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MASTERARBEIT

Titel der Masterarbeit

Geometric Morphometrics of Clypeasteroids

verfasst von

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Ich bedanke mich bei Univ. Prof. Mag. Dr. Martin Zuschin für die Betreuung der Masterarbeit, beim Naturhistorischen Museum Wien für die Bereitstellung des Materials, bei Dr. Andreas Kroh für die fachliche Unterstützung sowie bei Priv. Doz. Dr. Philipp Mitteröcker für die Hilfe bei der Erarbeitung einer geeigneten Methode.

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Abstract

The complex skeleton of echinoids shows a close relationship between structure and function that makes this clade a textbook example for the analysis of functional morphology. Clypeasteroids (“sand dollars”) are a group of irregular echinoids with flat body shape, which live as detritus feeders on marine softground. Rapid expansion, geographical separation and occupation of similar niches in different regions have led to a certain amount of convergence among lineages. In this study I applied Geometric Morphometrics (GM), a method based on landmarks and semilandmarks, to photographs of 13 species (68 individuals) of clypeasteroids to test the currently accepted phylogeny of this clade. The main aim of my study was to identify characters that are appropriate to distinguish species. For this purpose 205 landmarks and semilandmarks were placed mostly on the petals and outline of the clypeasteroids. In a process called „Procrustes Superimposition“, shape was separated from position, size and orientation. The resulting Procrustes shape coordinates were used for statistical analysis.
Clypeasteroids are well suited for GM analysis. The test is flat with an approximatley circular outline and provides many structures to place landmarks and semilandmarks on. In the Principal Components Analysis (PCA) characters are computed and listed in order of the amount of variation they explain. These major characters are then applied to particular problems. All analyzed species are well separated by at least one of the first three Principal Components (PCs), which explain 84.6% of the variation in the data set and which are the size of the petals in relation to test size (PC1), the shape of the petals (PC2) and the position of the madreporic plate in relation to the petals (PC3). Also higher order relationship is recognizable. Just the way individuals of one species cluster, species of the same family group together, but overlap between families is more common than between species. The currently accepted phylogeny is supported by the analysis. Moreover it is possible to use GM to quantify within-species variance. The closer individuals group in the PC-plots, the higher is their similarity.

1. Introduction

Echinoids are a diverse group of marine benthic animals. They exploit habitats ranging from the equator to the poles and thrive in intertidal zones as well as the deep sea. Regular echinoids live epifaunally as algal grazers and are important bioeroders including

many keystone-taxa. Most irregular echinoids live infaunally as bioturbating deposit feeders (KROH & SMITH 2010). The echninoid test is composed of high-magnesium-calcite. The single plates of post-paleozoic echinoids are more or less well interlocked, resulting in a fairly robust test and a good fossil record (SMITH 1984). By 1970, 124 paleozoic species, 3672 mesozoic species and 3250 cenozoic species were known (LAMBERT & THIERY 1909-25, KIER 1965 and KIER & LAWSON 1978). In regular echinoids the plates are arranged pentamerically. These animals are able to move in any direction, while irregular echinoids move unidirectional. The oral surface of irregular echinoids is flattened in order to bring more spines in contact with the substrate. Spines on the aboral side of burrowing echinoids are fine and densely spaced. They keep away sediment from the body, allowing the organism to take up oxygen. The more densely spaced the spines are, the finer the particles they can hold off. Most burrowing echinoids, however, are restricted to sand and fine gravel. Today only spatangoids can cope with clay or silt (SMITH 1984). *Togoyamus* from the Upper Paleocene of West Africa is the oldest known clypeasteroid. Sand-dollars rapidly attained world-wide distribution by the Oligocene, by the Miocene all of today's families had evolved (SMITH 1984). The skeleton of echinoids is a complex structure with a close relationship between structure and function. Rapid expansion, geographical separation and occupation of similar niches in different regions have led to a certain amount of convergence among different lineages (SMITH 1984). The test of an irregular echinoid consists of hundreds of small plates arranged pentamerically in twenty rows. Each plate bears spines and pedicellariae. The ambulacral zones consist of pairwise plates that are perforated. The echinoid body bears a water vascular system adapted to many purposes. Through the pores in the test the vascular system reaches into tube feet, allowing them to be moved. In between the ambulacral zones are the interambulacral zones, areas with pairwise plate columns that lack pores. They are usually larger and comprise most of the surface. The mouth opening or peristome lies ventrally, usually in the center. The anal opening or periproct is located dorsally, at the margin, or ventrally. Since in irregular echinoids the bilateral symmetry of the larvae is maintained, we also speak of anterior and posterior. Through the gonopores the gonads are connected to the outside (Fig. 1). Within the last few years a lot of work has been done on the phylogeny of echinoids (KROH & MOOI 2011, KROH & SMITH 2010, COPPARD & CAMPBELL 2006, MIHALJEVIC et al. 2011, SMITH & KROH (editors) 2011). In this study I am applying Geometric Morphometrics (GM) to test the currently accepted phylogeny of clypeasteroids. GM is a popular method in fields like anthropology and fish evolution (KERSCHBAUMER &

STURMBAUER 2011, MADERBACHER et al. 2008, MITTERÖCKER et al. 2013), but has found little use in echinoderms so far. To answer the question if the tests of echinoderms are suitable for a GM analysis, I compiled a set of landmarks and semilandmarks to cover as many significant characters as possible. The main aim of my study is to identify characters that are appropriate to distinguish species. It is also of interest to see if it is possible to use GM for quantifying within-species variance.

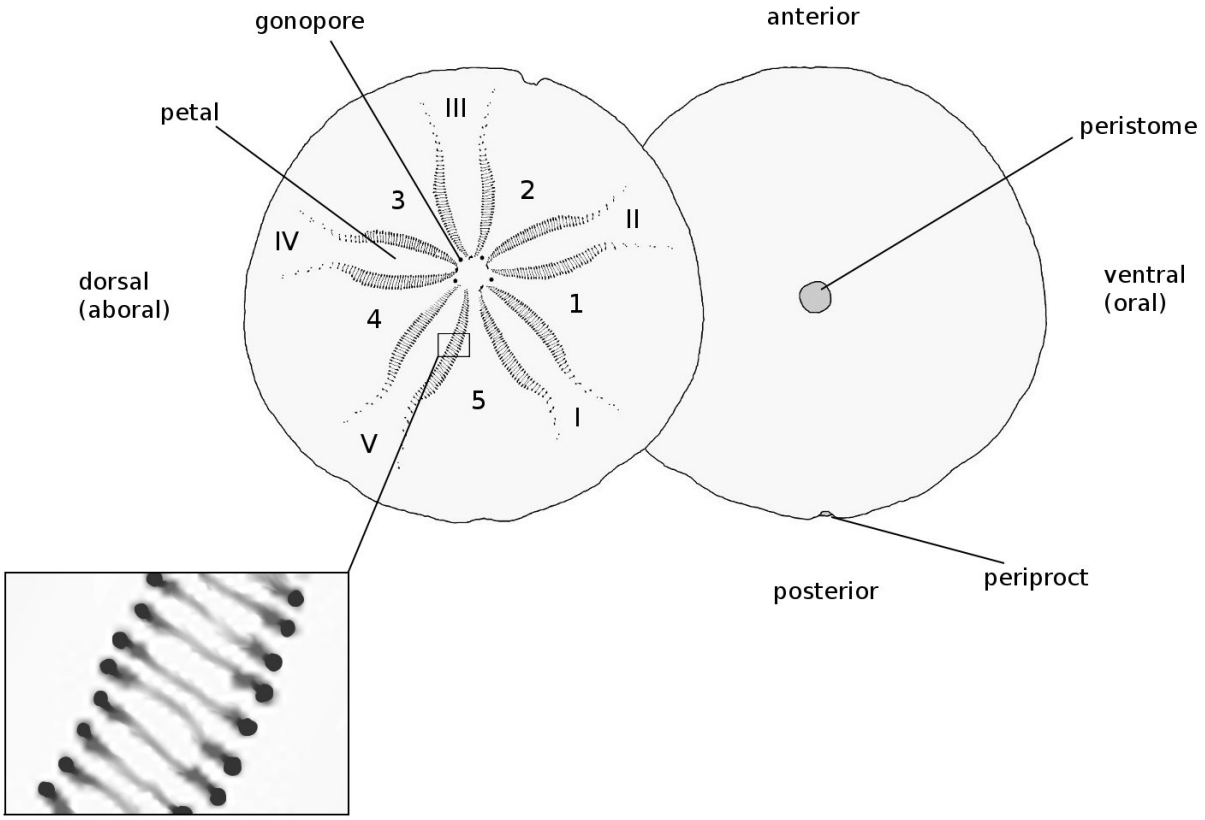


Fig. 1: Simplified drawing showing relevant morphological features of a clypeasteroid.

Morphometrics, the measurement (metron) of shape (morphe), is a subfield of statistics (MITTERÖCKER & GUNZ 2009). In traditional Morphometrics, distances between homologous points or angles are measured. In Geometric Morphometrics (GM) landmarks are placed on homologous points. The shape coordinates of these landmarks are then analyzed (GUNZ & MITTERÖCKER 2012). Though modern GM arose in the 1980s when coordinate-based methods were invented and the computational realization of deformation grids became possible, it's roots go way back (MITTERÖCKER & GUNZ 2009). In 1528, for example, Albrecht Dürer already used hand-drawn deformation grids for comparing face shape.

2. Material

The material studied was put at my disposal by the Natural History Museum Vienna. It contains thirteen species and one subspecies in seven families and three suborders of the Clypeasteroida (Tab. 1, Fig. 2). For the fourth suborder Rotulina no material was available. Wherever possible the type species was included. In the Mellitidae the use of *Mellita quinquesperforata* was not possible, *Encope emarginata* was used instead. All selected species are recent. The length of the tests ranges from 22.14 to 157.84 mm. Number of individuals, mean and standard deviation of the mean are listed in Tab. 2. Figures 3 and 4 show representatives of all fourteen groups. Size range is affected by the availability of material. It is narrow in some groups, but in *Clypeaster humilis* it is extremely wide with the biggest specimen being almost seven times as big as the smallest one. Whenever size range of the available material was wide, small and large individuals were chosen for the analysis.

Clypeasterina	Arachnoididae	*Arachnoides placenta* *
		Arachnoides tenuis
	Clypeasteridae	*Clypeaster rosaceus* *
		Clypeaster humilis
		Clypeaster reticulatus
Laganina	Laganidae	*Laganum laganum* *
		Peronella lesueuri
		Peronella lesueuri rostrata
Scutellina	Astriclypeidae	*Astriclypeus mannii**
		Echinodiscus auritus
		Echinodiscus bisperforatus
	Dendrasteridae	*Dendraster excentricus* *
	Echinarachniidae	*Echinarachnius parma* *
	Mellitidae	*Encope emarginata*

Tab. 1: Suborder, family and species of the studied material. * = type species.

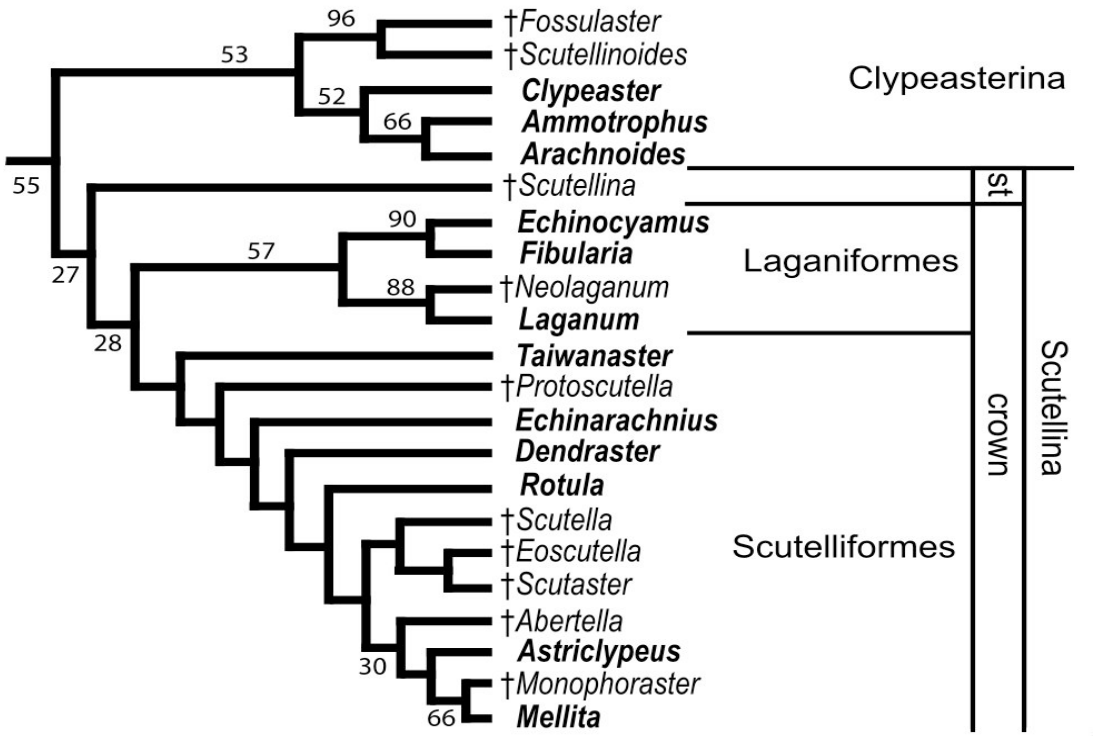


Fig. 2: Phylogeny of clypeasteroids, modified from KROH & SMITH (2010).

species	no.	mean	stdev.	stdev./mean
Arachnoides placenta	7	59.36	17.37	0.29
Arachnoides tenuis	5	33.57	1.41	0.04
Clypeaster rosaceus	5	111.85	8.12	0.07
Clypeaster humilis	6	82.42	49.38	0.60
Clypeaster reticulatus	5	48.05	7.98	0.17
Laganum laganum	5	32.03	3.29	0.10
Peronella lesueuri	4	99.12	7.62	0.08
Peronella lesueuri rostrata	1	114.28	-	-
Astriclypeus manni	5	115.97	6.50	0.06
Echinodiscus auritus	7	132.19	27.11	0.21
Echinodiscus bisperforatus	4	57.31	16.36	0.29
Dendraster excentricus	5	60.86	8.5	0.14
Echinarachnius parma	5	41.50	10.82	0.26
Encope emarginata	4	129.04	11.16	0.09

Tab. 2: Number of individuals and size [mm] of the studied species.

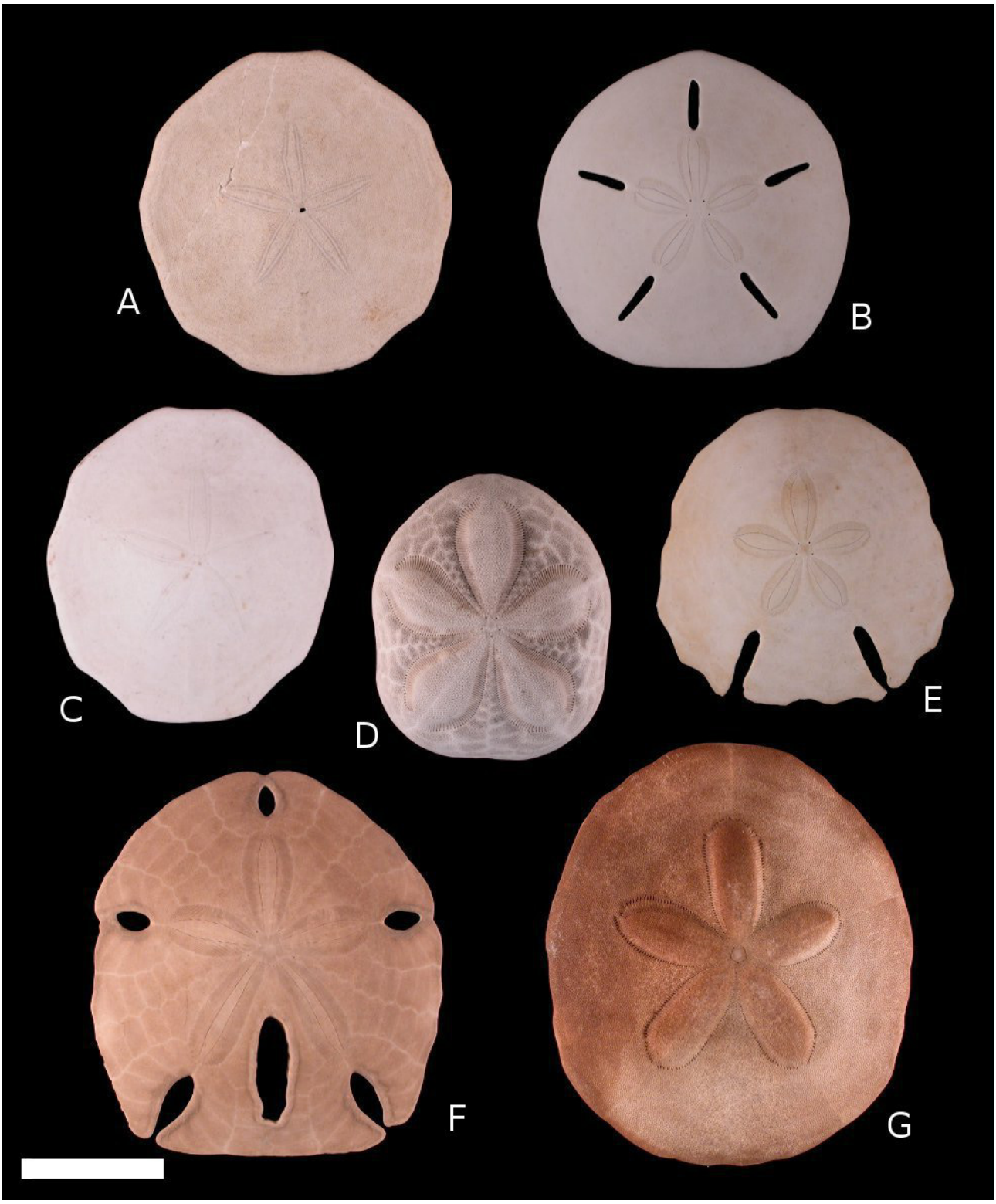


Fig. 3: Representative individuals of the species studied, part one: A *Peronella lesueuri rostrata*, B *Astriclypeus manni*, C *Peronella lesueuri*, D *Clypeaster rosaceus*, E *Echinodiscus auritus*, F *Encope emarginata*, G *Clypeaster humilis.* Scale bar equals 5 cm.

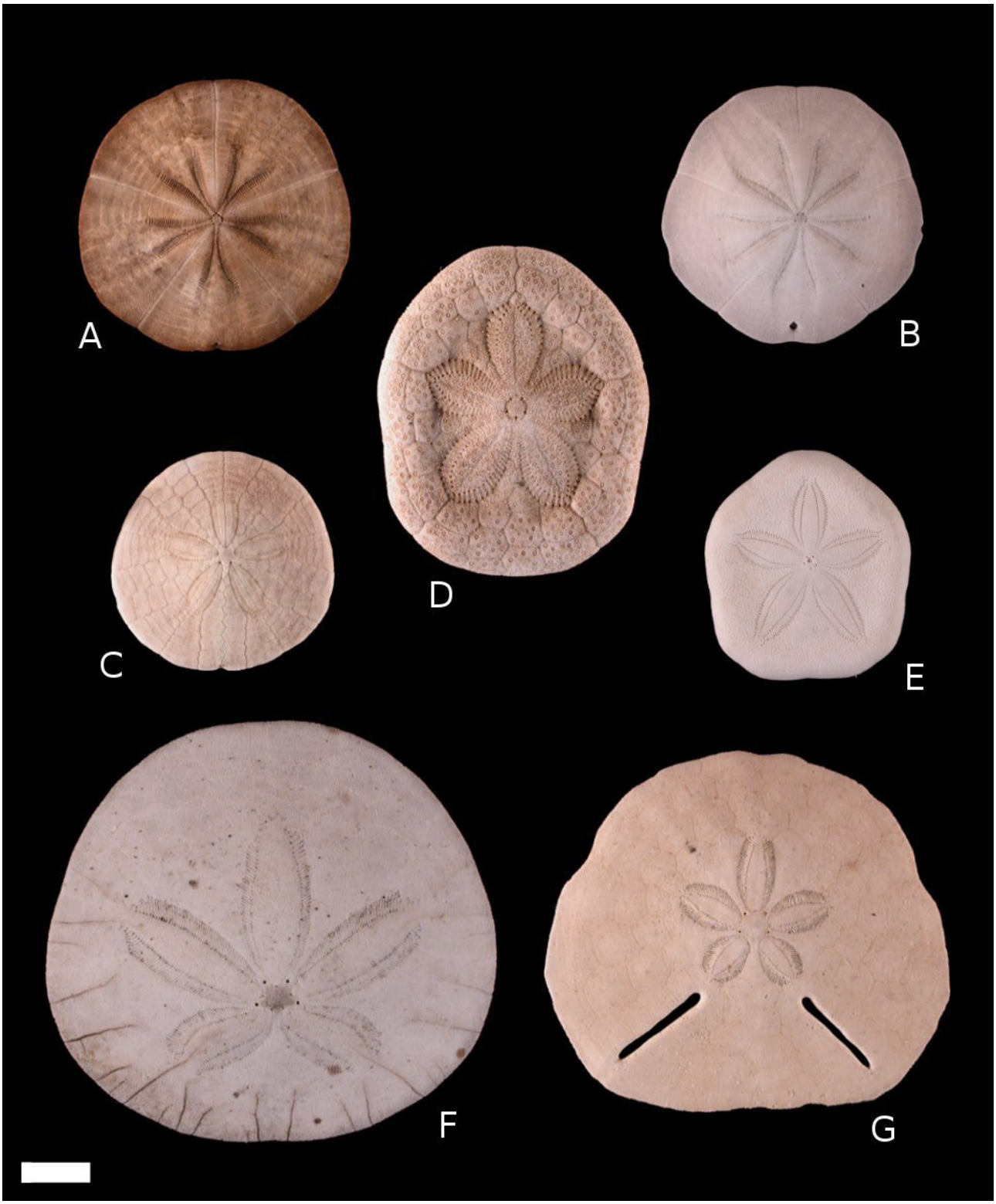


Fig. 4: Representative individuals of the species studied, part two: A *Arachnoides placenta*, B *Arachnoides tenuis*, C *Echinarachnius parma*, D *Clypeaster reticulatus*, E *Laganum laganum*, F *Dendraster excentricus*, G *Echinodiscus bisperforatus*. Scale bar equals 1 cm.

All sixty-eight specimens studied are listed in Table 3. Labels from the collection did not always correspond with currently acknowledged names. They were checked against the World Echinoidea Database (KROH & MOOI 2011) and corrected if necessary.
Three images were taken of each specimen (Figures 6 to 19). One of the ventral side, one of the dorsal side and one of petal IV. In *Peronella lesueuri rostrata*, the fourth petal was broken and petal II was used instead (Fig. 19c). Shape variability is high. Several species (*Astriclypeus manni* (Fig. 8)*, Echinodiscus auritus* (Fig. 14)*, Echinodiscus bisperforatus* (Fig. 15)*, Encope emarginata* (Fig. 16)) have slits or breakthroughs in their tests. These lunules (SMITH & GHIOLD 1982) were not considered in the outline analysis, because variation is too high and would lead to a breakdown of the thin plate splines since landmarks cannot switch places and all specimens need to have the same amount of landmarks.
Petals can be open (diverging distally) or closed (converging). In species with closed petals, there are usually no pores between the distal tip of the petal and the margin (for example Fig. 10., Fig. 11). In species with open petals, pore rows can pull all the way to the margin, but pores become smaller and the distance between pore pairs suddenly grows bigger (Fig. 6, Fig. 7). In this case, the outermost landmark was placed on the first pore pair that is separated by a gap from the others, which are more or less equally spaced (Fig.5).
Dendraster excentricus is different, because its madreporic plate is not situated in the center (Fig. 12). In life it is dug into the sand with its anterior end in an inclined position for suspension feeding (TIMKO 1976).

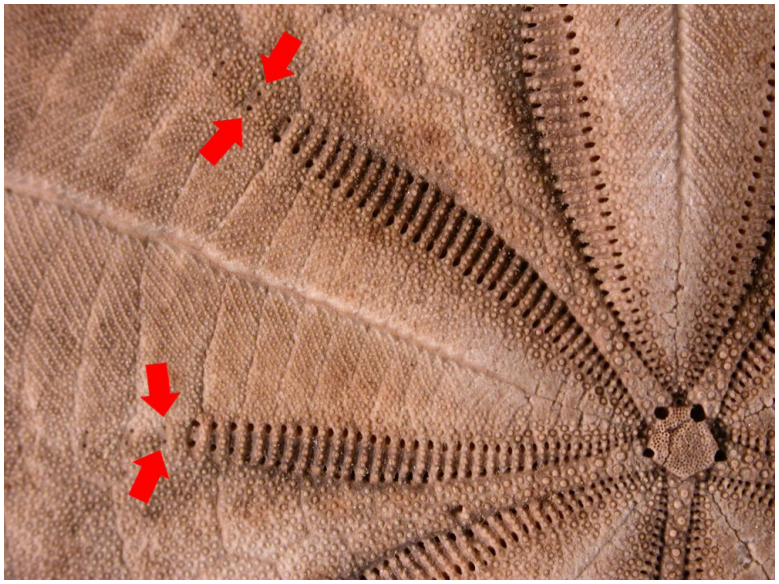


Fig. 5: Open petal IV of *Arachnoides placenta*. Arrows indicate position of outermost landmarks.

***Arachnoides placenta* Linnaeus, 1758 (Clypeasterina: Arachnoididae)**		
NHMW-Zoo12359	New Zealand	96.51
NHMW-Zoo12361-1	New Zealand	42.26
NHMW-Zoo12361-2	New Zealand	61.58
NHMW-Zoo13009	Java	57.41
NHMW-Zoo12360	Singapore	60.5
NHMW-Zoo12357	Singapore	58.58
NHMW-Zoo12358	Cebu Island	38.67
***Arachnoides tenuis* H.L. Clark, 1938 (Clypeasterina: Arachoididae)**		
NHMW-Geo 2010/0246/0003	Western Australia	31.57
NHMW-Geo 2010/0246/0004	Western Australia	27.27
NHMW-Geo 2010/0246/0005	Western Australia	35.63
NHMW-Geo 2010/0246/0006	Western Australia	35.76
NHMW-Geo 2010/0246/0007	Western Australia	43.59
***Clypeaster rosaceus* Linnaeus, 1758 (Clypeasterina: Clypeasteridae)**		
NHMW-Geo 2008z0162/0003	Roatan Island, Honduras	101.29
NHMW-Geo 2008z0167/0006	Roatan Island, Honduras	122.76
NHMW-Geo 2008z0167/0007	Roatan Island, Honduras	117.47
NHMW-Geo 2008z0167/0008	Roatan Island, Honduras	103.87
NHMW-Geo 2008z0162/0002	Roatan Island, Honduras	113.87
***Clypeaster humilis* Leske, 1778 (Clypeasterina: Clypeasteridae)**		
NHMW-Zoo13012-1	Red Sea	149.42
NHMW-Zoo13012-2	Red Sea	147.53
NHMW-Geo 2013/0279/0001	Dahab, Janub Sina', Egypt	22.14
NHMW-Geo 2013/0279/0003	Dahab, Janub Sina', Egypt	41.44
NHMW-Geo 2013/0279/0004	Dahab, Janub Sina', Egypt	59.5
NHMW-Geo 2013/0279/0002	Dahab, Janub Sina', Egypt	74.5
***Clypeaster reticulatus* Linnaeus, 1758 (Clypeasterina: Clypeasteridae)**		
NHMW-Zoo112392-1	Lord Hood's Island	56.26
NHMW-Zoo112392-2	Lord Hood's Island	54.99
NHMW-Zoo112393	Amboina Doleschal	33.86
NHMW-Zoo112395-1	Red Sea, Gulf of Akaba	46.92
NHMW-Geo 2013/0280/0001	Al Bahr al Ahmar, Egypt	48.22
***Laganum laganum* Leske, 1778 (Scutellina: Laganidae)**		
NHMW-Geo 2011/0346/0002	Olango Island, Philippines	36.85
NHMW-Geo 2011/0346/0003	Olango Island, Philippines	34.5
NHMW-Geo 2011/0346/0004	Olango Island, Philippines	31.66
NHMW-Geo 2011/0346/0005	Olango Island, Philippines	29.21
NHMW-Geo 2011/0346/0006	Olango Island, Philippines	27.93
***Peronella lesueuri* L. Agassiz, 1841 (Scutellina: Laganidae)**		
NHMW-Geo 2011/0361/0001	Cubian Island, Philippines	111.1
NHMW-Geo 2011/0362/0001	Cubian Island, Philippines	100.2
NHMW-Geo 2011/0363/0001	Cubian Island, Philippines	93.64

NHMW-Geo 2011/0364/0001	Cubian Island, Philippines	91.53
***Peronella lesueuri rostrata* L. Agassiz, 1841 (Scutellina: Laganidae)**		
NHMW-Geo 2011/0335/0002	Western Australia	114.28
***Astriclypeus manni* Verrill, 1867 (Scutellina: Astriclypeidae)**		
NHMW-Geo 2009z0005/0007	Bohol,Philippines	115.7
NHMW-Geo 2009z0005/0008	Bohol,Philippines	117.63
NHMW-Geo 2009z0005/0009	Bohol,Philippines	111.77
NHMW-Geo 2009z0005/0010	Bohol,Philippines	127.04
NHMW-Geo 2009z0005/0012	Bohol,Philippines	107.72
***Echinodiscus auritus* Leske, 1778 (Scutellina: Astriclypeidae)**		
NHMW-Geo 2009z0005/0013	Bohol,Philippines	156.08
NHMW-Geo 2009z0005/0015	Bohol,Philippines	135.91
NHMW-Geo 2009z0005/0016	Bohol,Philippines	157.84
NHMW-Geo 2009z0005/0017	Bohol,Philippines	152.75
NHMW-Geo 2011/0331/0008	Poro Island, Philippines	137.7
NHMW-Geo 2008z0004/0007	Safaga, Egypt	104.75
NHMW-Geo 2008z0004/0005	Safaga, Egypt	80.28
***Echinodiscus bisperforatus* Leske, 1778 (Scutellina: Astriclypeidae)**		
NHMW-Zoo12427	Red Sea	84.42
NHMW-Zoo12431	S'Urban (Natal)	40.79
NHMW-Zoo20071-1	Margarita Island, Venezuela	50.19
NHMW-Zoo20071-2	Margarita Island, Venezuela	53.85
***Dendraster excentricus* Eschscholtz, 1829 (Scutellina: Dendrasteridae)**		
NHMW-Geo 2011/0355/0005	Washington, USA	50.01
NHMW-Geo 2011/0355/0006	Washington, USA	54.04
NHMW-Geo 2011/0355/0007	Washington, USA	59.31
NHMW-Geo 2011/0355/0008	Washington, USA	68.18
NHMW-Geo 2011/0355/0009	Washington, USA	72.74
***Echinarachnius parma* Lamarck, 1816 (Scutellina: Echinarachniidae)**		
NHMW-Zoo12434-1	Grand Manan	60.73
NHMW-Zoo12434-2	Grand Manan	41.65
NHMW-Zoo13019-1	Grand Manan	42.79
NHMW-Zoo13019-2	Grand Manan	30.54
NHMW-Zoo13019-3	Grand Manan	31.8
***Encope emarginata* Leske, 1778 (Scutellina: Mellitidae)**		
NHMW-Zoo12487-1	Brazil	116.3
NHMW-Zoo12487-2	Brazil	135.92
NHMW-Zoo12487-3	Brazil	143.62
NHMW-Zoo12708	Brazil	120.31

Tab. 3: List of studied specimens with inventory number, area of collection and test length [mm].

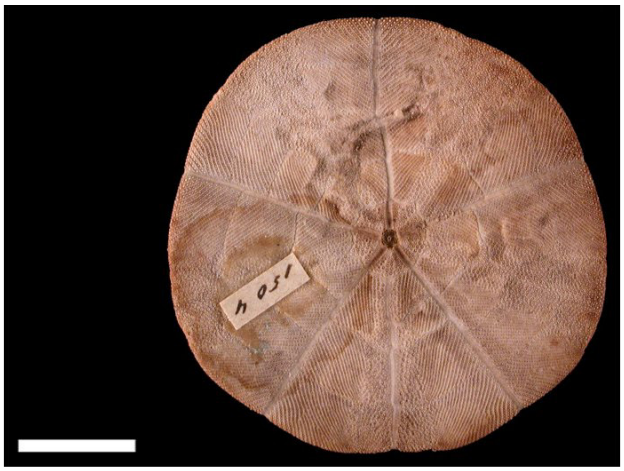


Fig. 6a: NHMW-Zoo 12358
Arachnoides placenta, oral view

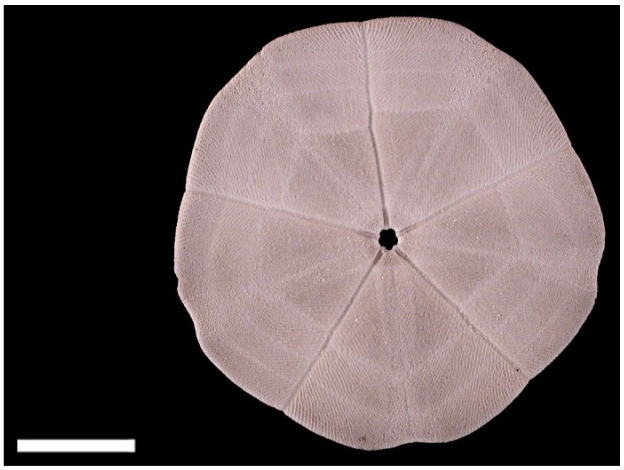


Fig. 7a: NHMW-Geo 2010/0246/0005
Arachnoides tenuis, oral view

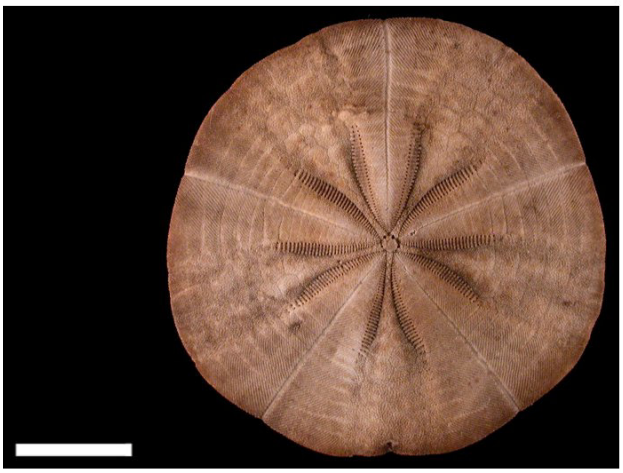


Fig. 6b: NHMW-Zoo 12358
Arachnoides placenta, aboral view

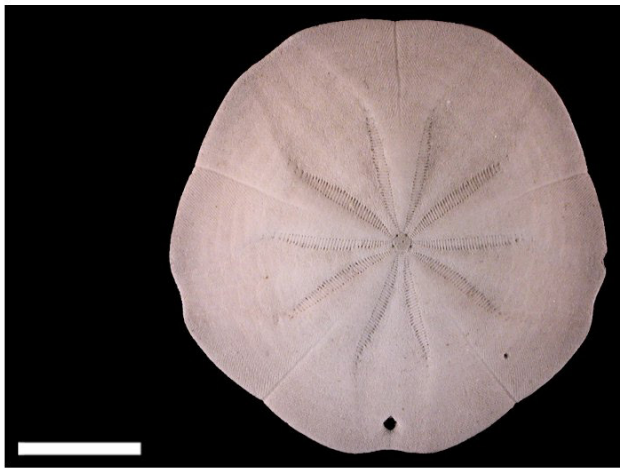


Fig. 7b: NHMW-Geo 2010/0246/0005
Arachnoides tenuis, aboral view

Fig. 6c: NHMW-Zoo 12358
Arachnoides placenta, petal IV

Fig. 7c: NHMW-Geo 2010/0246/0005
Arachnoides tenuis, petal IV

scale bar equals 1 cm

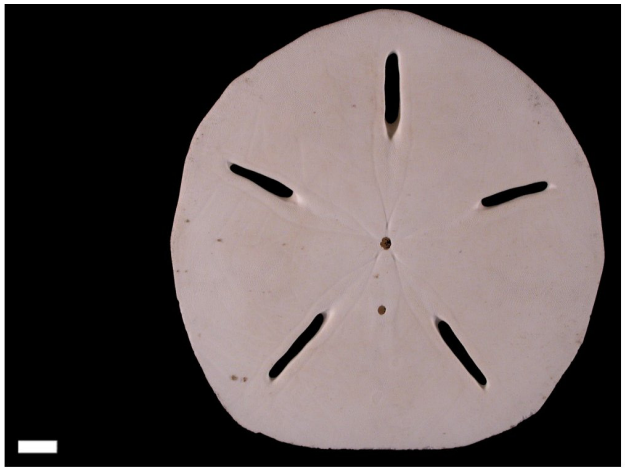


Fig. 8a: NHMW-Geo 2009z0005/0009
Astriclypeus manni, oral view

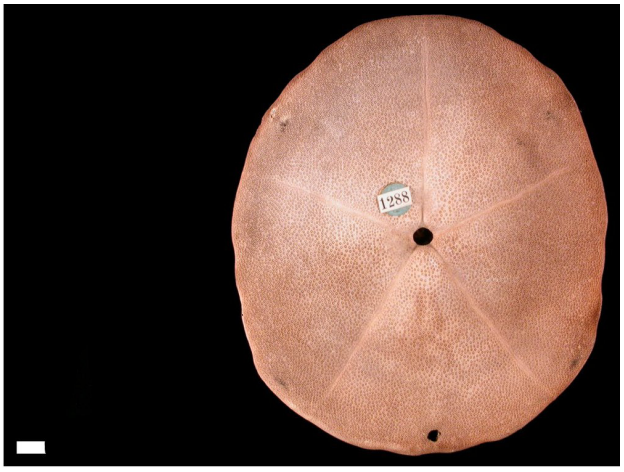


Fig. 9a: NHMW-Zoo 13012-1
Clypeaster humilis, oral view

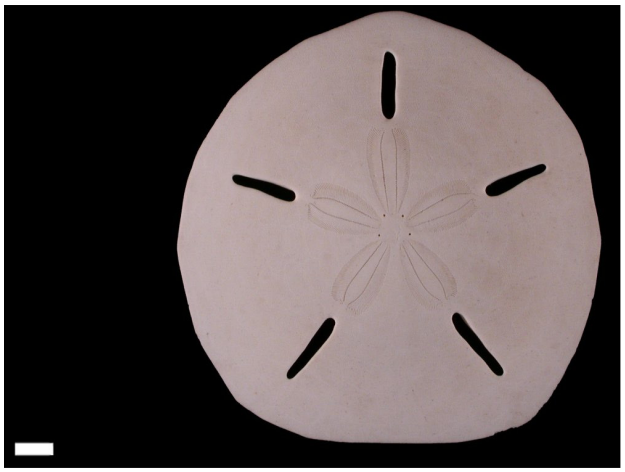


Fig. 8b: NHMW-Geo 2009z0005/0009
Astriclypeus manni, aboral view

Fig. 9b: NHMW-Zoo 13012-1
Clypeaster humilis, aboral view

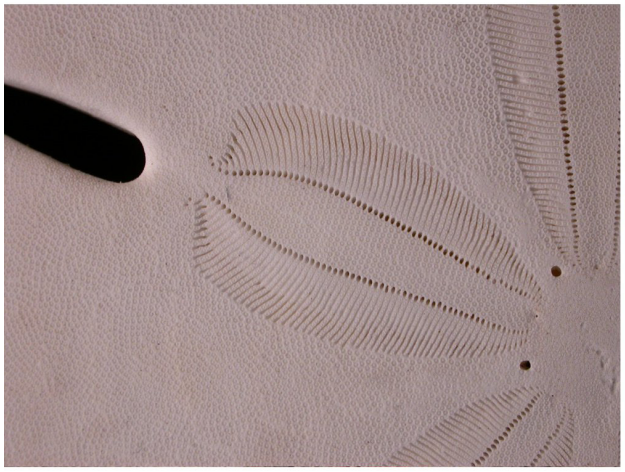


Fig. 8c: NHMW-Geo 2009z0005/0009
Astriclypeus manni, petal IV

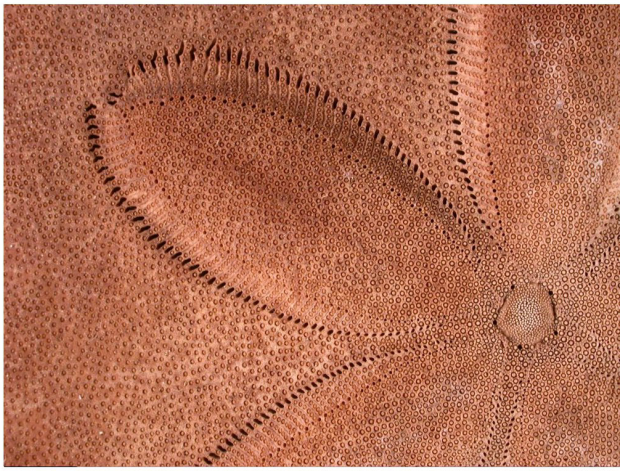


Fig. 9c: NHMW-Zoo 13012-1-1
Clypeaster humilis, petal IV

scale bar equals 1 cm

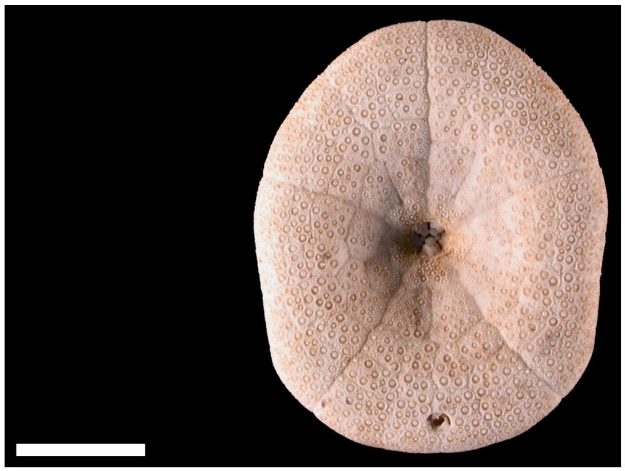


Fig. 10a: NHMW-Zoo112395-1
Clypeaster reticulatus, oral view

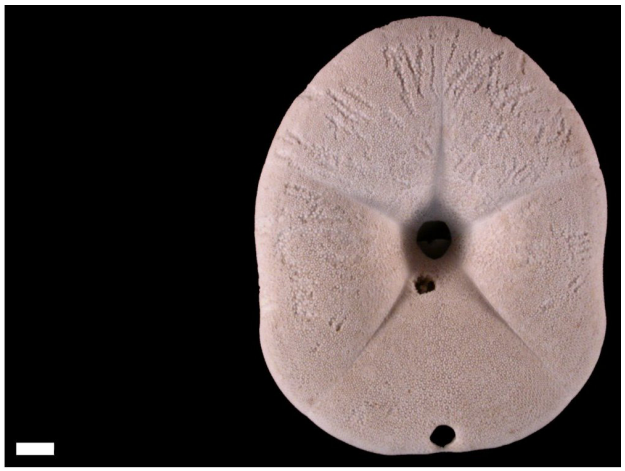


Fig. 11a: NHMW-Geo 2008z0162/0003
Clypeaster rosaceus, oral view

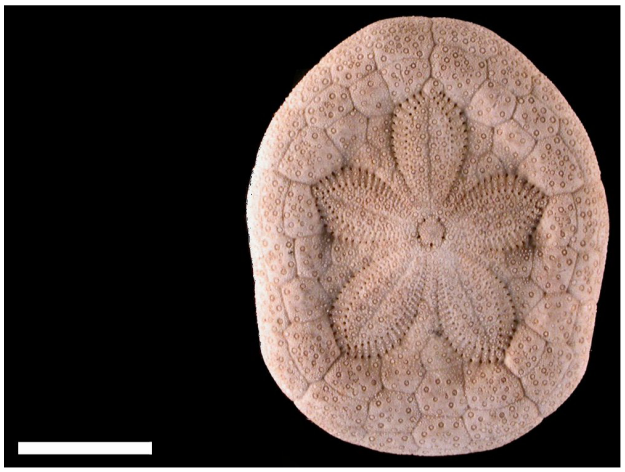


Fig. 10b: NHMW-Zoo112395-1
Clypeaster reticulatus, aboral view

Fig. 11b: NHMW-Geo 2008z0162/0003
Clypeaster rosaceus, aboral view

Fig. 10c: NHMW-Zoo112395-1
Clypeaster reticulatus, petal IV

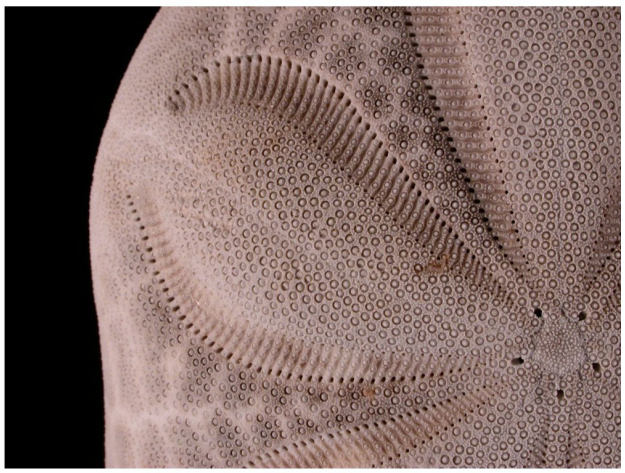


Fig. 11c: NHMW-Geo 2008z0162/0003
Clypeaster rosaceus, petal IV

scale bar equals 1 cm

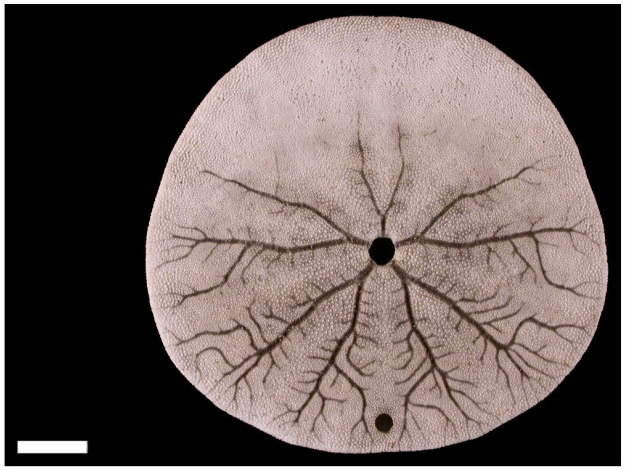


Fig. 12a: NHMW-Geo 2011/0355/0007
Dendraster excentricus, oral view

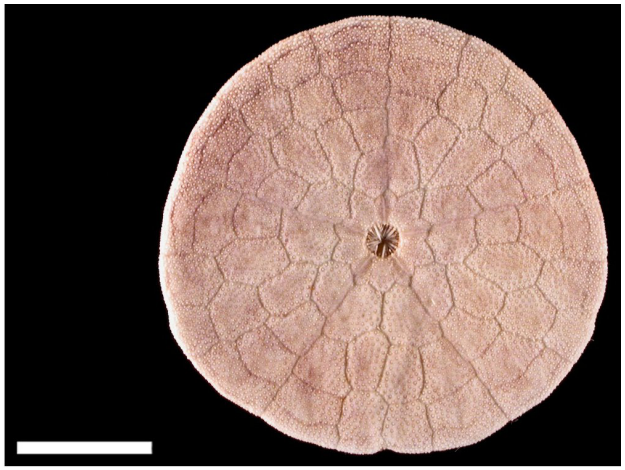


Fig. 13a: NHMW-Zoo13019-2
Echinarachnius parma, oral view

Fig. 12b: NHMW-Geo 2011/0355/0007
Dendraster excentricus, aboral view

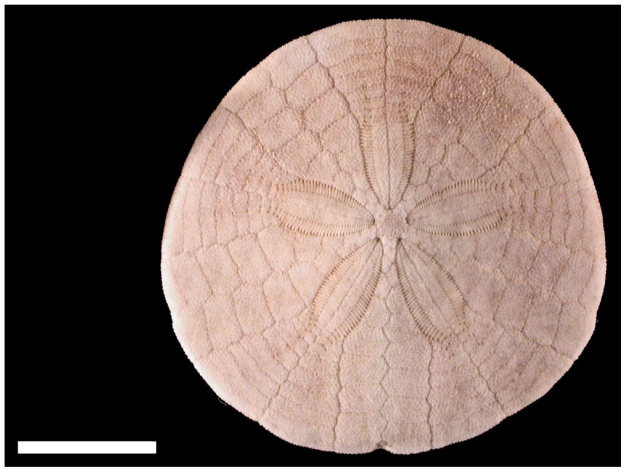


Fig. 13b: NHMW-Zoo13019-2
Echinarachnius parma, aboral view

Fig. 12c: NHMW-Geo 2011/0355/0007
Dendraster excentricus, petal IV

Fig. 13c: NHMW-Zoo13019-2
Echinarachnius parma, petal IV

scale bar equals 1 cm

Fig. 14a: NHMW-Geo 2008z0004/0007
Echinodiscus auritus, oral view

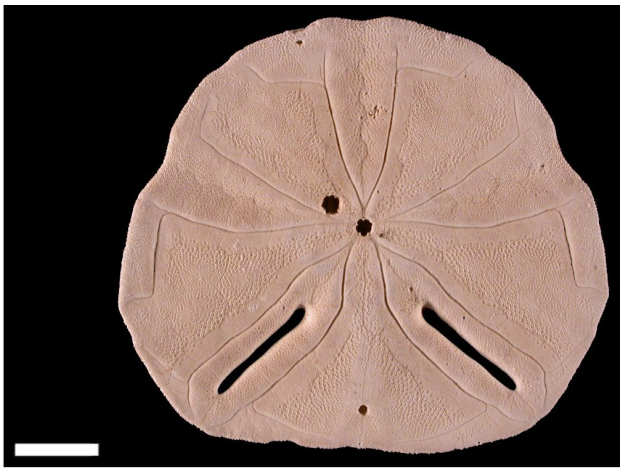


Fig. 15a: NHMW-Zoo20071-1
Echinodiscus bisperforatus, oral view

Fig. 14b: NHMW-Geo 2008z0004/0007
Echinodiscus auritus, aboral view

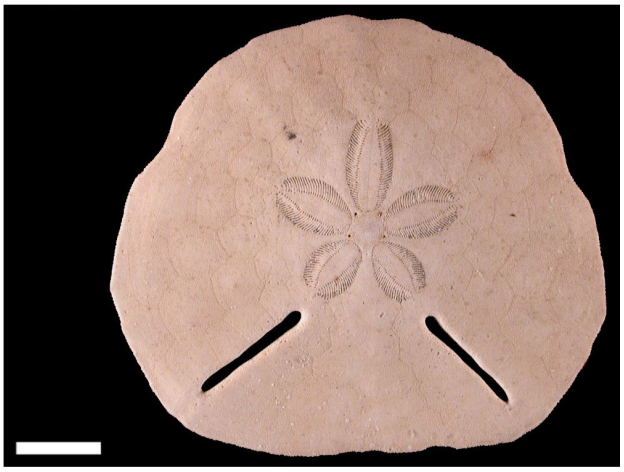


Fig. 15b: NHMW-Zoo20071-1
Echinodiscus bisperforatus, aboral view

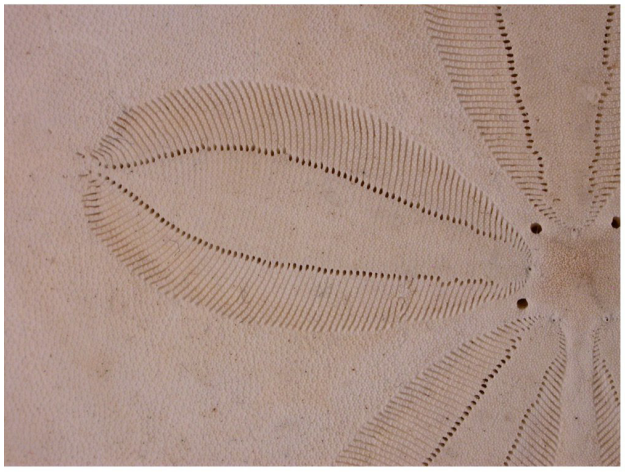


Fig. 14c: NHMW-Geo 2008z0004/0007
Echinodiscus auritus, petal IV

Fig. 15c: NHMW-Zoo20071-1
Echinodiscus bisperforatus, petal IV

scale bar equals 1 cm

Fig. 16a: NHMW-Zoo12487-2
Encope emarginata, oral view

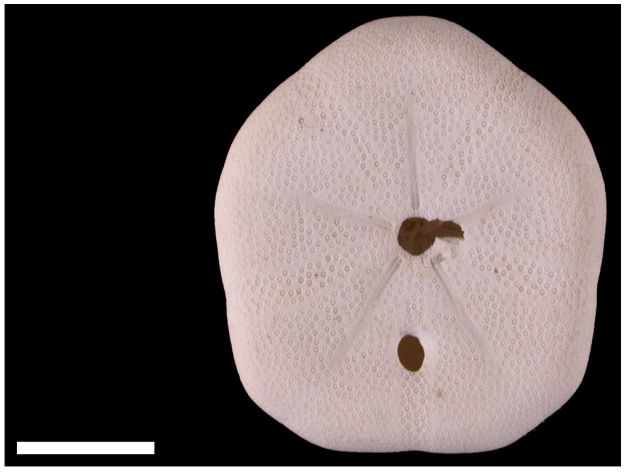


Fig. 17a: NHMW-Geo 2011/0346/0004
Laganum laganum, oral view

Fig. 16b: NHMW-Zoo12487-2
Encope emarginata, aboral view

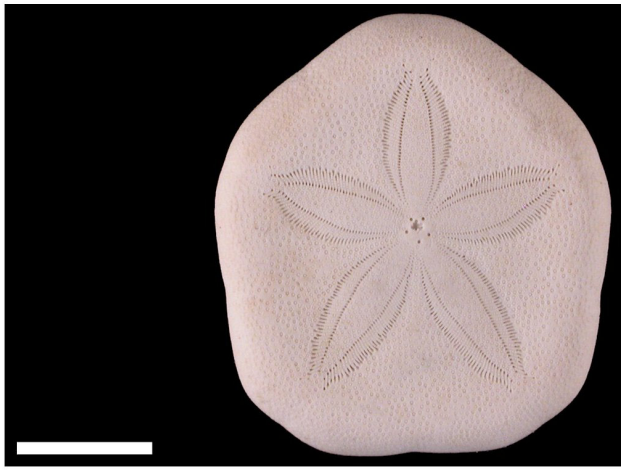


Fig. 17b: NHMW-Geo 2011/0346/0004
Laganum laganum, aboral view

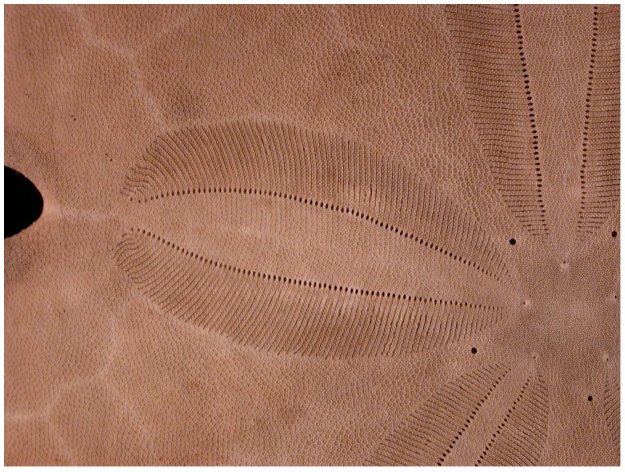


Fig. 16c: NHMW-Zoo12487-2
Encope emarginata, petal IV

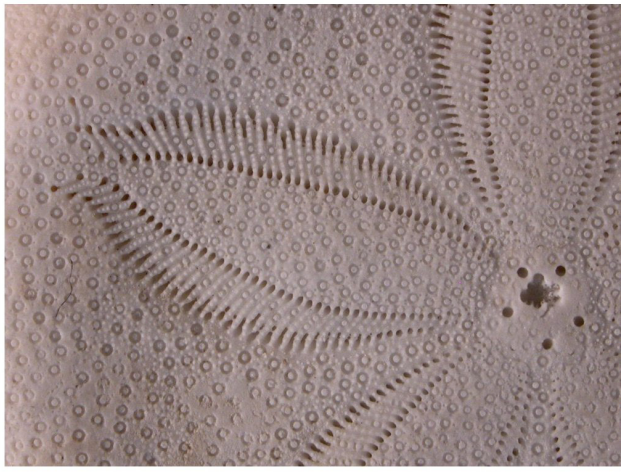


Fig. 17c: NHMW-Geo 2011/0346/0004
Laganum laganum, petal IV

scale bar equals 1 cm

Fig. 18a: NHMW-Geo 2011/0361/0001
Peronella lesueuri, oral view

Fig. 18b: NHMW-Geo 2011/0361/0001
Peronella lesueuri, aboral view

Fig. 18c: NHMW-Geo 2011/0361/0001
Peronella lesueuri, petal IV

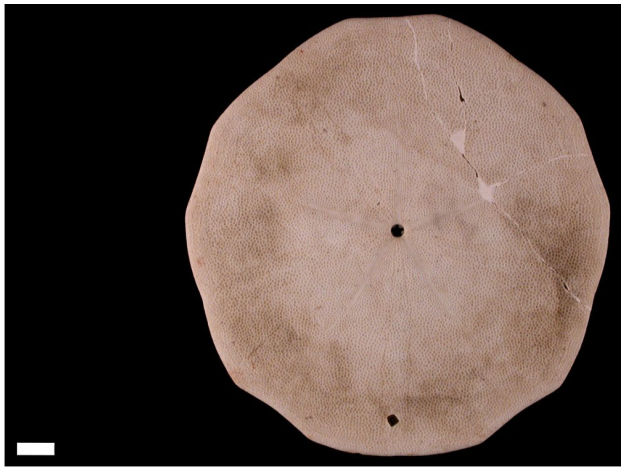


Fig. 19a: NHMW-Geo 2011/0335/0002
Peronella lesueuri rostrata, oral view

Fig. 19b: NHMW-Geo 2011/0335/0002
Peronella lesueuri rostrata, aboral view

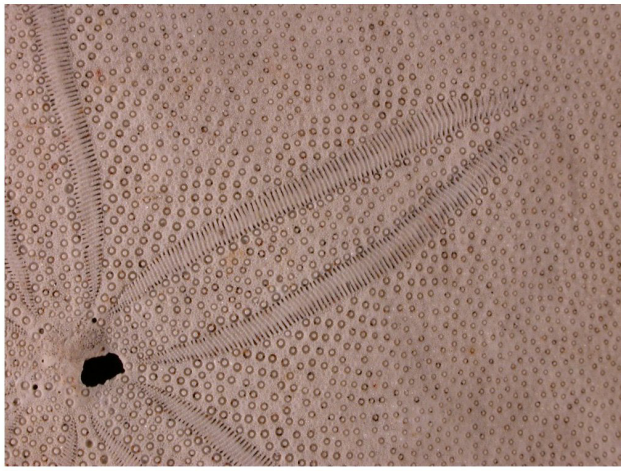


Fig. 19c: NHMW-Geo 2011/0335/0002
Peronella lesueuri rostrata, petal II

scale bar equals 1 cm

Landmarks are placed in a computer program and objects need to be digitized beforehand. Data can be two- or threedimensional. Twodimensional data collection usually is simple, quick and cheap (e.g. x-rays, cameras or scanners), but often needs to be treated with caution. In this study, images were taken of the clypeasteroids. Methods of three-dimensional data aquisition (e.g. Microscribe, 3D-scanners, CT) are more expensive and time consuming. They were not considered for this work.
A landmark has to be a homologous anatomical locus that can be recognized on each specimen in the study. The set of landmarks should be selected to offer an adequate summary of overall morphology (WEBSTER & SHEETS 2010). Sliding landmarks, also called semilandmarks, are used for areas, where landmarks are required but homologous points are hard to find, for example outlines. They are allowed to slide along the curve until the shape difference between individuals is minimized (MITTERÖCKER & GUNZ 2009). To make the computation tractable, the semilandmarks slide on tangent lines to the respective curve, instead of the complex curve itself (GUNZ & MITTERÖCKER 2013).

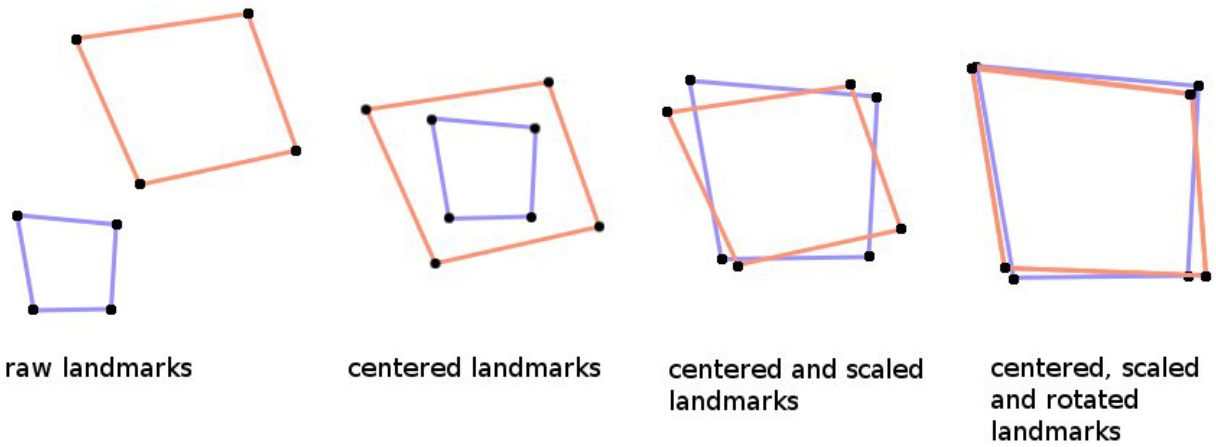


Fig. 20: Three steps of Procrustes Superimposition. Modified from MITTERÖCKER & GUNZ 2009.

Procrustes Superimposition converts the raw landmark coordinates into shape coordinates by standardizing position, scale and orientation of the landmark configurations (GUNZ & MITTERÖCKER 2013). In Fig. 20 the red figure and the blue figure represent two individuals with four landmarks each. The first image shows the raw landmarks. In the first step, the position of the centroid of each figure, which is the arithmetic mean of all landmark coordinates, is calculated. The figures are then shifted, so their centroids come to lay in one place (image two). Next is the scaling step. Centroid size is calculated. It is the square

root of the sum of squared distances between every landmark and the centroid. Figures are scaled so all have a centroid size of one (image three). In the third step, figures are rotated around their centroids until the sum of squared distances between corresponding landmarks of the different shapes becomes a minimum (image four).

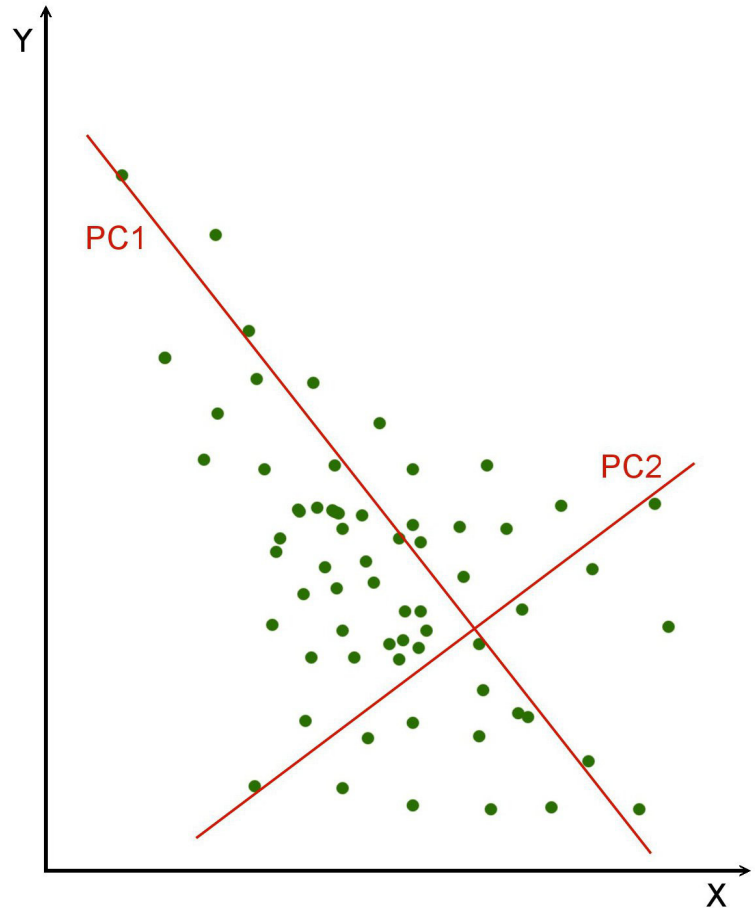


Fig. 21: Simplified visualisation of the computation of Principal Components (PC). Twodimensional data space with characters X and Y, PC1 and PC2.

After the Procrustes Superimposition every individual is represented by a point in a multidimensional space, the number of dimensions corresponding to the number of recognized character traits. Now the Principal Components (PC) are calculated. An axis is placed through the point cloud along the direction of greatest variance. The second axis is positioned at a right angle to the first axis and again along the direction of greatest possible variance. This step is repeated for all dimensions of the data space, although it is not possible to visualize the process in more than three dimensions. It is visualized for two dimensions in Fig. 21. In the scree plot (Tab. 4) the PCs are listed according to the amount of variance they explain. Usually the first three to four PCs explain over 90% of total variance. This way, a multidimensional data space can be reduced to three or four relevant

dimensions. The PCs can be plottet against each other. Any position in the morphospace created by two PCs can then be viewed as a thin plate spline.

Images were taken of all specimens using a compact camera. Beforehand, the camera was tested for barrel and pincushion distortion, which was found to be minimal.
Sand dollars are usually flat, but it is still crucial to make sure all images are taken from the same angle. Some species like *C. rosaceus* are more bulged, which leads to a distortion in the marginal areas because the three-dimensional surface is flattened by projection (Fig. 22).
Additionally, the length of the specimens was measured using a digital sliding caliper.

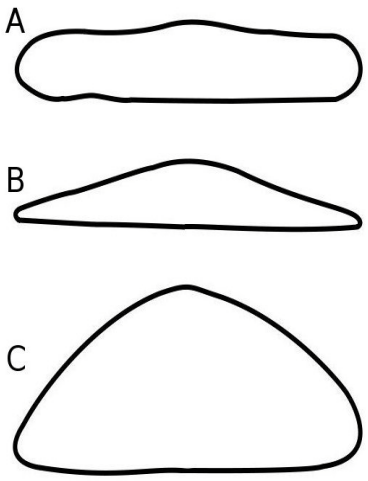


Fig. 22: Profile of A) *Laganum laganum*, B) *Echinarachnius parma* and C) *Clypeaster rosaceus*. Drawings not to scale.

A total of 205 landmarks were placed, 180 of which are sliding landmarks (Fig. 23).

landmarks:		sliding landmarks:	
1	centre	2-21	innermost semilandmarks
22-41	tips of petals	42-69	petal IV
202-205	gonopores	70-97	petal III
		98-125	petal II
		126-153	petal I
		154-181	petal V
		182-201	outline

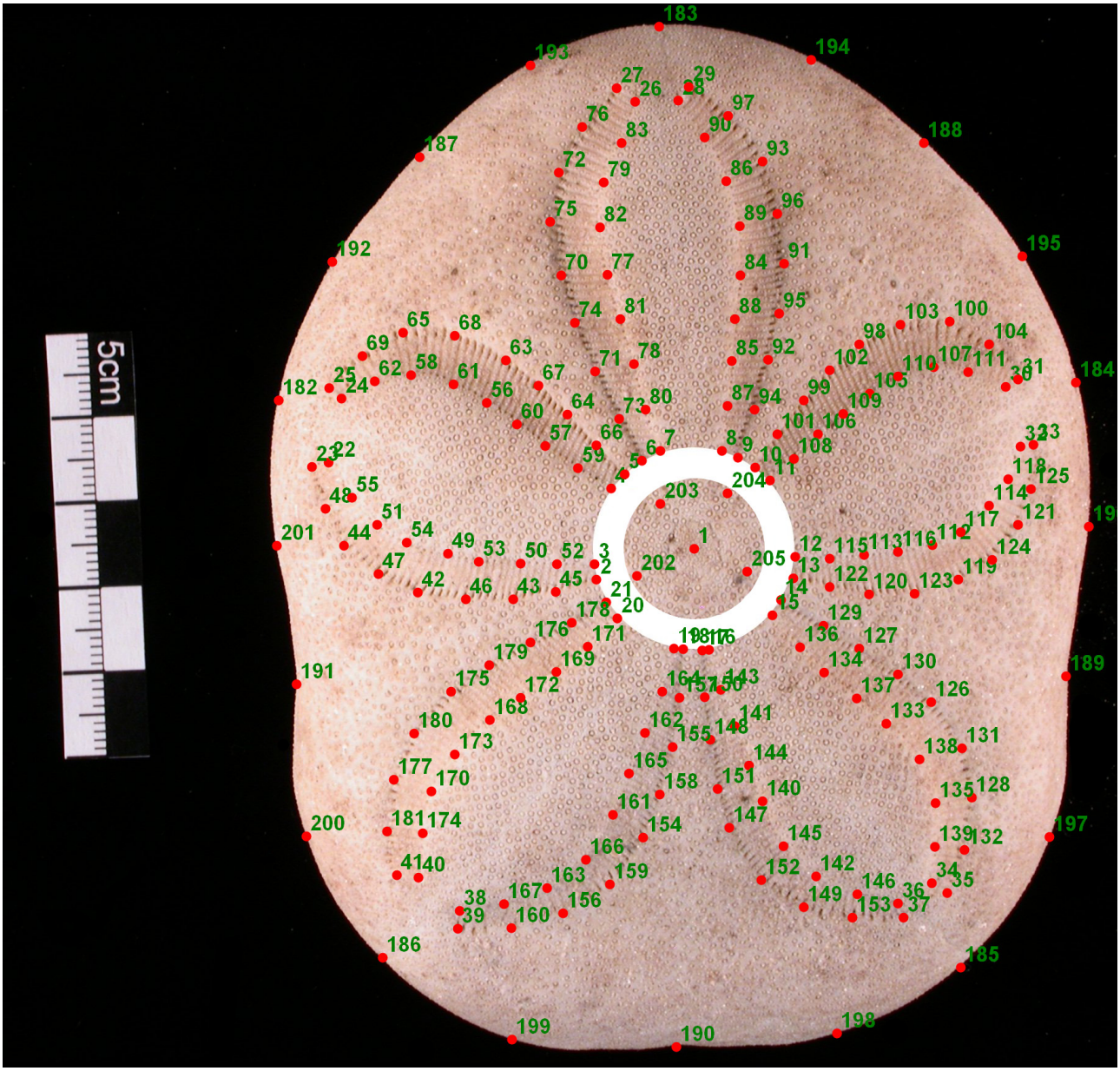


Fig. 23: Position of landmarks before sliding.

Morphological features of clypeasteroids considered in this study include general outline, size and shape of petals in relation to size and shape of the test. Several pre-analyses were made in the process of finding the right position and number of landmarks. The method was intended to be simple and applicable to many specimens in short time. Although only recent species are considered in this study, chosen characters are recognizable on well-preserved fossils too. Plate boundaries are often difficult to see and their analysis is time consuming. For these reasons they were not considered in the present study. Morphological features of clypeasteroids considered in this study include general outline and size and shape of petals in relation to size and shape of the test.

The plan of doing a separate outline analysis (Fourier) or additional measurements of the oral side were abandoned as well. The outline found consideration in the main analysis by placing 20 sliding landmarks along the margin. The oral side was left aside as a whole.
GM methods require all specimens to have the same number of landmark and semilandmark coordinates. Poorly or partially preserved specimens are a big methodological challenge. One can either restrict the analysis to the subset of landmarks and semilandmarks available on all specimens, or estimate the missing data (GUNZ & MITTERÖCKER 2013). I measured the length of petal IV and placed a circle with a diameter of half that length over the center of each specimen. Semilandmarks were not placed inside this circle. This measure was taken, because some specimens have damaged centers and in some species the adapical part of the petals is not clearly visible on the photograph. With the available equipment it was not possible to take images of the whole test in a quality good enough to allow the smallest pores to be seen. On the image showing the detail of the fourth petal it is possible to follow the pore rows all the way to their adapical end in most species, but that would have meant to restrict the whole analysis to that particular petal. Restricting analysis to petal IV would have led to different results, since the position and size of the petals in relation to the outline would have been lost. Moreover, one of the benefits of any GM analysis lies in the presentation of the results. Landmarks can be connected with lines for better recognition. By using the whole test, when looking at the thin plate splines, main features are recognized intuitively.
The central landmark 1 is important because the innermost semilandmarks are sliding between landmark 1 and the second-to-innermost semilandmarks. Treating the innermost semilandmarks (2-21) as landmarks would lead to an artifact.
The four landmarks on the gonopores (202-205) prevent the innermost semilandmarks from sliding too far towards the center. In a pre-analysis without these four landmarks, the semilandmarks of the petals of some species slid too far, causing an artifact that was so strong, it even dominated PC1.
On first sight the pores seem to be ideal places for landmarks. However, not all Clypeasterids have the same number of pores, it is not even constant within species. Finding biologically homologous pores, as is neccessary for landmarks, would require plate counting. Therefore I decided to place landmarks only on the outermost pore of every row and place a constant amount of semilandmarks along the row. Strictly speaking, the outermost pores are not homologous points either, but every line of semilandmarks needs at least two landmarks at its ends; in between the semilandmarks are allowed to slide.

Landmarks were placed in TPS Dig2. TPS is a free sofware series by F. James Rohlf and can be downloaded at http://life.bio.sunysb.edu/ee/rohlf/software.html (GUNZ & MITTERÖCKER 2012). Afterwards the links-file and the sliders-file were created using TPS Util. In the sliders-file semilandmarks and their tangents are defined. In the links-file, landmarks are connected with lines. These lines only serve better visualization and have no further meaning. The landmarks, the sliders and links are then loaded into TPS Relw. Procrustes Superimposition converts the raw landmark coordinates into shape coordinates by standardizing scale, position and orientation of the landmark configurations. To make the computation of the semilandmark sliding computationally tractable, the semilandmarks slide on tangent lines to the respective curve (GUNZ & MITTERÖCKER 2013).
TPS Relw produces a consensus, which is the intermediate of all individuals. It also computes the principal components and plots them against each other. Any position in the PC plots can be viewed as a thin plate spline of the mean.

4. Results

The first three Principal Components (PCs) explain 84.61% of total variance. PC4 adds another 4.73%. The consensus is the intermediate form of all specimens considered in the analysis. It lies at the origin of the coordinate system. Figures 25 to 32 show pairs of thin-plate splines. Each pair shows the variation along a particular PC. All thin plate splines are warped from the consensus (Fig. 24). Warps have not been exaggerated. For the PC plots in Figures 33 to 35 all species were color coded to indicate their systematic placement. Figure 35 was chosen because of the interesting three way distribution it displays, though PC2 and PC3 are accounted for in Figures 33 and 34, respectively. In Figure 33, *E. auritus* and *P. lesueuri rostrata*, *E. emarginata* and *C. humilis, C. humilis* and *C. reticulatus* and *A. placenta* and *A. tenuis* are overlapping. But they are well separated by PC1 and PC3 (Fig. 34). In fact, only two species overlap in Fig. 34, which are *E. emarginata* and *A. tenuis*. Although PC2 explains a higher percentage of variation than PC3 (Tab. 4), PC3 in combination with PC1 serves well for separating species. In all three PC-plots one specimen is very close to 0/0, that is *E. parma* no. 63. When comparing it to the consensus, they are very much alike, though the apical ends of the pore rows are a bit more closed in this specimen. The area covered by *A. placenta* is unusually big while those of *L. laganum* and *P. lesueuri* are very small. *P. lesueuri rostrata* does not overlap or group with P*. lesueuri* in Figures 33 or 34. Only in Figure 35 they are close, but this occurs to most species. In Figure 35 the area covered by *A. placenta* is nearly as big as the area within which all of the other species minus *D. excentricus* are clustering. Additionally, the Arachnoididae are clearly separated from the cluster. *D. excentricus* is far off, too. Although *Dendraster* dominates PC3 it is well separated from the rest by PC1 and PC2 as well.

PC	% expl.	cum. %
1	45.66	45.66
2	24.22	69.87
3	14.74	84.61
4	4.73	89.34

Tab. 4: Percentage of variance explained by Principal Components.

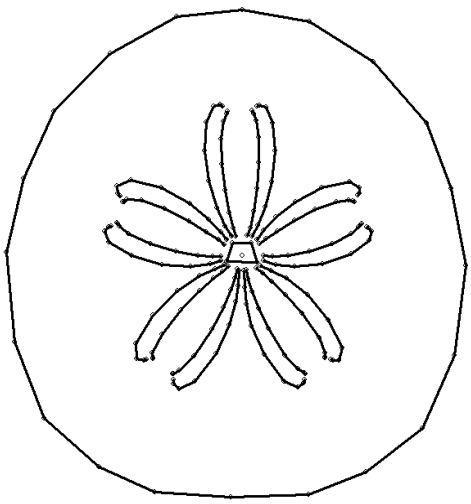


Fig. 24: Consensus resulting from GM analysis of of 68 specimens.

Main features of the first four PCs are as follows:

PC1 (Fig. 25, Fig. 26, Fig. 33, Fig. 34)
The two species showing the most extreme values along PC1 are *E. bisperforatus* and *C. rosaceus*. The Astriclypeidae group together below the consensus, the Clypeasteridae above the consensus. *C. humilis* and *C.reticulatus* overlap with *D. excentricus*. The Arachnoididae, *E. parma* and *E. emarginata* lie close to the consensus, the Laganiformes scatter loosely around it. The main characteristic of PC1 is the size of the petals in relation to test size. On Fig. 26 the petals almost touch the margin. The distances between the gonopores (the small, four-sided figure in the center) do not change. The outline of Figure 26 is oblong and the position of greatest width lies in front of the madreporic plate. Figure 25 is more rounded with the position of greatest width being posterior to the madreporic plate.

PC2 (Fig. 27, Fig. 28, Fig. 33, Fig. 35)
The extreme ends of PC2 are occupied by *A. placenta* and *E. emarginata*. *A. tenuis* overlaps with *A. placenta*. *D. excentricus* lies halfway between these two and the consensus. Almost all of the other species are located above the consensus.
Main characteristic of PC2 is the transition from open, straight petals to closed, curved petals. The area enclosed by the gonopores is smaller in Figure 27. Also the madreporic plate is shifted slightly towards the posterior. Test width is larger than test length.

PC3 (Fig. 29, Fig. 30, Fig. 34, Fig. 35)
PC3 is dominated by *D. excentricus*. The main feature is the position of the madreporic plate in relation to outline and the apical ends of the petals. In Figure 29 petal I and petal V are short, while they are longer than the others in Figure 30. Petals are closed on the dendrasterid side, the gonopores are wider apart. In Figure 34 *D. excentricus* stands alone, while all other species group together. Of the bulk opposing *D. excentricus, E. bisperforatus* is closest to it, while *A. placenta* lies on the other side.

PC4 (Fig. 31, Fig. 32)
PC4 shows an interesting variation, though it is of little significance (explaining only 4.73% of total variation). It is the transition from straight, slender pore rows to broad and heavily curved ones. Also the madreporic plate is smaller in Fig. 31.

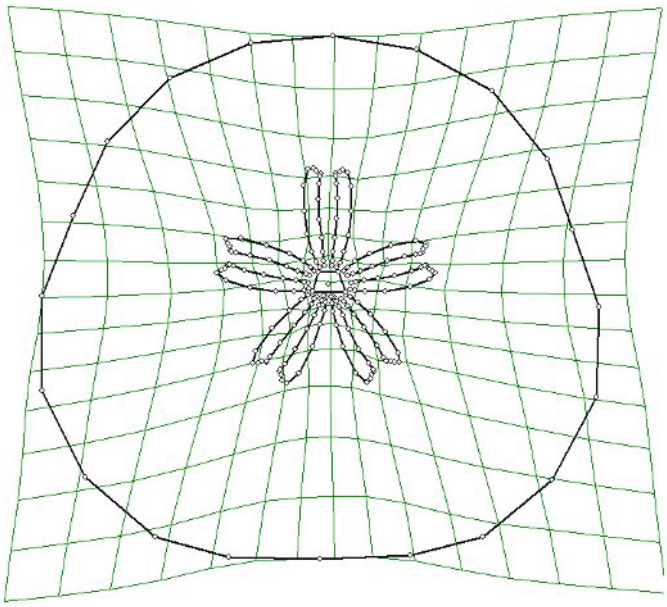


Fig. 25: Variation along PC1 (-0,2349).

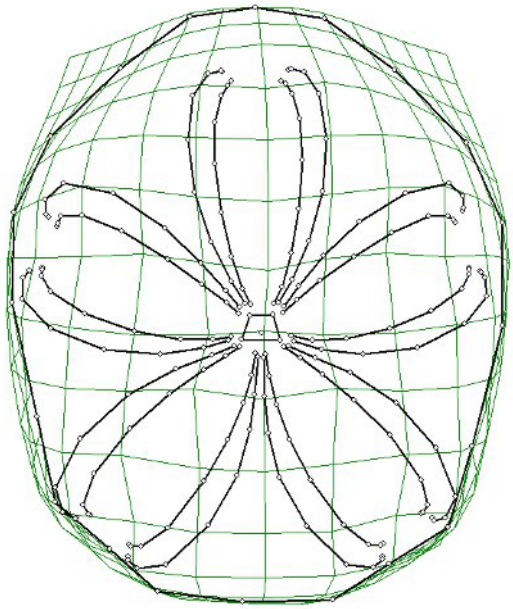


Fig. 26: Variation along PC1 (0,2280).

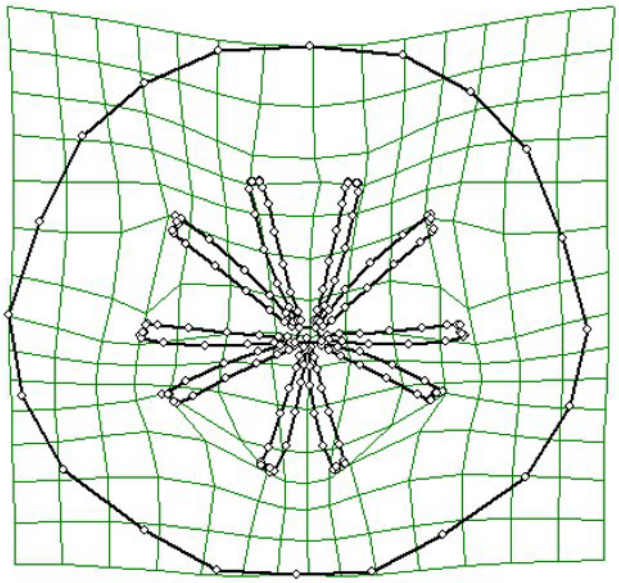


Fig. 27: Variation along PC2 (-0,1930).

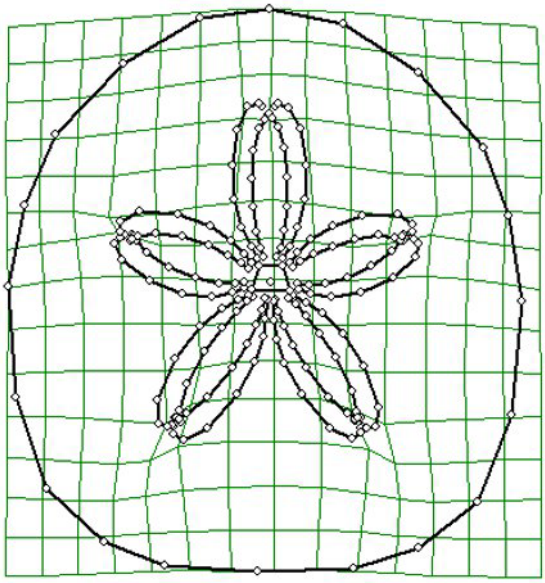


Fig. 28: Variation along PC2 (0,0802).

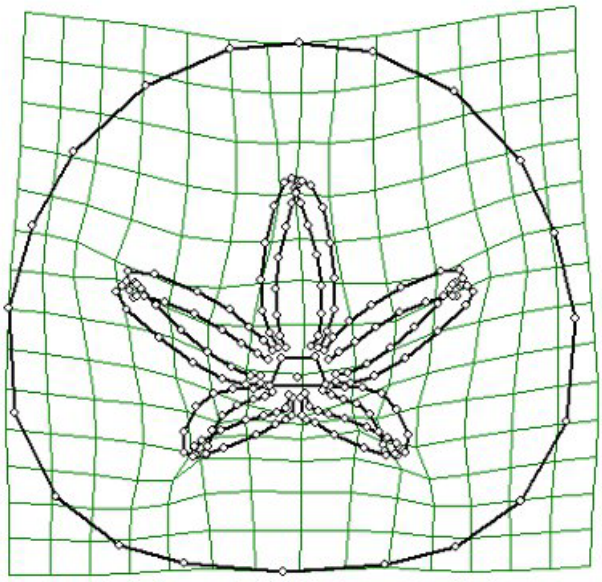


Fig. 29: Variation along PC3 (-0,2015).

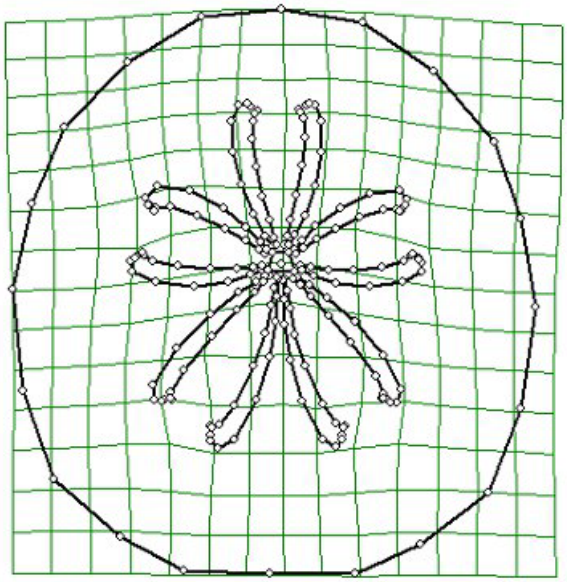


Fig. 30: Variation along PC3 (0,0887).

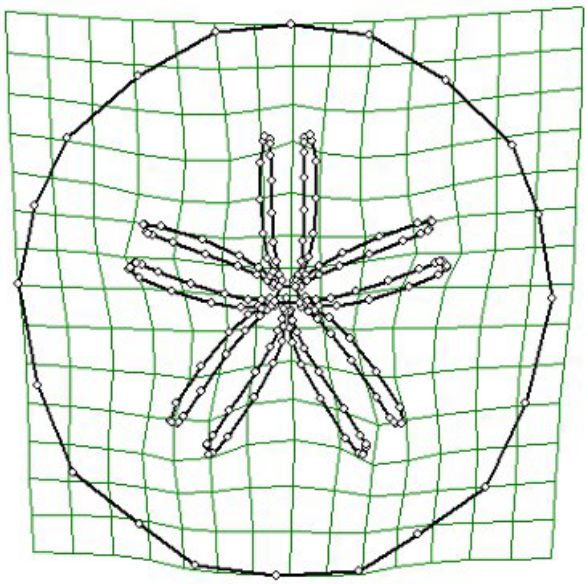


Fig. 31: Variation along PC4 (-0,0772).

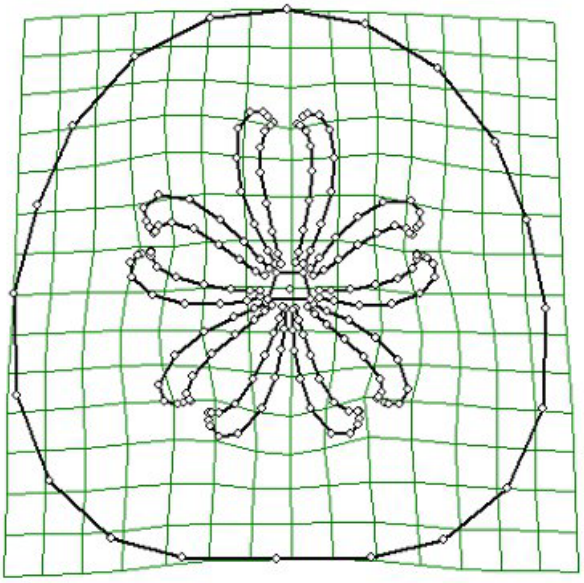


Fig. 32: Variation along PC4 (0,0545).

Fig. 33: Plot of PC1/PC2.

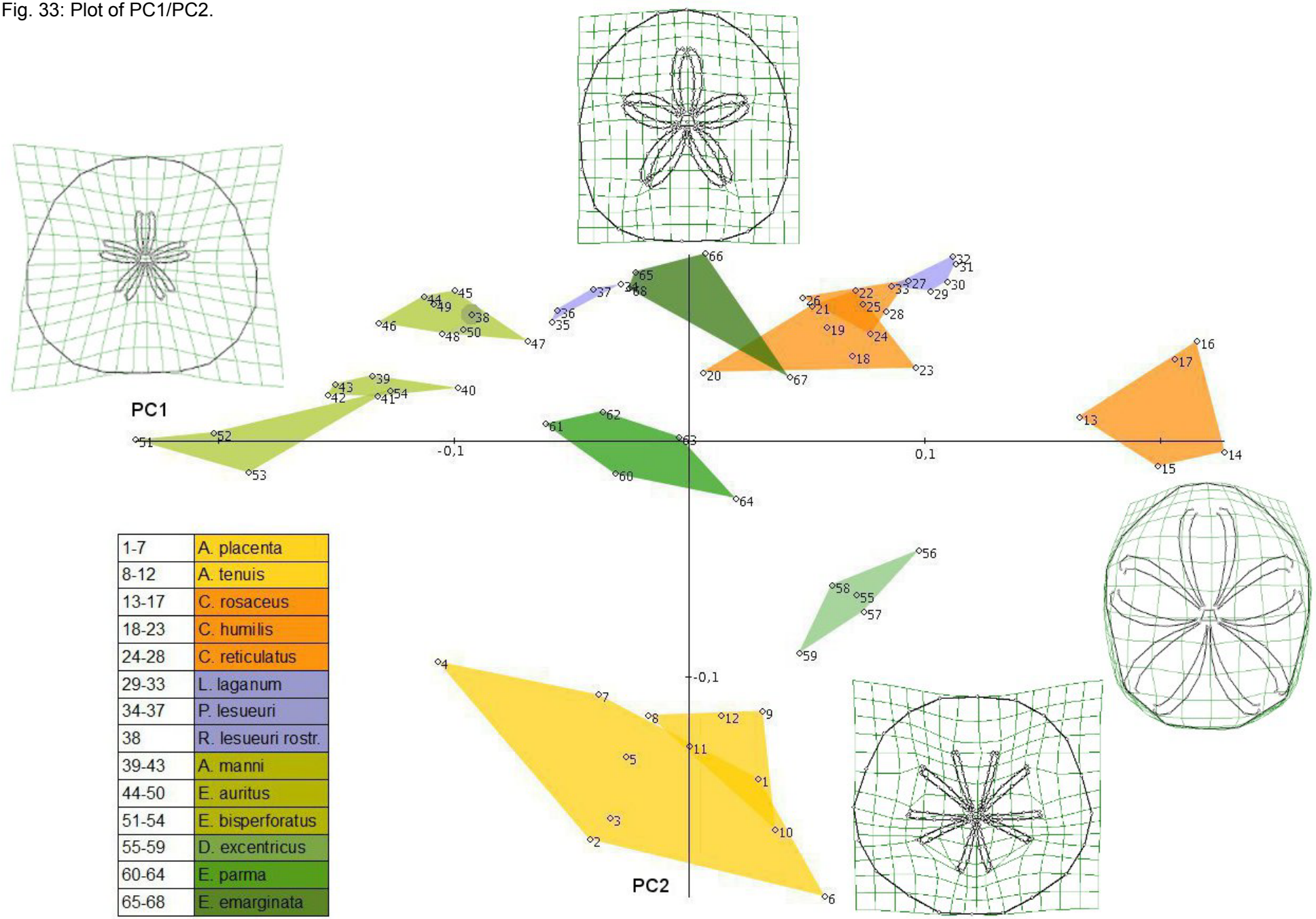
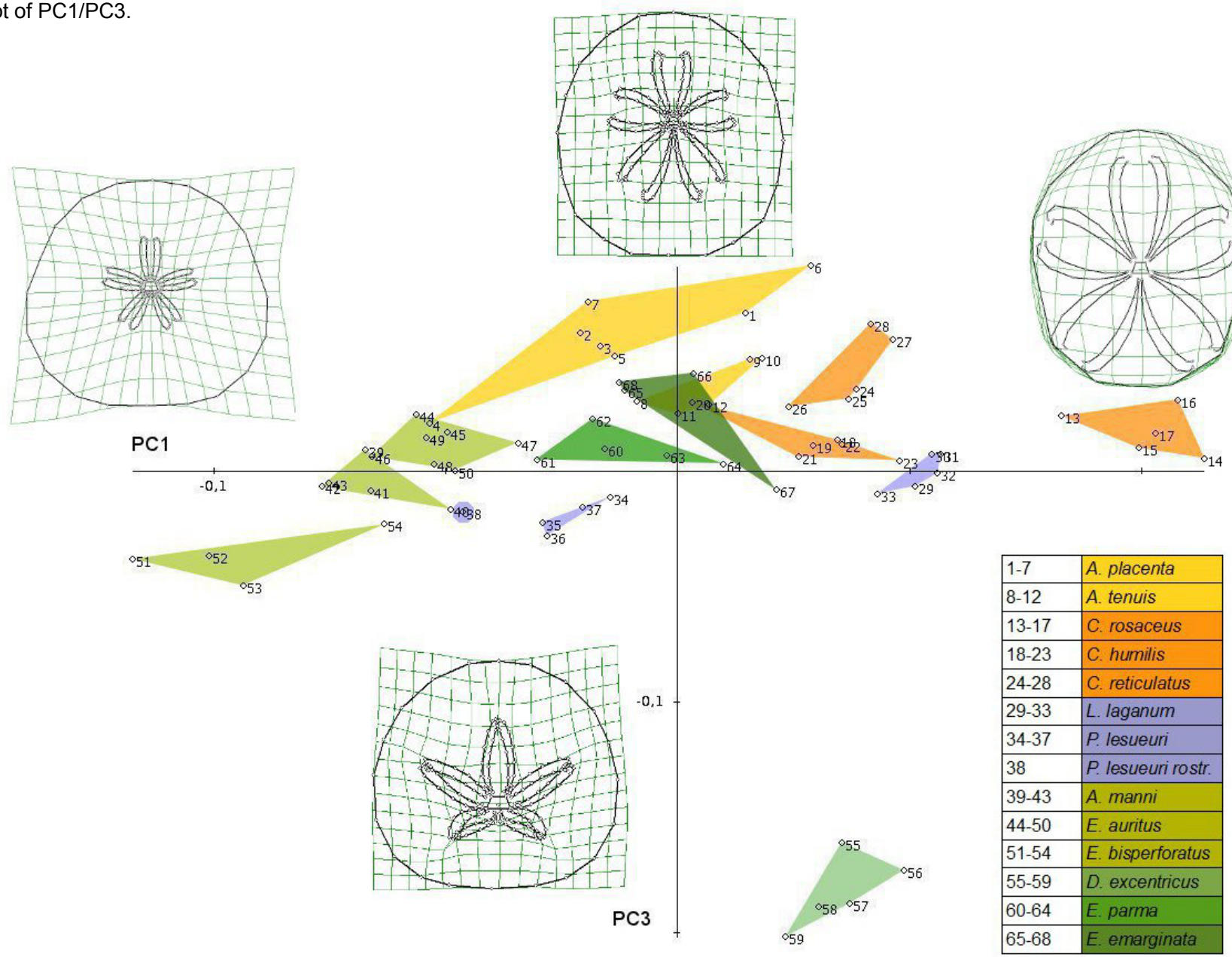
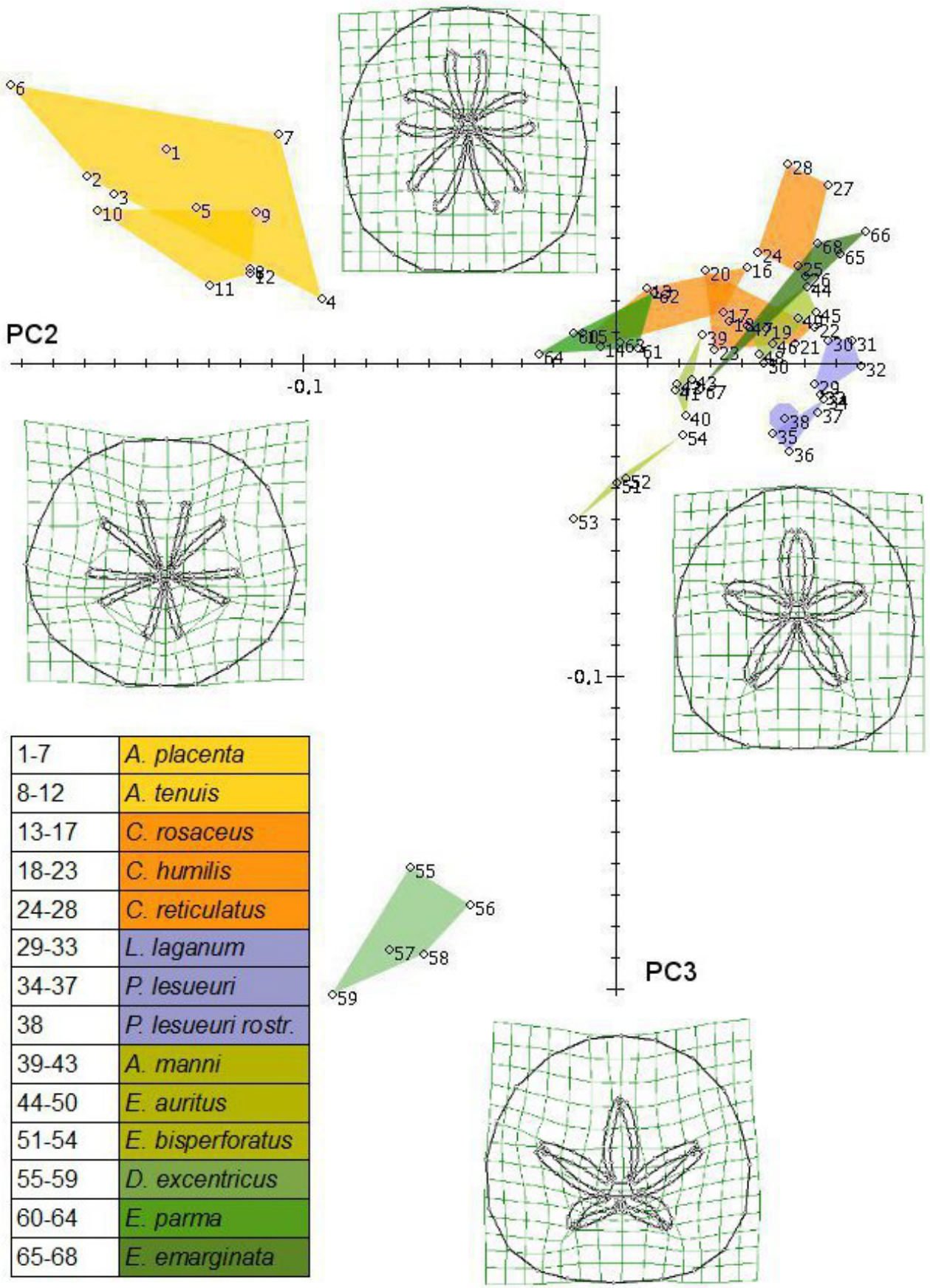


Fig. 34: Plot of PC1/PC3.





1-7	*A. placenta*
8-12	*A. tenuis*
13-17	*C. rosaceus*
18-23	*C. humilis*
24-28	*C. reticulatus*
29-33	*L. laganum*
34-37	*P. lesueuri*
38	*P. lesueuri rostr.*
39-43	*A. manni*
44-50	*E. auritus*
51-54	*E. bisperforatus*
55-59	*D. excentricus*
60-64	*E. parma*
65-68	*E. emarginata*

Fig. 35: Plot of PC2/PC3.

5. Discussion

Clypeasteroids are well suited for GM in some aspects, but not all. If data is acquired in two-dimensional form, homologous points for landmarks should be at the same level of height. Most Clypeasteroids more or less meet these requirements. In this sample, only *C. rosaceus* is an exception. On Figure 33 *C. reticulatus* and *C humilis* are overlapping, but *C. rosaceus* ist further off, though the three groups are closely related. Images are taken straight from above, leading to distortion of three-dimensional objects. The fact that the petals of *C. rosaceus* are larger than those of *C. humilis* and *C. reticulatus* is increased by its bulged dorsal surface. Nevertheless two-dimensional data acquisition was chosen because the few drawbacks of the method are made up for by its simplicity and effectiveness.

All landmarks have to be present on all specimens, which is why lunules found no consideration. For the same reason the fifth gonopore was excluded.

Landmarks should be biologically homologous points. Echinoids have plenty, but finding them is often time consuming. Structures like the petals and outline, however, are readily visible and can easily be traced. This is why only few landmarks (25) and many semilandmarks (180) were placed.

In one aspect, Clypeasteroids are especially well suited for GM: since their outline is approximately circular, there is no distance between any two landmarks that spans an area that is not part of the organism. In fish, for example, the line between the landmark on the tip of the dorsal fin and the upper tip of the caudal fin lies outside the specimens outline. Since the program does not differ between specimen and background, deformation for areas outside the outline is calculated the same way as would be for areas within the specimen.

Individuals of one species group together quite nicely and also higher order relationships are recognizable. Within a group of closely related species it would probably be possible to assign an unknown individual to one of them.

GM data is not suited for making a phylogeny. But an existing one can be supported. GM produces continuous data, which needs to be transformed since a phylogenetic analysis requires discrete values. Transformation is always affected by personal interpretation. For recommendations on how this can be done see SCHOLS et al. (2004). In Figures 33 to 35 species were given a color code. The Clypeasterina are yellow or orange, the Laganina are blue and the Scutellina were given various shades of green.

In Figure 34, the plot of PC1 and PC3, higher order relationship is visible best. Respective colors group together (*Dendraster* being left aside) and except for *E. emarginata* and *A. tenuis* there is no overlap.

D. excentricus is exceptional due to the eccentricity of its madreporic plate, which strongly affects the shape of the petalodium. PC3 is dominated by that character. *Dendraster* emerged in the lower Pliocene (RAUP 1956). In time it became more and more eccentric. In the PC-plots the fossil forms would be likely to show up between the recent *D.excentricus* and the 'normal' forms. *D. excentricus* lives as a suspension feeder in an inclined position with the anterior end of its test dug into the sand, so that the shifted madreporic plate is not covered so easily (TIMKO 1976).

Different PCs serve for separating different groups. *C. rosaceus* for example is clearly separated from *C. humilis* and *C. reticulatus* by PC1 alone, representing petal size in relation to test size (Fig. 33, Fig. 34). For separating *A. tenuis* and *A. placenta* both PC1 and PC3 are necessary (Fig. 34). The petals of *A. placenta* are more open and the madreporic plate is slightly shifted to the anterior, also petals are slightly smaller. The Laganidae differ much along PC1 but only slightly along PC2 and PC3.

P. lesueuri rostrata is a single specimen which is not determined with certainty. It could be *P. lesueuri* as well. Along PC2 and PC3, this specimen groups with *P. lesueuri*, but they are clearly separated by PC1. The results indicate that this specimen does indeed belong to a different taxon.

In Figures 33 to 35 the area covered by *A. placenta* strikes the eye. The size of the polygon indicates high within-species variance. But it is also influenced by the number of specimens: the more specimens, the larger the polygon. Especially when numbers are very small, as is the case in this study, one or two specimens can make a huge difference. *A. placenta* is represented by seven specimens, *E. auritus* by seven, *C. humilis by six*, all of the others by four or five, except for *P. lesueuri rostrata*, which is present with a single individual. By dividing the standard deviation of every species by its mean, within-species size variability can be compared (Table 5). Size variation is especially high in *A. placenta, C. humilis, E. auritus, E. bisperforatus* and *E. parma*. Moreover the specimens of some species come from multiple collections, while others were collected at one time in one place. Specimens of *A. tenuis, C. humilis, C. reticulatus, E. auritus* and *E. bisperforatus* come from multiple localities.

Table 5 shows that not only *A. placenta* but also *C. humilis* and *E. auritus* have elevated values in all three categories.

species	no. of indiv.	stdev./mean	no. of loc.
Arachnoides placenta	7	0.29	4
Arachnoides tenuis	5	0.04	1
Clypeaster rosaceus	5	0.07	1
Clypeaster humilis	6	0.60	2
Clypeaster reticulatus	5	0.17	5
Laganum laganum	5	0.10	1
Peronella lesueuri	4	0.08	1
Peronella lesueuri rostrata	1	-	1
Astriclypeus manni	5	0.06	1
Echinodiscus auritus	7	0.21	3
Echinodiscus bisperforatus	4	0.29	3
Dendraster excentricus	5	0.14	1
Echinarachnius parma	5	0.26	1
Encope emarginata	4	0.09	1

Tab. 5: Characters that might increase within-species variability.

Unlike in phylogenetic analysis, in GM characters are not chosen beforehand. Landmarks are placed all over the specimen, covering as many characters as possible. Relevant characters are filtered from the mass of data by a program, not a person. Afterwards the PCs can be checked for characters that serve well for a particular purpose, for example assigning a specimen to a certain group.

Observed within-species variation throws up further questions. In this study very few specimens have been analyzed. Nevertheless it is unlikely that that observed variation is entirely the result of unequal availability of material, because variance expected from values in Table 5 does not correspond with observed variance.

Although only recent species are treated in this study, the method is suited for fossils, too. Most species are morphospecies. Assignment to a group is based on morphology. The study of within-species variation of well-determined species can help with recent and fossil species determination.

6. Conclusio

The method used in this study is simple, efficient and cheap. Although only recent species are considered in this study, it applies to fossils, too. Placing the landmarks takes ten to fifteen minutes per specimen, allowing for larger numbers to be analysed.
In the Principal Component Analysis characters are computed and listed in order of importance. The first three Principal Components (PCs) explain 84.6% of total variance in this study. PC1 (45.66%) is the size of the petals in relation to test size, PC2 (24.22%) is the shape of the petals (being open or closed) and PC3 (14.74%) is the position of the madreporic plate in relation to the petals. All analyzed species are well separated by at least one of these PCs. Higher order relationship is visible, too. Just like individuals of the same species, species of the same familiy form clusters, although there is more overlap on the family level. Results support the currently accepted phylogeny of the clade, although *Dendraster*, whose morphology is strongly adapted to life as a filter feeder, is an outlier. Within-species variance is well visible on the PC-plots and can be quantified with shape coordinates. Individuals of some species form loose clusters, like *A. placenta*, while others, for example from the Laganidae, group closely. This signal could be caused by small sample size and unequal availability of material, but after looking at the number of localities, standard deviation of test size and number of individuals for every species, it seems unlikely. Clypesteroids are well suited for two-dimensional GM analysis. They are mostly flat, more or less circular and provide many structures on which few landmarks and many semilandmarks can be placed. The flat test allows for data to be acquired in a two-dimansional way, which is much cheaper and faster than three-dimensional methods like Computer Tomography or Microscribe. On a more or less circular object there is no line between any two points that could lie outside the objects outline. Space outside the specimens outline is warped the same way as the specimen itself, causing problems in objects with complex shape.

References

BEADLE, S. C. 1991. The Biogeography of Origin and Radiation: Dendrasterid Sand Dollars in the Northeastern Pacific. Paleobiology, 17(4): 325-339.

BEADLE, S. C. 1995. Retrodisplacement of the Oral and Anal Openings in Dendrasterid Sand Dollars. Ecolution, 49(6): 1203-1214.

COPPARD, S. E., CAMPBELL, A. C. 2006. Systematic significance of tridentate pedicellariae in the echinoid genera *Diadema* and *Echinothrix*. Invertebrate Biology, 125(4): 363-378.

DODD, J. R., ALEXANDER, R. R., STANTON, R. J. 1985. Population Dynamics in *Dendraster*, *Merriamaster*, and *Anadara* from the Neogene of the Kettleman Hills, California. Paleogeography, Paleoclimatology, Paleoecology, 52: 61-76.

GUNZ, P., MITTERÖCKER, P. 2012. Semilandmarks: A method for quantifying curves and surfaces. Hystix, the Italian Journal of Mammalogy, 24(1): 103-109.

KERSCHBAUMER, M., STURMBAUER, C. 2011. The Utility of Geometric Morphometrics to Elucidate Pathways of Cichlid Fish Evolution. International Journal of Evolutionary Biology, 2011: ID 290245, 8 p.

KROH, A., MOOI, R. 2011. World Echinoidea Database. Available online at http://www.marinespecies.org/echinoidea.

KROH, A., SMITH, A. B. 2010. The phylogeny and classification of post-Palaeozoic echinoids. Journal of Systematic Palaeontology, 8(2): 147–212.

MADERBACHER, M., BAUER, C., HERLER, J., POSTL, L., MAKASA, L., STURMBAUER, C. 2008. Assessment of traditional versus geometric morphometrics for discriminating populations of the *Tropheus moorii* species complex (Teleostei: Cichlidae), a Lake Tanganyika model for allopatric speciation. Journal of Zoological Systematics and Evolutionary Research, 46(2): 153–161.

MARSHALL, C., R. 1992. Character Analysis and the Integration of Molecular and Morphological Data in an Understanding of Sand Dollar Phylogeny. Molecular Biology and Evolution, 9(2): 309-322.

MIHALJEVIC, M., JERJEN, I., SMITH, A. B. 2011. The test architecture of *Clypeaster* (Echinoidea, Clypeasteroida) and its phylogenetic significance. Zootaxa, 2983: 21–38.

MITTERÖCKER, P., GUNZ, P. 2009. Advances in Geometric Morphometrics. Journal of Evolutionary

Biology, 36: 235-247.

MITTERÖCKER, P., GUNZ, P., WINDHAGER, S., SCHÄFER, K. 2013. A brief review of shape, form and allometry in geometric morphometrics, with applications to human facial morphology. Hystix, the Italian Journal of Mammalogy, 24(1): 59-66.

MITTERÖCKER, P., HUTTEGGER, S. M. 2009. The Concept of Morphospaces in Evolutionary and Developmental Biology: Mathematics and Metaphors. Biological Theory, 4(1): 54-67.

MOOI, R. 1986. Non-respiratory podia of clypeasteroids (Echinodermata, Echinoides): I. Functional Anatomy. Zoomorphology, 106: 21-30.

MOOI, R. 1986. Non-respiratory podia of clypeasteroids (Echinodermata, Echinoides): II. Diversity. Zoomorphology, 106: 75-90.

MOOI, R. 1990. Paedomorphosis, Aristotle's Lantern, and the Origin of the Sand Dollars (Echinodermata:Clypeasteroida). Paleobiology, 16(1): 25-48.

MOOI, R. 1997. Sand Dollars of the Genus *Dendraster* (Echinoidea: Clypeasteroidea): Phylogenetic Systematics, Heterochrony, and Distribution of extant Species. Bulletin of Marine Science, 61(2): 343-375.

MOOI, R. 1989. Living and Fossil genera of the Clypeasteroida (Echinoidea, Echinodermata). Smithsonian contributions to Zoology, 488.

MOOI, R., BRESLIN, C. M. 2007. Multiple origins of respiratory structures in sea urchins. Integrative and Comparative Biology, 47(1): e210.

NAKAMURA, R. K. 1995. Morphological variation in the Pacific sand dollar *Dendraster excentricus*. Canadian Journal of Zoology, 73: 576-583.

RAUP, D. M. 1956. *Dendraster*: a problem in echinoid taxonomy. Journal of Paleontology, 30: 685-694.

RAUP, D. M. 1958. The relation between water temperature and morphology in *Dendraster*. Journal of Geology, 66: 667-677.

SCHOLS, P., D'HONDT, C., GEUTEN, K., MERCKX, V., JANSSENS, S., SMETS, E. 2004. MorphoCode: coding quantitative data for phylogenetic analysis. PhyloInformatics, 4: 1-4.

SMITH, A. B. 1984. Echinoid Paleobiology. George Allen & Unwin, London, 190p.

SMITH, A. B. 1987. A Functional Classification of the Coronal Pores of Regular Echinoids. Paleontology, 21(4): 759-789.

SMITH, A. B. 1980. The Structure, Function, and Evolution of Tube Feet and Ambulacral Pores in Irregular Echinoids. Paleontology, 23(1): 39-83.

SMITH, A. B. 2001. Probing the cassiduloid origins of clypeasteroid echinoids using stratigraphically restricted parsimony analysis. Paleobiology, 27(2): 392–404.

SMITH, A. B., GHIOLD, 1982. Roles for Holes in Sand Dollars (Echinoidea): A Review of Lunule Function and Evolution. Paleobiology, 8(3): 242-253.

SMITH, A. B., KROH, A. (editor) 2011. The Echinoid Directory. World Wide Web electronic publication. http://www.nhm.ac.uk/research-curation/projects/echinoid-directory.

STANTON, R. J., DODD, J. R., ALEXANDER, R. R. 1979. Eccentricity in the clypeasteroid echinoid *Dendraster*: environmental significance and application in Pliocene paleoecology. Lethaia, 12: 75-87.

TELFORD, M., MOOI, R., HAROLD, A. S. 1987. Feeding Activities of two Species of *Clypeaster* (Echinoides, Clypeasteroida): Further Evidence of Clypeasteroid Resource Partitioning. Biological Bulletin, 172: 324-336.

Timko, P. L. 1976. Sand dollars as suspension-feeders: a new description of feeding in *Dendraster excentricus*. Biological Bulletin 151, 247-259.

WEBSTER, M., SHEETS, H. D. 2010. A practical Introduction to landmark-based Geometric Morphometrics. Quantitative Methods in Paleobiology, 163-188.

Summary

The complex skeleton of echinoids shows a close relationship between structure and function that makes this clade a textbook example for the analysis of functional morphology. Clypeasteroids (“sand dollars”) are a group of irregular echinoids with flat body shape, which live as detritus feeders on marine softground. Rapid expansion, geographical separation and occupation of similar niches in different regions have led to a certain amount of convergence among lineages. In this study I applied Geometric Morphometrics (GM), a method based on landmarks and semilandmarks, to photographs of 13 species (68 individuals) of clypeasteroids to test the currently accepted phylogeny of this clade. The main aim of my study was to identify characters that are appropriate to distinguish species. For this purpose 205 landmarks and semilandmarks were placed mostly on the petals and outline of the clypeasteroids. In a process called „Procrustes Superimposition“, shape was separated from position, size and orientation. The resulting Procrustes shape coordinates were used for statistical analysis.
Clypeasteroids are well suited for GM analysis. The test is flat with an approximatley circular outline and provides many structures to place landmarks and semilandmarks on. In the Principal Components Analysis (PCA) characters are computed and listed in order of the amount of variation they explain. These major characters are then applied to particular problems. All analyzed species are well separated by at least one of the first three Principal Components (PCs), which explain 84.6% of the variation in the data set and which are the size of the petals in relation to test size (PC1), the shape of the petals (PC2) and the position of the madreporic plate in relation to the petals (PC3). Also higher order relationship is recognizable. Just the way individuals of one species cluster, species of the same family group together, but overlap between families is more common than between species. The currently accepted phylogeny is supported by the analysis. Moreover it is possible to use GM to quantify within-species variance. The closer individuals group in the PC-plots, the higher is their similarity.

Zusammenfassung

Das komplexe Skelett von Echiniden weist eine enge Beziehung zwischen Struktur und Funktion auf, die diese Organismen zu einem Paradefall für funktionsmorphologische Untersuchungen macht. Clypeasteroiden (“sand dollars”) sind eine Gruppe flacher irregulärer Seeigel, die als Detritusfresser marine Weichböden besiedeln. Rasche Verbreitung, geografische Isolation und die Besiedelung ähnlicher Nischen in unterschiedlichen Regionen führten zu einem gewissen Maß an Konvergenz zwischen den Abstammungslinien. In dieser Studie habe ich geometrische Morphometrie (GM) an Fotografien von 13 Arten (68 Individuen) von Clypeasteroiden angewandt, um die derzeit anerkannte Phylogenie der Klade zu prüfen. GM ist eine auf Landmarken und Semilandmarken basierende Methode. Hauptziel meiner Studie war es, Merkmale aufzuzeigen, die sich dazu eignen, die untersuchten Arten zu unterscheiden. Zu diesem Zweck wurden 205 Landmarken und Semilandmarken hauptsächlich auf die Petalodien und den Umriss der Clypeasteroiden gesetzt. Während eines Prozesses, der sich 'Procrustes Superimposition' nennt, wird die Form von Position, Größe und Orientierung “befreit”. Die resultierenden Procrustes-Formkoordinaten werden für die statistische Analyse verwendet.
Clypeasteroiden eignen sich gut für Analysen der geometrischen Morphometrie. Ihr Skelett ist flach und von mehr oder weniger kreisförmigem Umriss, verfügt aber gleichzeitig über eine Vielzahl an Strukturen, an denen Landmarken und Semilandmarken gesetzt werden können. In der Hauptkomponentenanalyse (Principal Components Analysis, PCA) werden Merkmale berechnet und nach dem Prozentsatz der von ihnen erklärten Variabilität gereiht. Diese Hauptmerkmale werden denn auf bestimmte Probleme angewandt. Alle analysierten Arten sind durch mindestens eine der ersten drei Hauptkomponenten (Principal Components, PCs) klar abgegerenzt. Diese sind das Verhältnis der Petalodienlänge zur Skelettgröße (PC1), die Form der Petalodien (PC2) und die Lage der Madreporenplatte im Verhältnis zu den Petalodien (PC3). Zusammen erklären sie 84.6% der beobachteten Variabilität. Auch Verwandtschaftsverhältnisse höherer Ordnung sind zu erkennen. Ähnlich den Individuen einer Art gruppieren auch die Arten einer Familie, aber Familien überlappen stärker als Arten. Die derzeitig anerkannte Phylogenie wird durch die Analyse unterstützt. Außerdem ist es möglich, geometrische Morphometrie zur Quanitifizierung innerartlicher Varianz zu verwenden. Je näher Individuen einer Gruppe in den Hauptkomponentendiagrammen beieinanderliegen, desto ähnlicher sind sie einander.

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