

Phylogeny, ancestral ranges and reclassification of sand dollars

Hsin Lee^{1,2,3+}, Kwen-Shen Lee^{4,+}, Chia-Hsin Hsu², Chen-Wei Lee², Ching-En Li², Jia-Kang Wang², Chien-Chia Tseng², Wei-Jen Chen³, Ching-Chang Horng², Colby T. Ford^{5,6,7,8}, Andreas Kroh⁹, Omri Bronstein^{10,11}, Hayate Tanaka¹², Tatsuo Oji¹³, Jih-Pai Lin^{2,*}, Daniel Janies^{7,8}

¹National Museum of Marine Biology and Aquarium, Pingtung, 944401, Taiwan

²Department of Geosciences, National Taiwan University, Taipei, 10617, Taiwan

³Institute of Oceanography, National Taiwan University, Taipei, 10617, Taiwan

⁴Biology Department, National Museum of Natural Science, Taichung, 40453, Taiwan

⁵Tuple LLC, 2413 Commonwealth Ave, Charlotte, North Carolina, 28205, USA

⁶School of Data Science, University of North Carolina at Charlotte, 9201 University City Blvd, Charlotte, North Carolina, 28223 USA

⁷Department of Bioinformatics and Genomics, University of North Carolina at Charlotte, 9201 University City Blvd, Charlotte, North Carolina, 28223 USA

⁸Center for Computational Intelligence to Predict Health and Environmental Risks (CIPHER), University of North Carolina at Charlotte, 9201 University City Blvd, Charlotte, North Carolina, 28223 USA

⁹Department of Geology and Palaeontology, Natural History Museum Vienna, Vienna, 1010, Austria

¹⁰School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, 6997801, Israel

¹¹Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, 6997801, Israel

¹²Department of Biological Sciences, Graduate School of Science, University of Tokyo, Tokyo, 113-0033, Japan

¹³University Museum, Nagoya University, Furo-cho, Nagoya, 464-8601, Japan

*Correspondence and requests for materials should be addressed to J.-P.L. (email: alexjplin@ntu.edu.tw; xyloplax1@gmail.com)

+These authors contributed equally to this work

Electronic Supplementary Material

Previous classifications of Clypeasteroida discussed

Mortensen 1948 (ref.¹)

Order Clypeasteroida

Suborder Clypeastrina

Family Clypeastridae

Family Arachnoididae

Suborder Laganina

Family Fibulariidae

Family Laganidae

Family Scutellidae

Durham 1955 (ref.²)

Order Clypeasteroida

Suborder Clypeasterina

Family Clypeasteridae

Family Arachnoididae

Suborder Laganina

Family Fibulariidae

Family Laganidae

†Family Neolaganidae

Suborder Scutellina

Family Scutellidae

†Family Protoscutellidae

†Family Eoscutellidae

Family Dendrasteridae

Family Echinarachniidae

†Family Monophorasteridae

Family Mellitidae

Family Astrictlypeidae

†Family Abertellidae

†Family Scutasteridae

Suborder Rotulina

Family Rotulidae

Wang 1984 (ref.³)

Order Clypeasteroida

Suborder Clypeasterina

Family Clypeasteridae

Family Arachnoididae

Suborder Scutellina

Infraorder Scutellidea

Family Scutellidae

Family Astrictlypeidae

Infraorder Laganidea

Superfamily Taiwanasteritida

Family Taiwansteridae

Family Fibulariidae

Superfamily Laganitida

Family Laganidae

†Family Neolaganidae

Superfamily Rotulitida

Family Rotulidae

Wang 1992 (ref.⁴)

Order Oligopygoida

†Family Oligopygidae

†Family Protolampadidae

Order Clypeasteroida

Suborder Lenitina

†Family Lenitidae

Suborder Laganina

Family Fibulariidae

†Family Sismondiidae

Family laganidae

†Family Neolaganidae

†Family Proescutellidae

†Family Tarphypygidae

Family Rotulidae

Suborder Clypeasterina

Family Clypeasteridae

Family Arachnoididae

†Family Fossulasteridae

Suborder Scutellina

†Family Eoscutidae

†Family Protoscutellidae

Family Scutellidae

Family Astrictlypeidae

Infraorder Kewiidea

- †Family Kewiidae
- Superfamily Dendrasteracea
 - Family Echinarachniidae
 - Family Dendrasteridae
 - Family Mellitidae
- Superfamily Eoscutellacea
 - †Family Eoscutellidae
 - †Family Abertellidae
 - †Family Monophorasteridae
 - †Family Scutasteridae

Schultz 2005 (ref.⁵)

Order Clypeasteroida

Suborder Clypeasterina

- Family Clypeasteridae
- Family Arachnoididae
- †Family Fossulasteridae
- †Family Scutellinoididae

Suborder Laganina

- Family Fibulariidae
- Family Laganidae
- †Family Neolaganidae
- Family Rotulidae

Suborder Scutellina

- †Family Scutellinidae
- †Family Protoscutellidae
- †Family Eoscutellidae
- †Family Scutellidae
- Family Echinarachniidae
- †Family Abertellidae
- Family Dendrasteridae
- †Family Scutasteridae
- Family Astrictypeidae
- †Family Monophorasteridae
- Family Mellitidae

Schultz 2017 (ref.⁶)

Clypeasteroida

Clypeasterina

Arachnoididae

Clypeasteridae

Scutellina

Scutelliformes

Taiwanasteridae

Echinarachniidae

Scutellidae

Echinarachniidae

Dendrasteridae

Astriclypeidae

Mellitidae

Laganiformes

Fibulariidae

Laganidae

Rotulidae

Kroh 2020 (ref.⁷)

Stem group Neognathostomata

†Family Clypeidae

†Family Nucleolitidae

Crown group Neognathostomata

Family Apatopygidae

†Family Pygaulidae

†Family Archiaciidae

†Family Clypeolampadidae

Order Clypeasteroida

Stem group Clypeasteroida

†Family Faujasiidae

†Family Plesiolampadidae

†Family Conoclypeidae

†Family Oligopygidae

Crown group Clypeasteroida

Family Clypeasteridae

†Family Fossulasterinae

Echinolampadacea

Order Cassiduloida

Suborder Cassidulina

Family Cassidulidae

Suborder Neolampadina

Family Neolampadidae

Order Echinolampadoida

Family Echinolampadidae

Order Scutelloida

Stem group Scutelloida

†Family Scutellinidae

Crown group Scutelloida

Infraorder Laganiformes

Family Fibulariidae

Family Laganidae

Infraorder Scutelliformes

Family Taiwanasteridae

Stem group Scutelliformes

†Family Protoscutellidae

Crown group Scutelliformes

Family Echinarachniidae

Family Dendrasteridae

Family Rotulidae

†Family Scutellidae

†Family Eoscutellidae

†Family Scutasteridae

†Family Abertellidae

Family Astrictlypeidae

†Family Monophorasteridae

Family Mellitidae

Mongiardino Koch et al. 2022 (ref.⁸)

Irregularia

Atelostomata

Holasteroidea

Spatangoida

Neognathostomata

Luminacea

Clypeasteroidea

Echinolampadacea

Cassiduloidea

Scutelloida

Scutelliformes

RASP DEC Analysis result

DEC result file of Name

[TAXON]

1	Rhyncholampas_pacificus	G
2	Conolampas_sigsbei	AH
3	Echinolampas_crassa	AHJ
4	Ech18_Arachnoides_placenta	A
5	Clypeaster_reticulatus	ABCDGHJK
6	Ech106_Clypeaster_virens	ABCDGHJK
7	Ech32_Clypeaster_japonica	ABCDGHJK
8	Echinocyamus_pusillus	ACDHIJ
9	Ech43_Laganum_fudsiyama	ABCD
10	Ech13_Peronella_lesueuri	ABCD
11	Peronella_japonica	ABCD
12	Ech30_Astriclypeus_manni	AC
13	Ech14_Sculpsitechinus_auritus	ABD
14	Ech49_Echinodiscus_bisperforatus	ACD
15	Ech29_Sinaechinocyamus_mai	AC
16	Dendraster_excentricus	EG
17	Echinarachnius_parma	CEF
18	Scaphechinus_mirabilis	C
19	Lanthonia_longifissa	G
20	Mellita_isometra	H
21	Mellita_notabilis	G
22	Mellitella_stokesii	G
23	Leodia_sexiesperforata	FH
24	Encope_aberrans	H
25	Encope_grandis	G

[TREE]

```
Tree=(((1:106.214225,(2:6.490878,3:6.490878):99.723346):8.551437,((4:39.028993,(5:18.015538
,(6:4.489178,7:4.489178):13.52636):21.013455):64.088521,(8:52.439209,(9:35.070895,(10
:18.000753,11:18.000753):17.070141):17.368315):50.678305):11.648147):5.138475,((12:5
0.388548,(13:39.354713,14:39.354713):11.033834):40.337605,((15:32.872547,(16:26.781
921,(17:20.996038,18:20.996038):5.785883):6.090626):10.672663,((19:15.7555,(20:5.410
499,21:5.410499):10.345001):3.852497,(22:17.564041,(23:15.345302,(24:12.062763,25:12
.062763):3.282539):2.218739):2.043956):23.937213):47.180942):29.177984);
```

[RESULT]

DEC results:

node 26 (LR): AHJ 74.23 AH 25.77

node 27 (LR): A 67.25 G 22.65 H 10.10

node 28 (LR): A 41.04 C 6.35 G 6.27 D 6.19 B 6.16 H 5.83 J 5.76 E 5.61 F 5.60 I 5.59 K 5.59

node 29 (LR): A 100.00

node 30 (LR): A 100.00
node 31 (LR): ABCD 27.17 A 6.82 ACD 6.69 ABC 6.69 ABD 6.64 AC 5.55 AD 5.51 AB 5.50 BCD
5.14 C 4.14 D 4.07 B 4.06 CD 4.03 BC 4.02 BD 3.98
node 32 (LR): ABCD 22.17 A 13.84 ACD 6.28 ABC 6.27 ABD 6.19 AC 6.16 AD 6.08 AB 6.06 C
4.74 D 4.52 B 4.48 BCD 3.83 CD 3.17 BC 3.15 BD 3.08
node 33 (LR): A 38.38 ABCD 14.15 C 9.41 D 8.73 B 8.60 AC 7.00 AD 6.88 AB 6.86
node 34 (LR): A 100.00
node 35 (LR): A 86.31 G 13.69
node 36 (LR): A 69.69 D 16.18 AD 14.13
node 37 (LR): A 68.76 AC 16.82 C 14.42
node 38 (LR): C 75.91 CE 24.09
node 39 (LR): C 28.04 CE 25.20 CG 24.77 CEG 13.58 E 8.40
node 40 (LR): C 42.27 CG 22.11 CE 12.95 AC 8.55 CEG 7.59 ACEG 6.52
node 41 (LR): GH 100.00
node 42 (LR): G 100.00
node 43 (LR): GH 100.00
node 44 (LR): GH 100.00
node 45 (LR): G 63.99 GH 36.01
node 46 (LR): G 68.29 GH 31.71
node 47 (LR): CG 31.02 G 17.28 CEG 10.06 ACEG 9.53 ACG 9.17 CGH 7.20 C 6.26 AG 5.20
CEFG 4.30
node 48 (LR): A 32.87 C 26.35 AG 10.00 AC 9.92 G 9.76 ACG 5.60 CG 5.50
node 49 (LR): A 3.26 ACG 2.24 AG 2.24 AC 2.18 ACDG 1.80 ACGH 1.73 ACEG 1.64 ABCG 1.57
ACGJ 1.49 ACFG 1.37 ADG 1.31 ACD 1.30 ACH 1.28 ACGI 1.28 ACGK 1.28 AGH 1.26
ABG 1.15 AEG 1.14 ABC 1.14 ACE 1.11 AH 1.10 ACJ 1.09 AGJ 1.09 AD 1.09 ACDH 1.03
ADGH 1.01 AFG 0.98 ABCD 0.98 ACF 0.97 ABDG 0.95 AE 0.95 AB 0.94 AGK 0.92 ACI
0.91 ACK 0.91 ADEG 0.91 ACDE 0.90 AJ 0.90 ABCH 0.90 ABGH 0.89 ADGJ 0.88 ACEH
0.88 AGHJ 0.88 AEGH 0.88 ACDJ 0.88 ACHJ 0.86 ABEG 0.80 AF 0.80 ACDF 0.79 ADFG
0.79 ABCE 0.78 ABGJ 0.78 ACFH 0.77 ABCJ 0.77 AFGH 0.76 AEGJ 0.76 ACDI 0.75
ACDK 0.75 ADGI 0.75 ADGK 0.75 AK 0.74 AI 0.74 ACEJ 0.74 ACHI 0.72 ACHK 0.72 AGHI
0.72 AGHK 0.72 ADH 0.71 ACFG 0.70 ABFG 0.69 ABCF 0.68 ACEF 0.68 AFGJ 0.66 ABGI
0.65 ABGK 0.65 AEGK 0.65 AEGI 0.65 ACFJ 0.65 ABCI 0.65 ABCK 0.65 ABD 0.64 ACEI
0.63 ACEK 0.63 AGJK 0.62 ABH 0.62 ADE 0.62 ACIJ 0.61 ACJK 0.61 AEH 0.61 ADJ 0.60
AHJ 0.59 CG 0.58 AFGK 0.56 AFGI 0.56 ACFI 0.55 ACFK 0.55 ABE 0.54 ADF 0.53 AFH
0.52 ABDH 0.52 AGIK 0.52 ABJ 0.52 ACIK 0.52 AEJ 0.51 ADK 0.50 ADI 0.50 ADEH 0.50
ADHJ 0.50 AHK 0.49 CDG 0.49 AEF 0.46 ABF 0.46 ABDE 0.45 CGH 0.45 ABDJ 0.44

Supplementary tables

Table S1. Fossils and references used in the divergence time analysis.

Taxa	Earliest fossil / Reference	Time interval	Ma	Locality
Split between outgroups and Luminacea	<i>Clypeust</i> sp. ⁹	Middle Jurassic	170.3–168.3	Dhurma Formation (Shaqra Group), Saudi Arabia
Cassiduloidea + Echinolampadoidea	Most recent common ancestor estimated in ref ¹⁰	Early Cretaceous	146.6–102.5	
Astriclypeidae	<i>Echinodiscus tiliensis</i> † ¹¹	Late Paleocene to	58.7–48.6	Tili Village, Nantou, Taiwan
	<i>Echinodiscus yeliuensis</i> † ¹¹	Early Eocene		Yeliu, Taiwan
Clypeasteridae	<i>Clypeaster profundus</i> † ¹²	Late Eocene	41.3–38.0	Turkey
Laganidae	<i>Peronella archerensis</i> † ¹³	Late Eocene	38.0–33.9	Inglis Limestone Formation, Florida
Mellitidae	<i>Mellita</i> sp. ¹⁴	Early Miocene	20.44–15.97	Baitoa Formation, Dominican Republic
<i>Encope</i>	<i>Encope</i> sp. ¹⁵	Middle Miocene	16–11.6	Lowest Gatun Formation, Sand Dollar Hill, Panama
<i>Mellita</i>	<i>Mellita acilensis</i> † ¹⁶	Early Pliocene	5.3–3.6	Tamiami Formation, Florida

Table S2. Habitat of sand dollars collected in this study

Species	habitat
<i>Colobocentrotus mertensii</i>	Intertidal or subtidal zone, rocky shore
<i>Maretia planulata</i>	Subtidal zone, sandy bottom
<i>Arachnoides placenta</i>	Intertidal to subtidal zone, sandy bottom
<i>Clypeaster japonicus</i>	Subtidal zone, sandy bottom
<i>Clypeaster reticulatus</i>	Subtidal zone, sandy bottom, with a depths range shallower than <i>C. virescens</i>
<i>Clypeaster virescens</i>	Subtidal zone, sandy bottom, with a depths range deeper than <i>C. reticulatus</i>
<i>Sinaechinocyamus mai</i>	Intertidal to subtidal zone, sandy bottom
<i>Astriclypeus manni</i>	Intertidal to subtidal zone, sandy bottom
<i>Echinodiscus bisperforatus</i>	Intertidal to subtidal zone, sandy bottom
<i>Sculpsitechinus auritus</i>	Intertidal to subtidal zone, sandy bottom
<i>Laganum fudsiyama</i>	Shallow water to deep sea (50–654 m) sandy bottom ¹⁷
<i>Peronella lesueuri</i>	Intertidal to subtidal zone, sandy bottom
<i>Scaphechinus mirabilis</i>	Intertidal to subtidal zone, sandy bottom

Table S3. Best-fit substitution models obtained from PartitionFinder 2. The suffix after each gene name denotes the codon position. The models of DNA substitution are: SYM (Zharkikh, 1994)¹⁸, HKY (Hasegawa et al., 1985)¹⁸, GTR (Rodríguez et al., 1990)¹⁸, F81 (Felsenstein, 1981)¹⁸, and JC (Jukes and Cantor, 1969)¹⁸.

Partition	cox1_1	cox1_2	cox1_3	16S	28S	H3_1	H3_2	H3_3
Best model	SYM+I+G	HKY+I	GTR+I+G	GTR+I+G	GTR+I+G	GTR	F81	JC+I

Supplementary figures

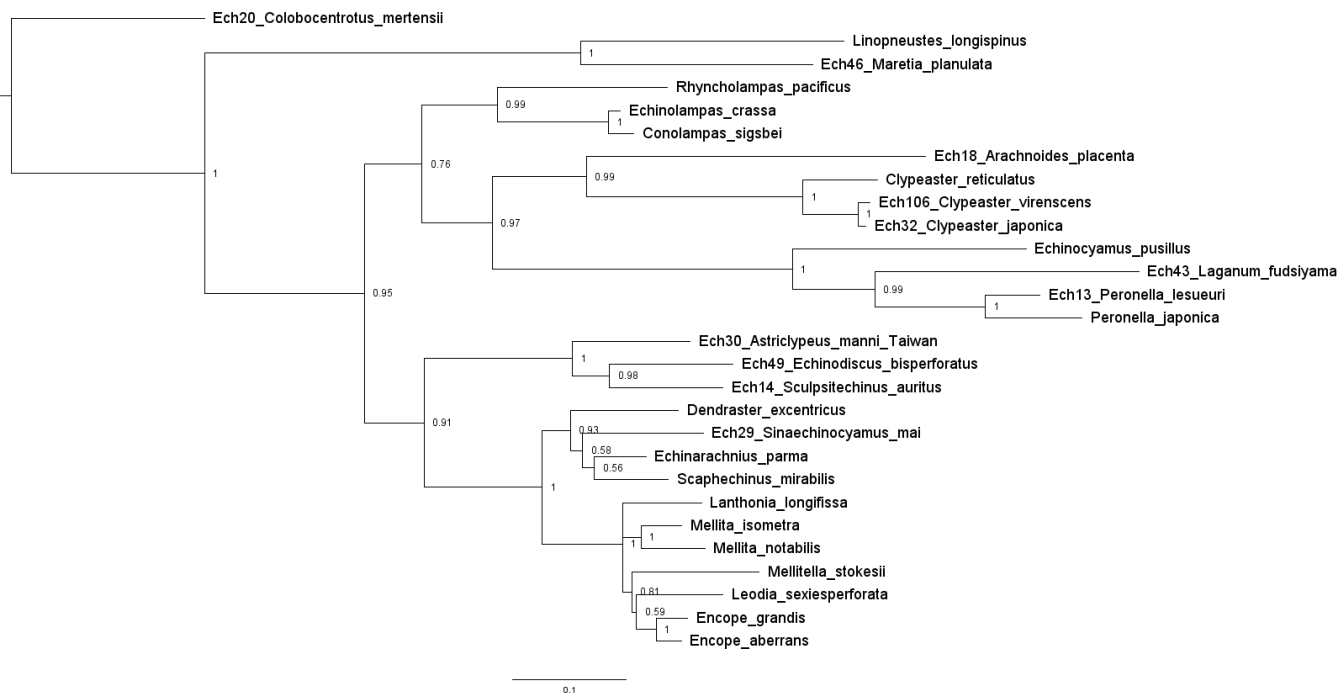


Fig. S1. Phylogenetic relationships of Neognathostomata based on Bayesian Inference analysis.

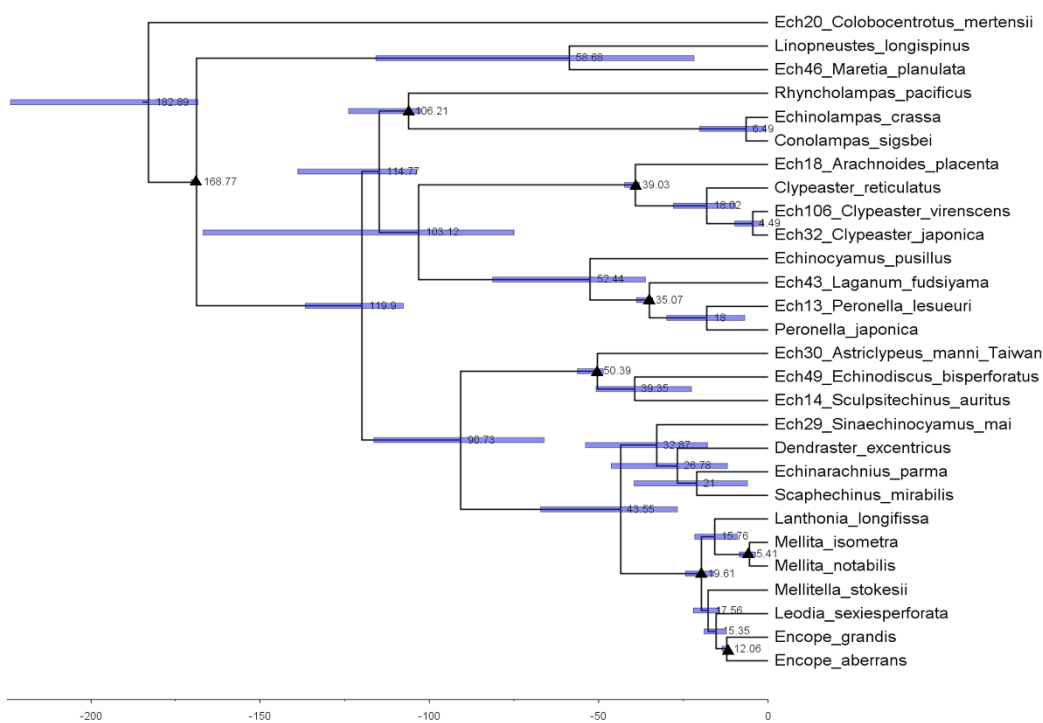


Fig. S2. Rates of evolution for studied echinoids with error bars representing 95% confidence Level (see Fig. 3 and related text). Nodes with black triangles represent the constrained and assigned age priors.

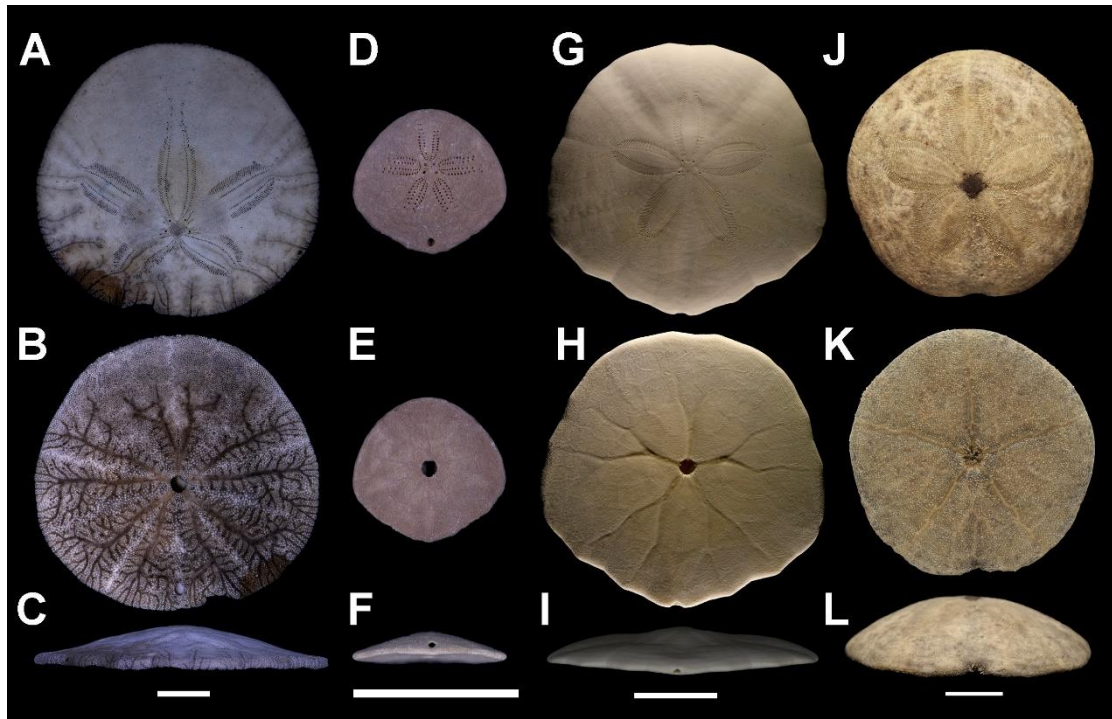


Fig. S3. Key non-lunulate scutelliformes included in this study. All scales = 10 mm. A-C. *Dendraster excentricus* (Eschscholtz, 1831). D-F. *Sinaechinocyamus mai* (Wang, 1984). G-I. *Scaphechinus mirabilis* A. Agassiz, 1864. J-L. *Echinarachnius parma* (Lamarck, 1816). Image credit: Jih-Pai Lin (A-C; G-I) and Kwen-Shen Lee (D-F; J-L).

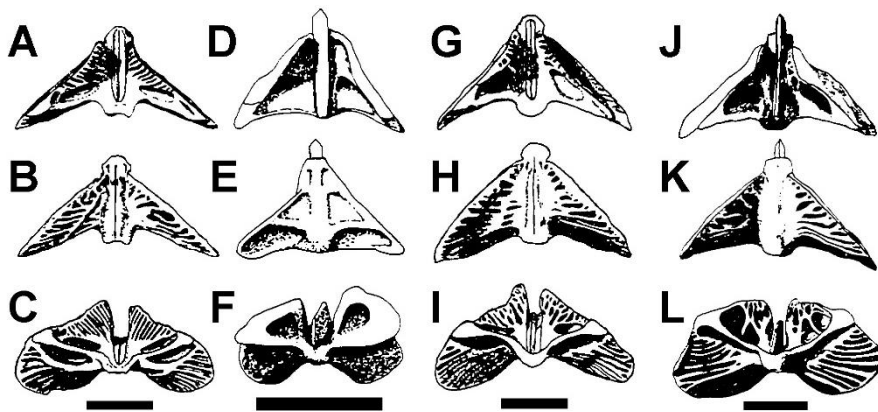


Fig. S4. Views of pyramid morphology of key non-lunulate scutelliformes discussed in this study (modified from Wang⁴). Scales = 0.5 mm (D-F); 3 mm (A-C; G-L). A-C. *Dendraster excentricus*; D-F. *Sinaechinocyamus mai*; G-I. *Scaphechinus mirabilis*; J-L. *Echinarachnius parma*.

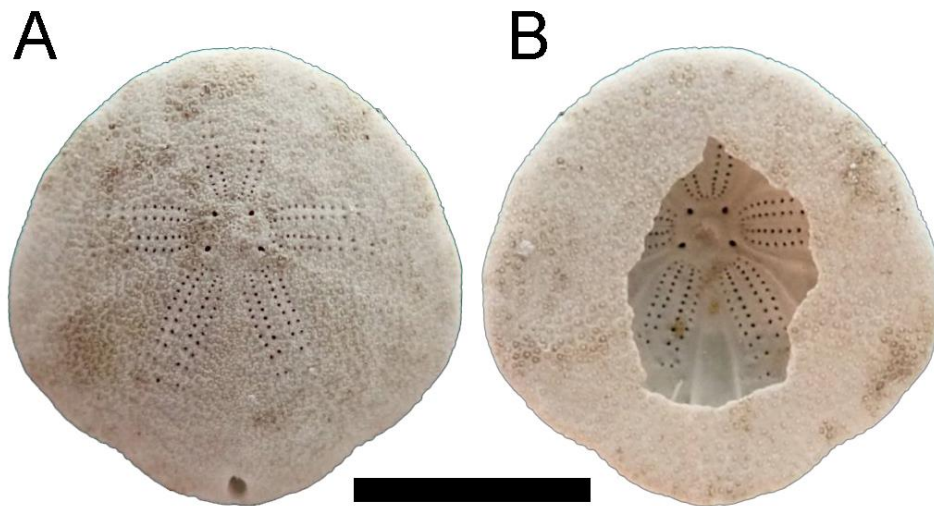


Fig. S5. New occurrence of *Sinaechinocyamus* sp. from Seto Inland Sea, Japan. Denuded test. Scale = 5mm. Image credit: Hayate Tanaka.

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