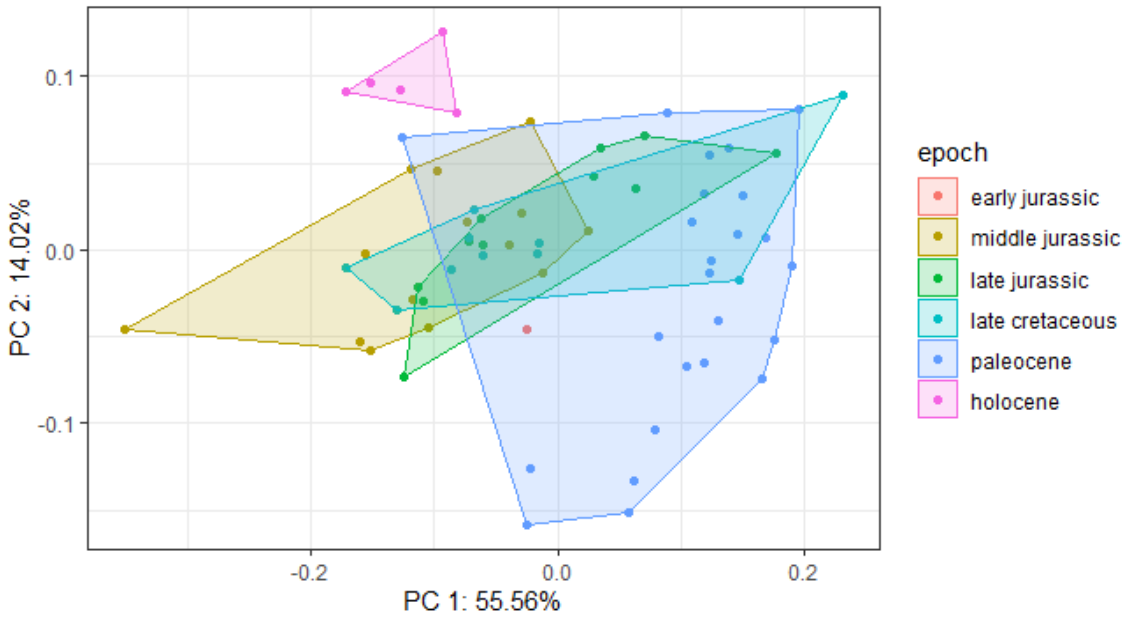


Figure 3.3. Psychocidaridae spines plotted in multivariate space grouped by epoch. Total variance: 69.58%. Specimen count: 65.

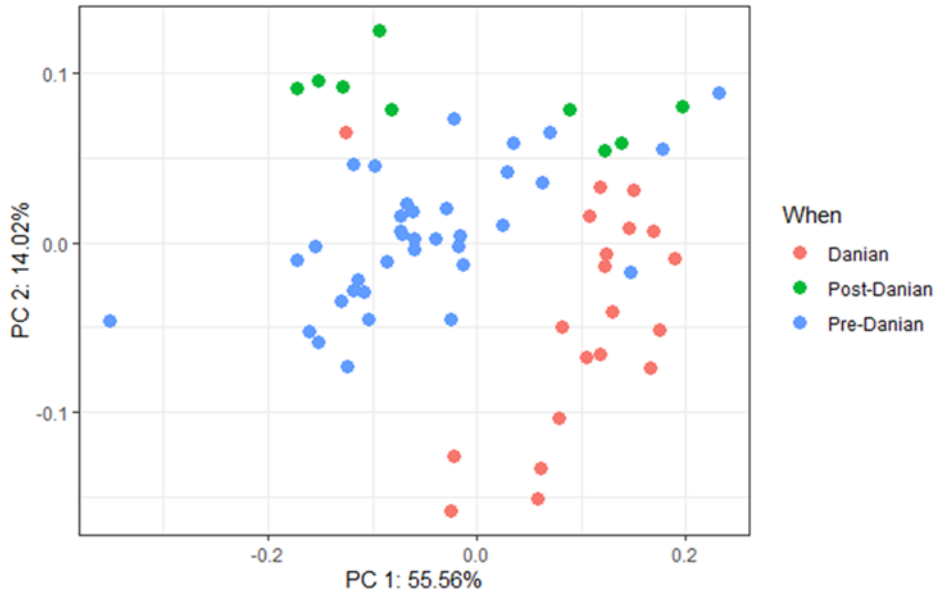


Figure 3.4. PCA of Psychocidaridae spines in time bins. Pre-Danian for specimens from the Jurassic and Cretaceous. Post-Danian representing Thanetian and Modern specimens. Total variance: 69.58%. Specimen count: 65.

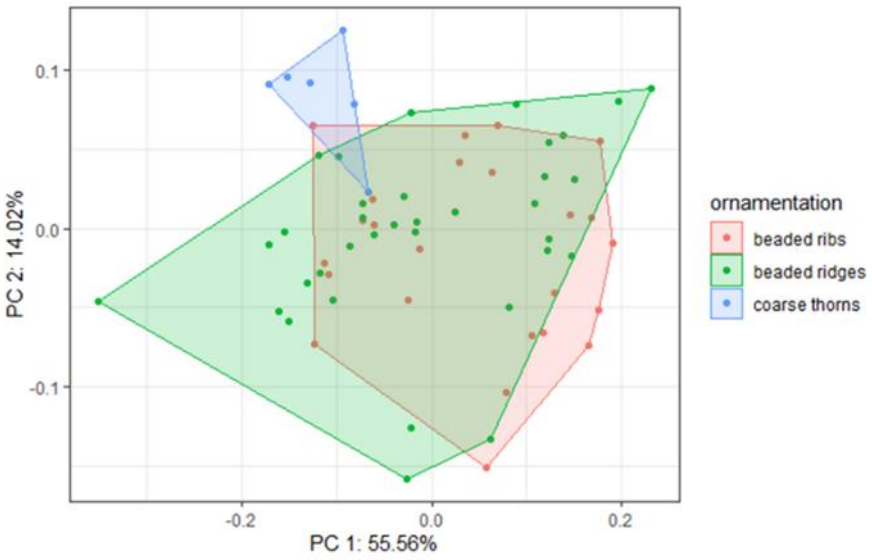


Figure 3.5. PCA of Psychocidaridae displaying spine ornamentation across the family. Total variance: 69.58%. Specimen count: 65.

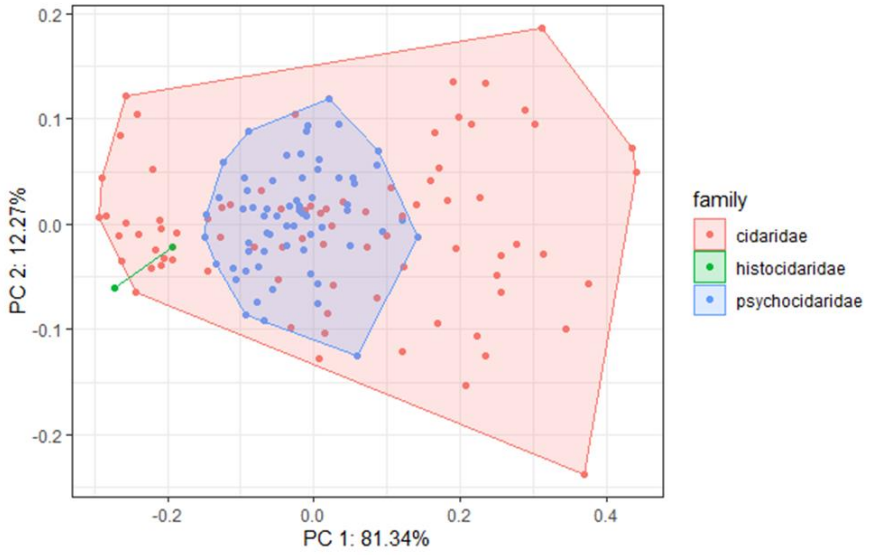


Figure 3.6. The three families plotted in a PCA. Psychocidaridae n = 65. Cidaridae n = 80. Histocidaridae n = 2. Total variance 93.61%. Total specimens: 147.

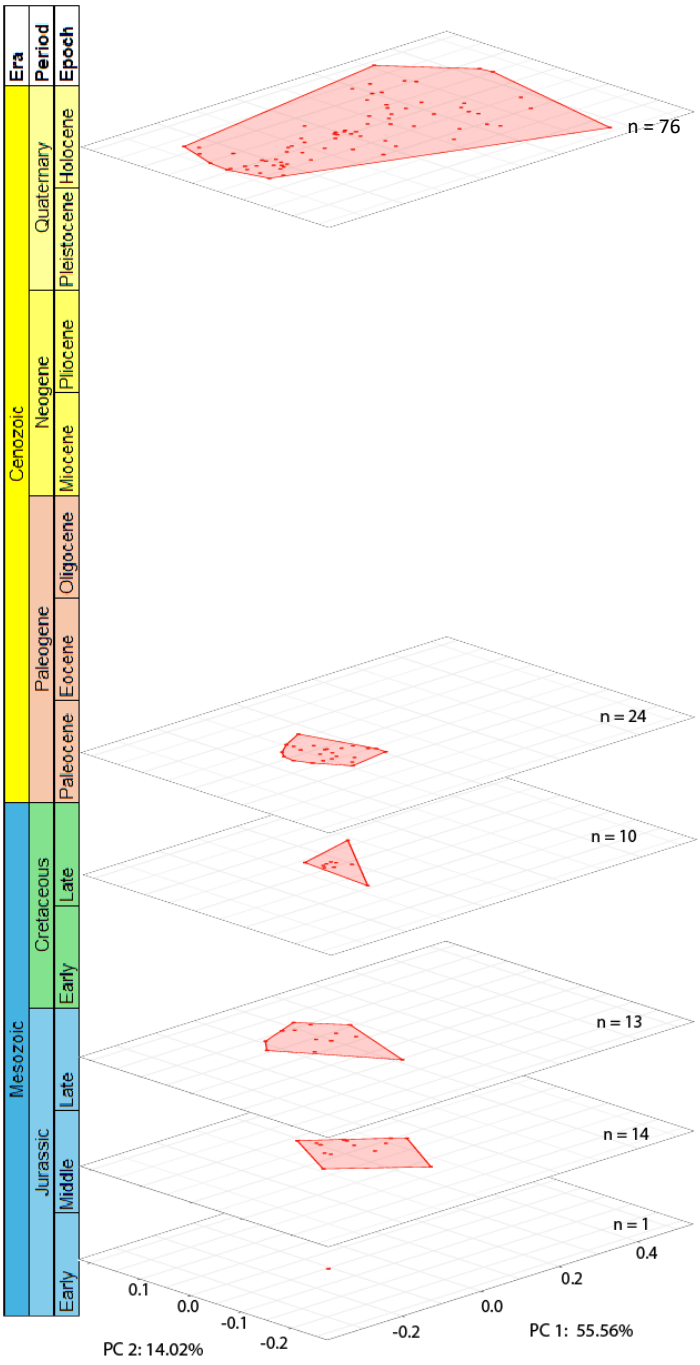


Figure 3.7. The three families of cidaroids of this study, Histocidaridae, Cidaridae, and Psychocidaridae, through time by epoch. Total variance: 93.61%. Specimen count: 147.

Danian (66.0 to 61.6 Ma) is Thanetian (59.2 to 56 Ma) in age, showing a shift across a relatively short period of time. The other grouping from modern spines belongs to *Tylocidris ohshimai*, which has a spine morphology distinct from all other Psychocidarids included in this study, as shown by where it plots in multivariate space. The general shape of these spines is similar to that of Mesozoic spines, being quite bulbous and thick throughout the length, and instead display differences in ornamentation (Fig. 3.5). Then, when exploring the ornamentation of Psychocidaridae, only three distinct ornamentation types were defined. Figure 3.5 shows that while there is little correlation between morphospace and the ornamentations of beaded ribs and beaded ridges, coarse thorns occur within a defined morphospace.

Once exploring the entire pool of data collected, the "Pull of the Recent" is more visible (Figs. 3.6 and 3.7) (Jablonski et al., 2003). This still allows for comparisons between Psychocidaridae and the other two families. Psychocidaridae fills much less morphospace than Cidaridae, with wholly unique spine morphologies to cidaroids. Histocidaridae, while included in this study, need more specimens for discussion of the morphology of cidaroid spines and allow for future directions for this study. Looking at morphospace regarding spine ornamentation across the entire pool of data and in modern cidaroids was done to glean additional information. Ornamentation in modern cidaroids was predominantly thorny in nature (78%) (Fig. 3.8). Most genera displayed a variety of ornamentation type, alongside overlaps in morphospace (Fig. 3.9). *Goniocidaris* was distinct in morphospace (Fig. 3.9A) and characteristically displayed coarse thorn rows (Fig. 3.9B).

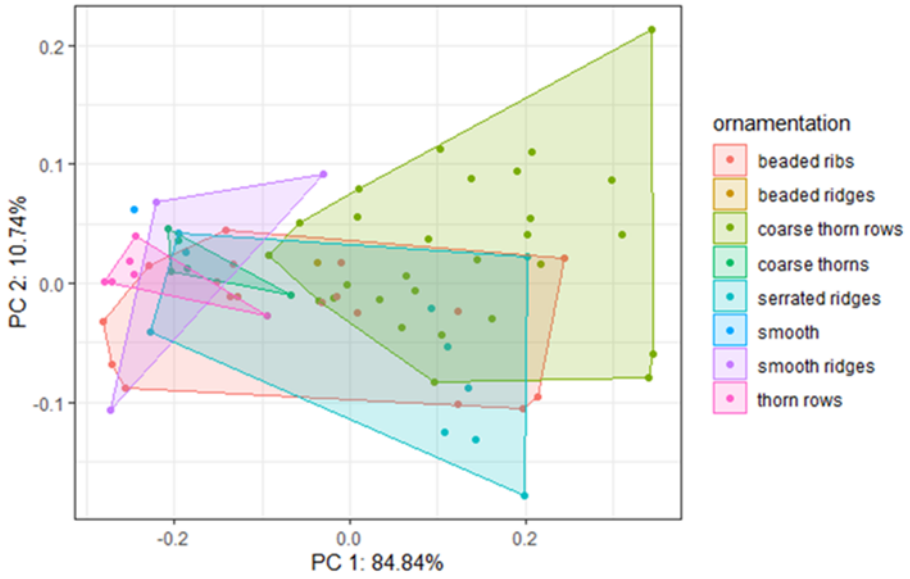


Figure 3.8. Ornamentation seen in modern crown group cidaroids. Total variance: 95.58%. Specimen count: 72.

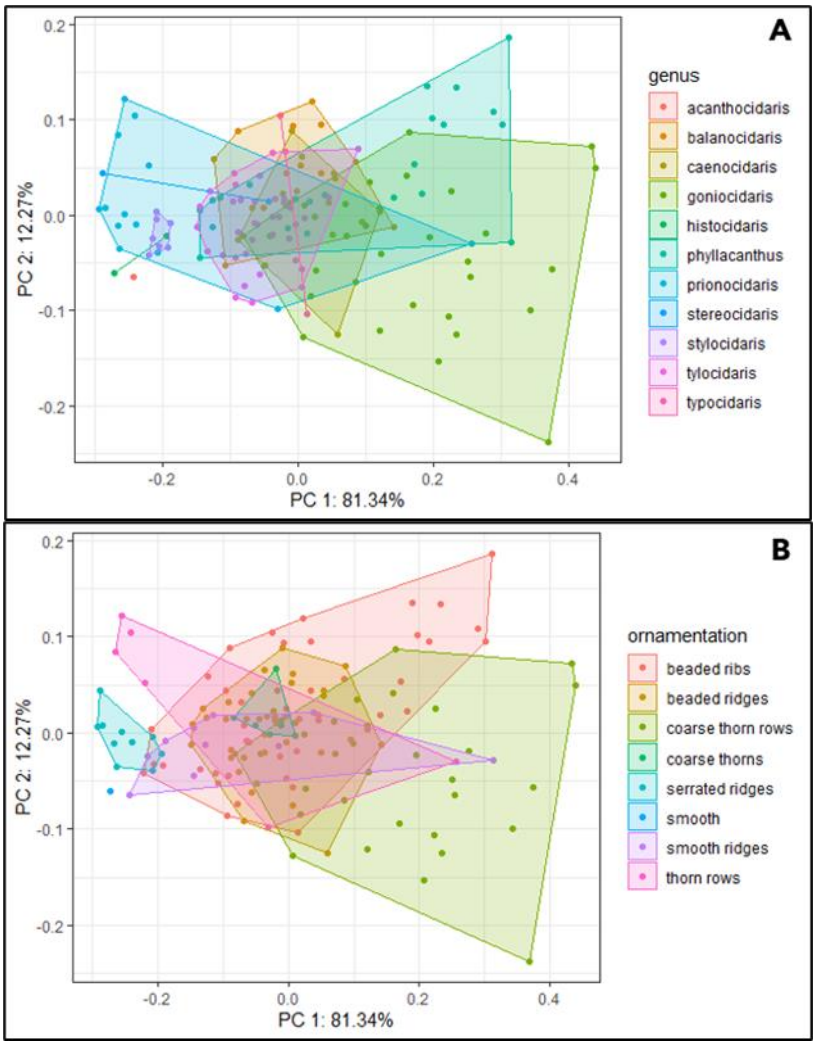


Figure 3.9. PCA of all 147 specimens across the 11 genera. Figure 3.9A displays each genus in a convex hull. Figure 3.9B displays the data with convex hulls representing the eight distinct ornamentation types. Total variance: 93.61%.

# CHAPTER FOUR

## Discussion

### *Mesozoic Marine Revolution*

In Figures 3.2 and 3.3, a shift in morphospace occurs through the Mesozoic. This coincides with the Mesozoic Marine Revolution (MMR), where marine communities underwent accelerated change driven by predation. This encapsulated the life habits of organisms and organismal interactions. This started in the Jurassic and continued into the Cretaceous (Vermeji, 1977). Echinoids are commonly preyed upon by a host of mammals, birds, fish, and marine invertebrates today. There is some recorded evidence of preying on regular echinoids during the MMR, potentially acting as a selective pressure on the shift in spine morphology observed. Middle Jurassic fish regurgitates from Poland were recorded to have fragmented cidaroid spines and mamelons. This study found that echinoid taxonomic diversity was not affected or driven by the rise of such predation, but with the evidence provided, morphological diversity shifts concurrently (Borszcz & Zaton, 2013). Wilson et al. (2015) found more evidence of fish predation through bite marks on cidaroid spines. These Middle Jurassic bite marks were remarkably similar to those of some modern fish known to prey on echinoids, attacking from above and twisting to remove the spines for access to the body of the echinoid (Wilson et al., 2015). Many marine echinoid predators, gastropods, asteroids, fish, and crustaceans, diversified during and after the MMR. Specifically rising in diversity in the Late Cretaceous, when we start to see the down trend in diversity for cidaroids. The type of predation would have different impacts on echinoid communities, potentially leading to different pressures

on morphology (Fig. 4.1) (Petsios et al., 2023). Vermeji (1977) noted that this intensity of predation would have led to exceptional species selection and skeletal morphologies of snails were adapting for such during it. Cidaroid spine morphology was shifting in response to pressures, which coincide closely with the predation of the MMR.

### *K-Pg Extinction Event*

Another distinct shift in morphospace is around the K-Pg, alluding to effects of the extinction event affecting cidaroids (Figs. 3.2 and 3.4). While a distinct change in shape is observed, diversity was not heavily altered from the end of the Cretaceous to the Paleocene (Smith & Jeffery, 1998). The diversity of cidaroids had already begun to drop towards the Late Cretaceous, and the K-Pg did not add much to this decrease, while morphological diversity in Psychocidaroids seems to increase (Fig. 4.1) (PBDB, 2025). Several factors played a part in echinoids, and more importantly cidaroids, retaining much of the group's diversity across the K-Pg boundary. Many of the regular echinoids that persisted across the boundary were omnivorous and held a more generalist life habit. Additionally, echinoids habitats at storm wave base and below were less affected by the K-Pg extinction event (Smith & Jeffery, 1998). Psychocidaridae displayed morphological diversification after the K-Pg before a loss in taxonomic and morphological diversity into the Holocene. The K-Pg event had a distinct effect on cidaroids, quite different from that of other marine fauna, allowing them to diversify the morphologies of their spines (example with Psychocidarids in Fig. 3.2).

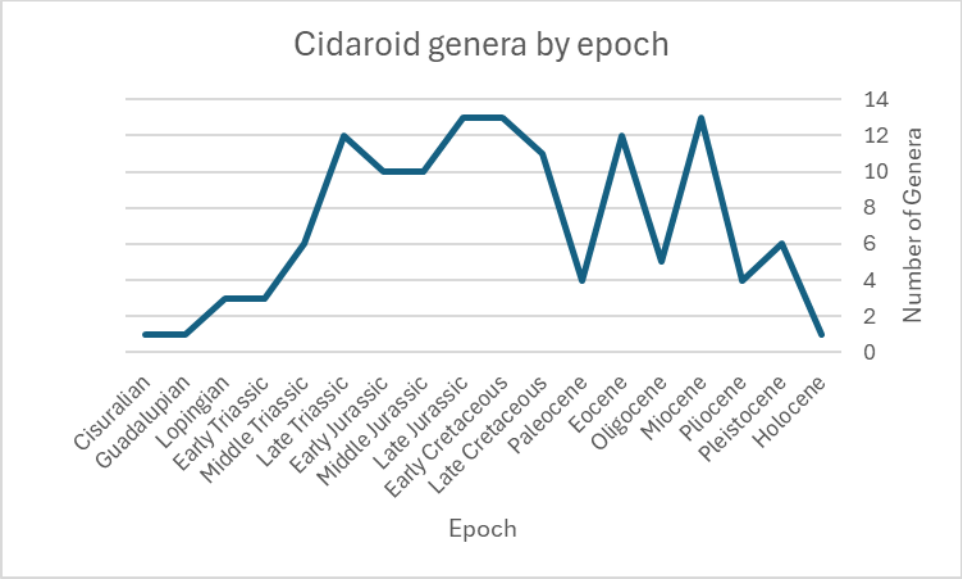


Figure 4.1. Cidaroid genera by epoch using PBDB data. The largest dip in diversity is across the K-Pg. The Holocene data is lacking as the PBDB pulls fossil data. (PBDB, 2024)

### *Spine Morphology in the Cenozoic*

Modern Cidaridae displays the greatest diversity amongst cidaroid clades, along with the highest diversity in spine morphologies (Fig. 3.7). With much overlap in morphospace and ornamentation, selective pressures that led to such features may be similar, leading to potential convergence or retention of morphology (Fig. 3.8 and 3.9). More data is needed to decipher the source of shared morphologies during the Holocene. The Cenozoic holds a lack of material of regular echinoids from the increased predation and poor preservation potential, alongside the constant shifting in sea level (Greenstein, 1992; Petsios et al., 2021). Even the fragments of cidaroids that do show up are regularly too fragmented for a study such as this that requires complete spines, or other common methods that require more than fragmental material (Owen & Portell, 2001). Through the increase in morphological diversity for Cidaridae, yet a decrease in taxonomic diversity, a decoupling of the two may be occurring and pressures are yet unknown, potentially

related to the increasing predation upon cidaroids throughout the Cenozoic. The cause of the constriction in Psychocidaridae taxonomic and morphological diversity may be related, as they may not be functionally fit enough in the communities they inhabit. Cidaroid clades are presenting multiple modes of morphological diversity today.

# CHAPTER FIVE

## Conclusion

Echinoid spine shapes, being highly adaptable, shift through time as selective pressures act upon them. This is seen across the Mesozoic as cidaroid spine shape shifts as the MMR takes place, potentially adapting to pressures from predation (Figs. 3.3 and 3.4). The next shift is after the K-Pg, where there is a morphological diversification in tandem with recovery from the extinction event (Figs. 3.4 and 4.1). Overall, there is a decrease in taxonomic diversity through the Cenozoic that can be seen through Psychocidaridae having only one species today, being highly constricted in morphospace (Figs. 3.3 and 4.1). However, there is an increase in morphological diversity in cidaroids today, through Cidaridae exploring unique morphologies (Fig. 37). The morphological diversity of cidaroid spines might be decoupled from the taxonomic diversity and should be further studied to assess this possibility. Ornamentation is an aspect of morphological diversity that needs to be analyzed for the controls and ecological importance. Both spine morphology and ornamentation have yet to be correlated to selective pressures and need to be understood to grasp why cidaroid spine morphology changes and how it will change in the future.

# APPENDIX

# APPENDIX A

| Genus | Species | Family | x | y | When | Stage | Epoch | Period | age_begin_ma | age_end_ma | Ornamentation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| balanocidaris | besairiei | psychocidaridae | -0.02483083 | -0.045307552 | Pre-Danian | torcian | early jurassic | jurassic | 182.7 | 174.1 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | 0.1770971 | 0.055148296 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | 0.06993433 | 0.065358949 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | 0.06286964 | 0.035686441 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | -0.12425052 | -0.072986915 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | -0.10873747 | -0.029172094 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | 0.03516075 | 0.058765082 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | -0.11360608 | -0.021449241 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | -0.06159221 | 0.018551567 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | -0.07209244 | 0.004958058 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | -0.06008724 | 0.002611646 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | glandifera | psychocidaridae | 0.02914079 | 0.042137507 | Pre-Danian | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| balanocidaris | gibberula | psychocidaridae | -0.06748347 | 0.023364058 | Pre-Danian | coniacian | late cretaceous | cretaceous | 89.8 | 86.3 | coarse thorns |
| balanocidaris | julii | psychocidaridae | -0.351766 | -0.045852802 | Pre-Danian | bathonian | middle jurassic | jurassic | 168.3 | 166.1 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.09773383 | 0.04581868 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.02194862 | 0.073658693 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.11869746 | 0.046883271 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.10417257 | -0.044778824 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | 0.02513497 | 0.010575687 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.1512522 | -0.058200826 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.11794093 | -0.028075695 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.02895043 | 0.020750162 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.0398447 | 0.0024082 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.1610195 | -0.052676644 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.15552686 | -0.002016624 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| caenocidaris | cucumifera | psychocidaridae | -0.07337406 | 0.01587577 | Pre-Danian | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| tylocidaris | abildgaardi | psychocidaridae | 0.07842716 | -0.103117079 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | abildgaardi | psychocidaridae | 0.17556794 | -0.051782092 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | abildgaardi | psychocidaridae | 0.14566286 | 0.008548014 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | abildgaardi | psychocidaridae | 0.05756932 | -0.151240794 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | clavigera | psychocidaridae | -0.06048745 | -0.003676179 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | clavigera | psychocidaridae | -0.13036996 | -0.034524356 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | clavigera | psychocidaridae | -0.08627579 | -0.01096608 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | clavigera | psychocidaridae | -0.01562715 | 0.004250721 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | clavigera | psychocidaridae | -0.0726498 | 0.006841115 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | clavigera | psychocidaridae | -0.17198401 | -0.009986319 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | clavigera | psychocidaridae | -0.01715946 | -0.001770134 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | clavigera | psychocidaridae | 0.14683099 | -0.017046432 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | clavigera | psychocidaridae | 0.23124507 | 0.088665527 | Pre-Danian | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tylocidaris | honorinae | psychocidaridae | -0.0126433 | -0.013116271 | Pre-Danian | bajocian-bathonian | middle jurassic | jurassic | 170.3 | 166.1 | beaded ribs |
| tylocidaris | herupensis | psychocidaridae | -0.12580347 | 0.065099111 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | odumi | psychocidaridae | 0.18990084 | -0.009149795 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | odumi | psychocidaridae | 0.12951487 | -0.040723032 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | odumi | psychocidaridae | 0.16586628 | -0.073727695 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | odumi | psychocidaridae | 0.16889705 | 0.006882394 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | odumi | psychocidaridae | 0.11791903 | -0.065321899 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | odumi | psychocidaridae | 0.10501273 | -0.06707379 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tylocidaris | ohshimai | psychocidaridae | -0.15231712 | 0.096003181 | Post-Danian | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| tylocidaris | ohshimai | psychocidaridae | -0.12816436 | 0.09202287 | Post-Danian | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| tylocidaris | ohshimai | psychocidaridae | -0.08216854 | 0.0790019 | Post-Danian | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| tylocidaris | ohshimai | psychocidaridae | -0.09356145 | 0.125792105 | Post-Danian | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| tylocidaris | ohshimai | psychocidaridae | -0.17207067 | 0.09103473 | Post-Danian | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| tylocidaris | rosenkrantzi | psychocidaridae | -0.02560001 | -0.15829903 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | rosenkrantzi | psychocidaridae | -0.02190463 | -0.125603033 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | rosenkrantzi | psychocidaridae | 0.08210559 | -0.049417689 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | rosenkrantzi | psychocidaridae | 0.06180041 | -0.133266463 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | rosenkrantzi | psychocidaridae | 0.11833219 | 0.032722338 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | rosenkrantzi | psychocidaridae | 0.12373104 | -0.006043287 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | rosenkrantzi | psychocidaridae | 0.12218918 | -0.013576058 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | rosenkrantzi | psychocidaridae | 0.14957902 | 0.031358241 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | rosenkrantzi | psychocidaridae | 0.10817129 | 0.01571015 | Danian | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tylocidaris | salina | psychocidaridae | 0.12271191 | 0.054473068 | Post-Danian | thanetian | paleocene | paleogene | 59.2 | 56 | beaded ridges |
| tylocidaris | salina | psychocidaridae | 0.13886094 | 0.058981243 | Post-Danian | thanetian | paleocene | paleogene | 59.2 | 56 | beaded ridges |
| tylocidaris | salina | psychocidaridae | 0.19610604 | 0.080796276 | Post-Danian | thanetian | paleocene | paleogene | 59.2 | 56 | beaded ridges |
| tylocidaris | walcotti | psychocidaridae | 0.08835529 | 0.079209675 | Post-Danian | thanetian | paleocene | paleogene | 59.2 | 56 | beaded ridges |

**Table A.1.** Table of the data used to group Psychocidaridae and plot into multivariate space.

| Specimen | Genus | Species | Family | x | y | Stage | Epoch | Period | age_begin_ma | age_end_ma | Ornamentation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| AcanthHast_gbif_1_mat, | acanthocidaris | hastigera | cidaridae | -0.24306 | -0.06508 | modern | holocene | quaternary | 0 | 0 | smooth ridges |
| bb_gb0_mat, | balanocidaris | besairiei | psychocidaridae | -0.10708 | -0.05278 | torcian | early jurassic | jurassic | 182.7 | 174.1 | beaded ribs |
| bg_r1_s1_mat, | balanocidaris | glandifera | psychocidaridae | -0.08958 | 0.088199 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r1_s2_mat, | balanocidaris | glandifera | psychocidaridae | 0.03409 | 0.095103 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r1_s3_mat, | balanocidaris | glandifera | psychocidaridae | 0.021264 | 0.118799 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r2_s4_mat, | balanocidaris | glandifera | psychocidaridae | -0.06756 | 0.007315 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r3_s5_mat, | balanocidaris | glandifera | psychocidaridae | -0.00265 | 0.025459 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r3_s6_mat, | balanocidaris | glandifera | psychocidaridae | 0.033377 | 0.043445 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r4_s7_mat, | balanocidaris | glandifera | psychocidaridae | 0.085222 | 0.056062 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r5_s10_mat, | balanocidaris | glandifera | psychocidaridae | -0.00825 | 0.093689 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r5_s8_mat, | balanocidaris | glandifera | psychocidaridae | -0.01668 | 0.044406 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r5_s9_mat, | balanocidaris | glandifera | psychocidaridae | 0.045995 | 0.013609 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bg_r6_s11_mat, | balanocidaris | glandifera | psychocidaridae | -0.1242 | 0.058405 | oxfordian-tithonian | late jurassic | jurassic | 163.5 | 145 | beaded ribs |
| bgib_gb0_mat, | balanocidaris | gibberula | psychocidaridae | -0.05138 | 0.00725 | coniacian | late cretaceous | cretaceous | 89.8 | 86.3 | coarse thorns |
| bjul_gb0_mat, | balanocidaris | julii | psychocidaridae | 0.141594 | -0.01211 | bathonian | middle jurassic | jurassic | 168.3 | 166.1 | beaded ridges |
| ccuc_ed0_1_mat, | caenocidaris | cucumifera | psychocidaridae | 0.006169 | 0.061788 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_ed0_2_mat, | caenocidaris | cucumifera | psychocidaridae | 0.004173 | 0.052545 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_ed0_3_mat, | caenocidaris | cucumifera | psychocidaridae | -0.00954 | 0.088172 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_1_mat, | caenocidaris | cucumifera | psychocidaridae | 0.09429 | -0.00718 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_10_mat, | caenocidaris | cucumifera | psychocidaridae | -0.08848 | -0.025 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_3_mat, | caenocidaris | cucumifera | psychocidaridae | 0.120791 | 0.00375 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_4_mat, | caenocidaris | cucumifera | psychocidaridae | 0.049843 | -0.02032 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_5_mat, | caenocidaris | cucumifera | psychocidaridae | -0.02342 | 0.022727 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_6_mat, | caenocidaris | cucumifera | psychocidaridae | 0.053381 | 0.04411 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_7_mat, | caenocidaris | cucumifera | psychocidaridae | 0.054572 | 0.03892 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_8_mat, | caenocidaris | cucumifera | psychocidaridae | 0.058939 | -0.12429 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| ccuc_gb0_9_mat, | caenocidaris | cucumifera | psychocidaridae | -0.02024 | 0.012997 | bajocian | middle jurassic | jurassic | 170.3 | 168.3 | beaded ridges |
| gonimp_inat1_1_mat, | goniocidaris | impressa | cidaridae | 0.10483 | 0.035026 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gonimp_inat1_2_mat, | goniocidaris | impressa | cidaridae | 0.343358 | -0.09988 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gonimp_inat1_3_mat, | goniocidaris | impressa | cidaridae | 0.434307 | 0.072756 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| GonNoet_mnhn_1_mat, | goniocidaris | noetlingi | cidaridae | 0.072083 | -0.02185 | NA | miocene | neogene | 23.03 | 5.333 | coarse thorn rows |
| GonNoet_mnhn_2_mat, | goniocidaris | noetlingi | cidaridae | -0.04225 | -0.02099 | NA | miocene | neogene | 23.03 | 5.333 | coarse thorn rows |
| GonNoet_mnhn_3_mat, | goniocidaris | noetlingi | cidaridae | 0.085482 | -0.06947 | NA | miocene | neogene | 23.03 | 5.333 | coarse thorn rows |
| GonNoet_mnhn_4_mat, | goniocidaris | noetlingi | cidaridae | 0.20789 | -0.15334 | NA | miocene | neogene | 23.03 | 5.333 | coarse thorn rows |
| GonNoet_mnhn_6_mat, | goniocidaris | noetlingi | cidaridae | 0.007137 | -0.1277 | NA | miocene | neogene | 23.03 | 5.333 | coarse thorn rows |
| gontub_inat1_1_mat, | goniocidaris | tubaria | cidaridae | -0.04927 | -0.0529 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat2_1_mat, | goniocidaris | tubaria | cidaridae | 0.122074 | -0.0402 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat3_1_mat, | goniocidaris | tubaria | cidaridae | 0.02452 | -0.00129 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat3_2_mat, | goniocidaris | tubaria | cidaridae | 0.09939 | -0.01118 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat3_3_mat, | goniocidaris | tubaria | cidaridae | 0.121392 | -0.12039 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat3_4_mat, | goniocidaris | tubaria | cidaridae | 0.019083 | -0.08449 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat3_5_mat, | goniocidaris | tubaria | cidaridae | -0.01213 | 0.013587 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat4_1_mat, | goniocidaris | tubaria | cidaridae | 0.234216 | -0.12428 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat4_2_mat, | goniocidaris | tubaria | cidaridae | 0.026147 | -0.05798 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat4_3_mat, | goniocidaris | tubaria | cidaridae | 0.374021 | -0.05629 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat4_4_mat, | goniocidaris | tubaria | cidaridae | 0.368852 | -0.23773 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat4_5_mat, | goniocidaris | tubaria | cidaridae | 0.169424 | -0.09392 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat4_6_mat, | goniocidaris | tubaria | cidaridae | 0.439384 | 0.0501 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat4_7_mat, | goniocidaris | tubaria | cidaridae | 0.222995 | -0.10651 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |

**Table A.2a.** The first part of the data for cidaroid families for grouping and plotting into multivariate space.

| Specimen | Genus | Species | Family | x | y | Stage | Epoch | Period | age_begin_ma | age_end_ma | Ornamentation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| gontub_inat4_8_mat, | goniocidaris | tubaria | cidaridae | 0.277029 | -0.01913 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat4_9_mat, | goniocidaris | tubaria | cidaridae | 0.250477 | -0.04875 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat5_1_mat, | goniocidaris | tubaria | cidaridae | 0.254694 | -0.06492 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat5_2_mat, | goniocidaris | tubaria | cidaridae | 0.225695 | 0.025856 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat5_3_mat, | goniocidaris | tubaria | cidaridae | 0.164782 | 0.086393 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat5_4_mat, | goniocidaris | tubaria | cidaridae | 0.120081 | 0.008074 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat5_5_mat, | goniocidaris | tubaria | cidaridae | 0.194662 | -0.02282 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat5_6_mat, | goniocidaris | tubaria | cidaridae | 0.159785 | 0.041912 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat6_1_mat, | goniocidaris | tubaria | cidaridae | -0.0812 | -0.02113 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat6_2_mat, | goniocidaris | tubaria | cidaridae | 0.070425 | 0.011799 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| gontub_inat6_3_mat, | goniocidaris | tubaria | cidaridae | 0.009555 | 0.010492 | modern | holocene | quaternary | 0 | 0 | coarse thorn rows |
| HistCob_gbif_1_mat, | histocidaris | cobosi | histocidaridae | -0.27229 | -0.05998 | modern | holocene | quaternary | 0 | 0 | smooth |
| HistPurpur_gbif_1_mat, | histocidaris | purpurata | histocidaridae | -0.19355 | -0.02228 | modern | holocene | quaternary | 0 | 0 | serrated ridges |
| phylhemig_ou_1_mat, | phyllacanthus | hemigranosus | cidaridae | -0.01568 | -0.01381 | cenomanian | upper cretaceous | cretaceous | 100.5 | 93.9 | smooth ridges |
| phylhemig_ou1_1_mat, | phyllacanthus | hemigranosus | cidaridae | 0.314009 | -0.02853 | cenomanian | upper cretaceous | cretaceous | 100.5 | 93.9 | smooth ridges |
| phylhemig_ou1_2_mat, | phyllacanthus | hemigranosus | cidaridae | 0.038836 | 0.021054 | cenomanian | upper cretaceous | cretaceous | 100.5 | 93.9 | smooth ridges |
| PhyllacanthusImperialis_ | phyllacanthus | imperialis | cidaridae | -0.11491 | 0.017927 | modern | holocene | quaternary | 0.0117 | 0 | smooth ridges |
| PhyllaDub_gbif_1_mat, | phyllacanthus | dubius | cidaridae | -0.12589 | 0.016401 | modern | holocene | quaternary | 0 | 0 | beaded ridges |
| phyllaimp_inat4_1_mat, | phyllacanthus | imperialis | cidaridae | -0.14477 | 0.004584 | modern | holocene | quaternary | 0.0117 | 0 | smooth ridges |
| phyllaimp_inat4_2_mat, | phyllacanthus | imperialis | cidaridae | -0.14587 | -0.04423 | modern | holocene | quaternary | 0.0117 | 0 | smooth ridges |
| phyllaimp_inat4_3_mat, | phyllacanthus | imperialis | cidaridae | -0.12691 | -0.01244 | modern | holocene | quaternary | 0.0117 | 0 | smooth ridges |
| phyllaparv_inat1_1_mat, | phyllacanthus | parvispinus | cidaridae | -0.00459 | 0.017512 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat1_2_mat, | phyllacanthus | parvispinus | cidaridae | 0.012839 | -0.01904 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat1_3_mat, | phyllacanthus | parvispinus | cidaridae | 0.016381 | 0.014503 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_1_mat, | phyllacanthus | parvispinus | cidaridae | 0.181824 | 0.022449 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_10_mat, | phyllacanthus | parvispinus | cidaridae | 0.28893 | 0.108529 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_2_mat, | phyllacanthus | parvispinus | cidaridae | 0.302264 | 0.095266 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_3_mat, | phyllacanthus | parvispinus | cidaridae | 0.197071 | 0.101616 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_4_mat, | phyllacanthus | parvispinus | cidaridae | 0.311299 | 0.186716 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_5_mat, | phyllacanthus | parvispinus | cidaridae | 0.140301 | 0.018642 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_6_mat, | phyllacanthus | parvispinus | cidaridae | 0.171272 | 0.053224 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_7_mat, | phyllacanthus | parvispinus | cidaridae | 0.233222 | 0.133772 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_8_mat, | phyllacanthus | parvispinus | cidaridae | 0.214302 | 0.095637 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat2_9_mat, | phyllacanthus | parvispinus | cidaridae | 0.19004 | 0.135224 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| phyllaparv_inat3_1_mat, | phyllacanthus | parvispinus | cidaridae | -0.07209 | 0.032382 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| prionbac_gbif1_2_mat, | prionocidaris | baculosa | cidaridae | -0.25596 | 0.001087 | modern | holocene | quaternary | 0 | 0 | serrated ridges |
| prionbac_gbif1_3_mat, | prionocidaris | baculosa | cidaridae | -0.26317 | -0.03483 | modern | holocene | quaternary | 0 | 0 | serrated ridges |
| prionbac_gbif1_4_mat, | prionocidaris | baculosa | cidaridae | -0.28407 | 0.007785 | modern | holocene | quaternary | 0 | 0 | serrated ridges |
| prionbac_gbif1_5_mat, | prionocidaris | baculosa | cidaridae | -0.26606 | -0.01124 | modern | holocene | quaternary | 0 | 0 | serrated ridges |
| prionbac_gbif1_6_mat, | prionocidaris | baculosa | cidaridae | -0.29328 | 0.006914 | modern | holocene | quaternary | 0 | 0 | serrated ridges |
| prionbac_gbif_3_mat, | prionocidaris | baculosa | cidaridae | -0.20829 | -0.03895 | modern | holocene | quaternary | 0 | 0 | serrated ridges |
| prionbis_gbif_1_mat, | prionocidaris | bispinosa | cidaridae | -0.22024 | 0.052569 | modern | holocene | quaternary | 0 | 0 | thorn rows |
| prionbis_gbif_2_mat, | prionocidaris | bispinosa | cidaridae | 0.25626 | -0.02935 | modern | holocene | quaternary | 0 | 0 | thorn rows |
| prionbis_gbif_3_mat, | prionocidaris | bispinosa | cidaridae | -0.24095 | 0.104322 | modern | holocene | quaternary | 0 | 0 | thorn rows |
| prionbis_gbif_4_mat, | prionocidaris | bispinosa | cidaridae | -0.26496 | 0.084278 | modern | holocene | quaternary | 0 | 0 | thorn rows |
| prionbis_gbif_5_mat, | prionocidaris | bispinosa | cidaridae | -0.0312 | -0.09854 | modern | holocene | quaternary | 0 | 0 | thorn rows |
| prionbis_gbif_6_mat, | prionocidaris | bispinosa | cidaridae | -0.25612 | 0.121914 | modern | holocene | quaternary | 0 | 0 | thorn rows |
| PrionocidarisBaculosa_g | prionocidaris | baculosa | cidaridae | -0.23914 | -0.00901 | modern | holocene | quaternary | 0 | 0 | serrated ridges |
| stereoingo_gbif_1_mat, | stereocidaris | ingolfiana | cidaridae | -0.28893 | 0.044055 | modern | holocene | quaternary | 0 | 0 | serrated ridges |

**Table A.2b.** The second part of the data for cidaroid families for grouping and plotting into multivariate space.

| Specimen | Genus | Species | Family | x | y | Stage | Epoch | Period | age_begin_ma | age_end_ma | Ornamentation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| stereoscept_idb1_1_mat, | stereocidaris | sceptrifera | cidaridae | -0.04408 | 0.014948 | coniacian | late cretaceous | cretaceous | 89.8 | 86.3 | beaded ridges |
| stylaff_gbif_1_mat, | stylocidaris | affinis | cidaridae | -0.20863 | -0.00407 | modern | holocene | quaternary | 0.0117 | 0 | serrated ridges |
| stylcal_gbif_1_mat, | stylocidaris | calacantha | cidaridae | -0.20546 | -0.03248 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| stylcal_gbif_2_mat, | stylocidaris | calacantha | cidaridae | -0.22132 | -0.0421 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| stylcing_nhmd1_1_mat, | stylocidaris | cingulata | cidaridae | -0.18818 | -0.00776 | modern | holocene | quaternary | 0 | 0 | smooth ridges |
| stylcing_nhmd1_2_mat, | stylocidaris | cingulata | cidaridae | -0.21549 | -0.02429 | modern | holocene | quaternary | 0 | 0 | smooth ridges |
| stylcon_gbif_1_mat, | stylocidaris | conferta | cidaridae | -0.19308 | -0.03379 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| stylcon_gbif_2_mat, | stylocidaris | conferta | cidaridae | -0.20983 | 0.003267 | modern | holocene | quaternary | 0 | 0 | beaded ribs |
| ta_b_r0_mat, | tylocidaris | abildgaardi | psychocidaridae | -0.01361 | -0.02469 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| ta_g_r0s1_mat, | tylocidaris | abildgaardi | psychocidaridae | -0.11084 | -0.04117 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| ta_g_r0s2_mat, | tylocidaris | abildgaardi | psychocidaridae | -0.1343 | -0.03796 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| ta_g_r2s3_mat, | tylocidaris | abildgaardi | psychocidaridae | 0.005851 | -0.05597 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tc_b_r0s1_mat, | tylocidaris | clavigera | psychocidaridae | -0.00365 | -0.01015 | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tc_b_r0s2_mat, | tylocidaris | clavigera | psychocidaridae | -0.02055 | 0.01787 | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tc_b_r0s3_mat, | tylocidaris | clavigera | psychocidaridae | -0.03362 | 0.016716 | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tc_b_r0s4_mat, | tylocidaris | clavigera | psychocidaridae | -0.03722 | -0.00136 | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tclav_gb2_1_mat, | tylocidaris | clavigera | psychocidaridae | -0.01695 | 0.011095 | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tclav_gb3_1_mat, | tylocidaris | clavigera | psychocidaridae | 0.087744 | 0.068954 | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tclav_gb4_1_mat, | tylocidaris | clavigera | psychocidaridae | -0.05661 | 0.041819 | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| tclav_ou_1_mat, | tylocidaris | clavigera | psychocidaridae | -0.06761 | -0.09192 | turonian-santonian | late cretaceous | cretaceous | 93.9 | 83.6 | beaded ridges |
| th_ed0_r0s1_mat, | tylocidaris | honorinae | psychocidaridae | 0.045684 | 0.018011 | bajocian-bathonian | middle jurassic | jurassic | 170.3 | 166.1 | beaded ribs |
| theru_gb2_1_mat, | tylocidaris | herupensis | psychocidaridae | -0.09488 | 0.044254 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tod_g1_r1s1_mat, | tylocidaris | odumi | psychocidaridae | -0.05959 | -0.00903 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tod_g1_r2s2_mat, | tylocidaris | odumi | psychocidaridae | -0.00382 | -0.04693 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tod_g1_r3s3_mat, | tylocidaris | odumi | psychocidaridae | -0.09304 | -0.08631 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tod_g1_r4s4_mat, | tylocidaris | odumi | psychocidaridae | -0.09228 | -0.04417 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tod_g2_r1s1_mat, | tylocidaris | odumi | psychocidaridae | -0.07871 | -0.07434 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| tod_g2_r2s2_mat, | tylocidaris | odumi | psychocidaridae | -0.06482 | -0.00851 | danian | paleocene | paleogene | 66 | 61.6 | beaded ribs |
| toh_ed0_r1s1_mat, | tylocidaris | ohshimai | psychocidaridae | -0.02815 | -0.0013 | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| toh_ed1_r1s1_mat, | tylocidaris | ohshimai | psychocidaridae | -0.08419 | 0.016344 | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| toh_ed1_r2s2_mat, | tylocidaris | ohshimai | psychocidaridae | -0.01109 | 0.007798 | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| toh_ed1_r3s3_mat, | tylocidaris | ohshimai | psychocidaridae | 0.01009 | -0.00299 | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| toh_ed1_r4s4_mat, | tylocidaris | ohshimai | psychocidaridae | -0.01887 | 0.067537 | modern | holocene | quaternary | 0 | 0 | coarse thorns |
| tr_1_r0s1_mat, | tylocidaris | rosenkrantzi | psychocidaridae | 0.005677 | -0.07486 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tr_1_r0s2_mat, | tylocidaris | rosenkrantzi | psychocidaridae | -0.03766 | -0.02042 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tr_1_r0s3_mat, | tylocidaris | rosenkrantzi | psychocidaridae | -0.14894 | -0.01168 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tr_1_r0s4_mat, | tylocidaris | rosenkrantzi | psychocidaridae | -0.05734 | -0.06181 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tr_2_r1s1_mat, | tylocidaris | rosenkrantzi | psychocidaridae | -0.14611 | 0.009138 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tr_2_r2s2_mat, | tylocidaris | rosenkrantzi | psychocidaridae | -0.13051 | 0.025181 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tr_2_r3s3_mat, | tylocidaris | rosenkrantzi | psychocidaridae | -0.07654 | -0.04086 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tr_2_r3s4_mat, | tylocidaris | rosenkrantzi | psychocidaridae | -0.06398 | 0.014096 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| tr_2_r4s5_mat, | tylocidaris | rosenkrantzi | psychocidaridae | -0.08868 | -0.01808 | danian | paleocene | paleogene | 66 | 61.6 | beaded ridges |
| ts_r0_s1_mat, | tylocidaris | salina | psychocidaridae | -0.09163 | 0.032176 | thanetian | paleocene | paleogene | 59.2 | 56 | beaded ridges |
| ts_r0_s2_mat, | tylocidaris | salina | psychocidaridae | -0.09669 | 0.01418 | thanetian | paleocene | paleogene | 59.2 | 56 | beaded ridges |
| ts_r0_s3_mat, | tylocidaris | salina | psychocidaridae | -0.06753 | -0.02558 | thanetian | paleocene | paleogene | 59.2 | 56 | beaded ridges |
| twal_z_r1s1_mat, | tylocidaris | walcotti | psychocidaridae | -0.0374 | 0.065457 | thanetian | paleocene | paleogene | 59.2 | 56 | beaded ridges |
| typomargin_gbif_1_mat, | typocidaris | marginata | cidaridae | 0.01393 | -0.10367 | oxfordian | late jurassic | jurassic | 163.5 | 157.3 | beaded ribs |
| typomargin_gbif_2_mat | typocidaris | marginata | cidaridae | -0.0259 | 0.104414 | oxfordian | late jurassic | jurassic | 163.5 | 157.3 | beaded ribs |

**Table A.2c.** The third part of the data for cidaroid families for grouping and plotting into multivariate space.

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