New Record of a Sea Urchin *Echinometra mathaei* (Echinoidea: Camarodonta: Echinometridae) from Jeju Island, Korea and Its Molecular Analysis

Taekjun Lee¹, Sook Shin^{2,*}

¹Department of Biotechnology, Korea University, Seoul 136-701, Korea ²Department of Life Science, Sahmyook University, Seoul 139-742, Korea

ABSTRACT

Echinoids were collected at depths of 5-10 m in Munseom, Jeju Island by SCUBA diving on November 23, 2008 and September 15, 2009. Two specimens were identified as *Echinometra mathaei* (Blainville, 1825) based on morphological characteristics and molecular analyses of mitochondrial cytochrome *c* oxidase subunit I partial sequences. *Echinometra mathaei* collected from Korea was redescribed with photographs and was compared with other species from GenBank based on molecular data. Phylogenetic analyses showed that no significant differences were between base sequences of *E. mathaei* from Korea and that from GenBank. To date, 13 echinoids including this species have been reported from Jeju Island, and 32 echinoids have been recorded in Korea.

Keywords: taxonomy, sea urchin, Echinometridae, molecular phylogeny, cytochorome c oxidase subunit I

INTRODUCTION

Genus Echinometra species generally occur throughout the tropical Pacific and also from East Africa to the Indian Ocean (Clark and Rowe, 1971). This genus contains seven extant species, including E. insularis, E. lucunter, E. l. polypora, E. mathaei, E. m. oblonga, E. vanbrunti, and E. viridis (Kroh and Mooi, 2012). Among them, E. mathaei is widely distributed over the Indo-Pacific region from the Red Sea to Hawaii, Australia, and southern Japan (Mortensen, 1943; Nisiyama, 1966). This species was first described by Blainville (1825) based on a single specimen from Mauritius, East Africa. He also described E. m. oblonga as a subspecies of E. mathaei without describing the type locality, and its body color was described as white or violet. Echinometra mathaei oblonga was elevated to the separate genus Mortensia by Döderlein (1906) because of the shape of gonadal spicules. But, Mortensen (1943) claimed these as shapes of E. mathaei, and gave the species a subspecies name, E. mathaei oblonga. Subsequently, Clark and Rowe (1971) and Kroh and Mooi (2012) followed the nomenclature of Mortensen (1943). Some morphological (Arakaki et al., 1998; Arakaki and Uehara, 1999) and molecular (Palumbi et al., 1997; McCartney et al.,

© This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (http://creativecommons.org/licenses/by-nc/3.0/) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

pISSN 2234-6953 eISSN 2234-8190

2000; Landry et al., 2003) studies were conducted due to the obscure relationship between these species. A morphological and molecular examination and identification of *Echinometra* specimens collected from Munseom of Jeju Island, Korea was performed in the present study.

MATERIALS AND METHODS

Echinoid specimens were collected at depths of 5-10 m in Munseom, Jeju Island by SCUBA diving on November 23, 2008 and September 15, 2009. The specimens were preserved in 95% ethanol, and their important morphological characters were photographed with a digital camera (Canon G12; Canon Co., Tokyo, Japan) and stereo and light microscopy (Nikon SMZ1000, Nikon Eclipse 80*i*; Nikon Co., Tokyo, Japan). The specimens were morphologically identified based on the descriptions of Mortensen (1943) and Clark and Rowe (1971).

Genomic DNA was extracted from the tubefeet of Korean echinoids using the DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany) for the molecular analysis. The mitochondrial cytochrome c oxidase subunit 1 (COI) gene fragment

^{*}**To whom correspondence should be addressed** Tel: 82-2-3399-1717, Fax: 82-2-3399-1729 E-mail: shins@syu.ac.kr

Table 1. List of taxa and GenBank accession numbers of mitochondrial cytochrome *c* oxidase subunit 1 (COI) sequences examined in this study

Family	Species	COI	Reference				
Echinometridae	Echinometra mathaei (Blainville, 1825)	JQ742945	This study				
		JQ742946	"				
		AY262888, AY262912,4,6	Landry et al. (2003)				
	Echinometra mathaei oblonga (Blainville, 1825)	AY262865-8	"				
	Echinometra insularis HL Clark, 1912	AY262902,4,6,8	"				
	Echinometra lucunter (Linnaeus, 1758)	AF255472, AF255506,8,10	McCartney et al. (2000)				
	Echinometra vanbrunti A Agassiz, 1863	AF255530,2,6,8	"				
	Echinometra viridis A Agassiz, 1863	AF255511, AF255522,4,6	"				
	Heliocidaris crassispina (A Agassiz, 1863)	JN716400	Lee and Shin (2011)				
Strongylocentrotidae	Mesocentrotus nudus (A Agassiz, 1863)	JQ716398	"				
	Strongylocentrotus purpuratus (Stimpson, 1857)	NC001453	Jacobs et al. (1988)				

was amplified using ECO1a and ECO1b, as suggested by Knott and Wray (2000). The COI gene fragment corresponding to the interval between sites 5921 to 6861 of the *Strongylocentrotus purpuratus* mitochondrial genome (NCBI ID: NC001453) was obtained for each specimen.

PCR analyses were conducted according to Lee and Shin (2011). DNA fragments were sequenced on an ABI 3730XL Sequencer (Applied Biosystems Inc., Foster City, CA, USA) using the ABI Prism Bigdye Terminator v3.1 (Applied Biosystems). The mitochondrial COI gene was sequenced, and the sequence data of five species that were not distributed in Korea were obtained from GenBank (Table 1). COI sequences were aligned using CLUSTAL X (Thompson et al., 1997), and genetic distances were calculated according to the Kimura 2-parameter model using MEGA5 (Tamura et al., 2011). The best-fit evolutionary model was identified using the Akaike Information Criterion (AIC) in jMODELTEST (Posada, 2008), and the result was GTR+G (α =0.238). A phylogenetic tree was drawn with neighbor joining (NJ), maximum likelihood (ML), and Bayesian inference (BI) methods. The NJ tree was inferred from the Kimura 2-parameter genetic distance and bootstrapped 1,000 times using MEGA5. The ML tree was analyzed with PHYML v.3.0 (Guindon and Gascuel, 2003) and 1,000 bootstrap replications. The BI analysis was conducted with the same model and analyzed by MrBayes 3.1.2 with 2×10^6 trees, sampling every 1,000th tree, and credibility values of the nodes were calculated with the 50% majority rule tree after discarding the first 500 trees (Ronquist and Huelsenbeck, 2003).

RESULTS

Systematic notes

Class Echinoidea Leske, 1778

Korean name: 1*만두성게속(신칭), 2*만두성게(신칭)

Order Camarodonta Jackson, 1912 Infraorder Echinidea Kroh and Smith, 2010 Family Echinometridae Gray, 1855

Key to the genera of family Echinometridae in Korea

1. Test oval shaped, with usually four pore-pairs to an arc *Echinometra* Test nearly circular shaped, with usually eight pore-pairs to an arc *Heliocidaris*

^{1*}Genus Echinometra Gray, 1825

Echinometra Gray, 1825: 426; Blainville, 1830: 206; L Agassiz and Desor, 1846: 372; A Agassiz, 1872-1874: 282;
Döderlein, 1906: 233; HL Clark, 1912: 370; Mortensen, 1943: 352; Nisiyama, 1966: 267; Kroh and Mooi, 2012: 179659.

Ellipsechinus Lütken, 1864: 165. *Mortensenia* Döderlein, 1906: 233.

Test more or less oval shaped, stout, longitudinal axis through interambulacral III to ambulacral 1. Ambulacrals with four pore-pairs per an arc. Apical system with all exserted ocular plates. Primary spines rather long, strong, pointed, Globiferous pedicellariae with one lateral tooth, tubefeet with C-shaped spicules.

Type species: Echinus lucunter Linnaeus, 1758.

^{2*}*Echinometra mathaei* (Blainville, 1825) (Fig. 1) *Echinus mathai* Blainville, 1825: 94; 1830: 206.

Echinometra mathaei Blainville, 1834: 225; Mortensen, 1903: 128; A Agassiz and HL Clark, 1907: 241; HL Clark, 1908: 303; 1912: 372; Koehler, 1914: 250; Mortensen, 1940: 103; 1943, 381; Nisiyama, 1966: 271; AM Clark and Rowe, 1971: 157; Arakaki et al., 1998: 159; Arakaki and Uehara, 1999: 551; Kroh and Mooi, 2012: 213383.



Fig. 1. *Echinometra mathaei*. A, Dorsal side; B, Ventral side; C, Lateral side; D, Apical system; E, Pore pairs; F, Primary spine on dorsal side (left) and secondary spine on ventral side (right); G, Globiferous pedicellaria; H, Heads of globiferous pedicellaria; I, Valve of tridentate pedicellaria; J, Valve of ophiocephalous pedicellaria; K, Valves of tripyllous pedicellaria; L, Spicules of tubefeet. Scale bars: A-C=1.5 cm, D, F=0.5 cm, E=1.5 mm, G, J=200 µm, H, I=100 µm, K=50 µm, L=25 µm.

Echinometra megastoma M'Clelland, 1840: 181.

Echinometra heteropora L Agassiz and Desor, 1846: 372. *Echinometra microtuberculata* A Agassiz, 1863: 22.

Echinometra picta A Agassiz and HL Clark, 1907: 241; HL Clark, 1912: 373.

Ellipsechinus decryi Lambert, 1933: 47.

Material examined. 1 specimen, Munseom, Jeju Island, 23 Nov 2008, at 5 m depth by SCUBA diving; 1 specimen, 15 May 2009, at 10 m depth by SCUBA diving.

Description. Test of small size, strong, hemispherical, oval shaped; ventral side flat, scarcely sunken towards peristome. Ambulacral with four pore-pairs, rarely five to one oblique and rather irregularly curved pore-arcs (Fig. 1E). One of tubercles in pore-zone enlarged and forms a fairly conspicuous vertical. In interambulacral, larger secondary tubercles usually form a distinct vertical series admedially and adradially to primary series. These secondaries vary in size, from almost as large as smaller than primaries. Apical system with all ocular plates exserted (Fig. 1D). Genital plates covered with some small spines, and genital pores developed (Fig. 1D).

Suranal plate indistinct, and anal opening acentric. Primary spines rather long, about as long as half test diameter, usually rather stout, tapering, and colors getting lighter at tips (Fig. 1F). Secondary spines rather short, with flat tips, looks like rolling pins (Fig. 1F). Globiferous pedicellariae very scarce: valve with a lateral tooth as long as two-thirds of apical tooth (Fig. 1H). Tridentate pedicellariae large: valve with curved tips (Fig. 1I). Ophiocephalous pedicellariae narrow in middle: valve with zigzag edges (Fig. 1J). Triphyllous pedicellariae small: valve width moderately as wide as basal part (Fig. 1K). Tubefeet with C-shaped spicules (Fig. 1L). Buccal plates with some small spines in peristome among a few assemblages of ophiocephalous pedicellariae.

Size. Test diameter, 19.0, 29.0 mm; test height, 9.0, 13.0 mm (44.8, 47.4% of test diameter); apical system, 3.8, 6.1 mm (18.0, 19.0% of test diameter); peristome, 9.8, 15.0 mm (51.6, 51.7% of test diameter); number of interambulacral plates, 9, 13; number of ambulacral plates, 11, 26.

Distribution. Korea (Jeju Island), Japan (Okinawa), China, Philippines, Hawaii, Solomon Islands, northern Australia, Indo-West Pacific, East Africa (Kenya, Mauritius, Mozam-

Table 2. Interspecific pairwise distance values (p) between six species of genus *Echinometra* and outgroups of *Heliocidaris crassispina*, *Mesocentrotus nudus*, and *Strongylocentrotus purpuratus* based on partial sequences of the mitochondrial cytochrome *c* oxidase subunit 1 (COI) gene

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	E. mathaei (JQ742945) ^a																													
2	E. mathaei (JQ742946) ^a	0.00																												
3	E. mathaei (AY262912)	0.00	0.00																											
4	E. mathaei (AY262913)	0.00	0.00	0.00																										
5	E. mathaei (AY262914)	0.00	0.00	0.00	0.00																									
6	E. mathaei (AY262915)	0.00	0.00	0.00	0.00	0.00																								
7	E. m. oblonga (AY262865)	0.03	0.03	0.03	0.03	0.03	0.03																							
8	E. m. oblonga (AY262866)	0.03	0.03	0.03	0.03	0.03	0.03	0.01																						
9	E. m. oblonga (AY262867)	0.03	0.04	0.04	0.04	0.04	0.04	0.00	0.01																					
10	E. m. oblonga (AY262868)	0.04	0.04	0.04	0.04	0.04	0.04	0.00	0.01	0.01																				
11	E. insularis (AY262902)	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.04	0.05	0.05																			
12	E. insularis (AY262904)	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.04	0.05	0.05	0.00																		
13	E. insularis (AY262906)	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.04	0.05	0.05	0.00	0.00																	
14	E. insularis (AY262908)	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.05	0.05	0.00	0.00	0.00																
15	E. lucunter (AF255472)	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.13	0.12	0.15	0.15	0.15	0.15															
16	E. lucunter (AF255506)	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.11	0.12	0.12	0.14	0.14	0.14	0.14	0.02														
17	E. lucunter (AF255508)	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.12	0.11	0.14	0.14	0.14	0.14	0.01	0.00													
18	E. lucunter (AF255510)	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.12	0.11	0.14	0.14	0.14	0.14	0.01	0.00	0.00												
19	E. viridis (AF255511)	0.13	0.13	0.13	0.13	0.13	0.13	0.14	0.13	0.14	0.14	0.16	0.16	0.16	0.16	0.08	0.07	0.07	0.07											
20	E. viridis (AF255522)	0.12	0.12	0.12	0.12	0.12	0.12	0.14	0.13	0.13	0.14	0.15	0.15	0.15	0.16	0.07	0.07	0.06	0.06	0.01										
21	E. viridis (AF255524)	0.12	0.12	0.12	0.12	0.12	0.12	0.13	0.12	0.13	0.13	0.15	0.15	0.15	0.15	0.07	0.06	0.06	0.06	0.01	0.00									
22	E. viridis (AF255526)	0.13	0.13	0.13	0.13	0.13	0.13	0.14	0.13	0.14	0.14	0.16	0.16	0.16	0.16	0.08	0.07	0.07	0.07	0.00	0.01	0.01								
23	E. vanbrunti (AF255530)	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.11	0.11	0.12	0.13	0.13	0.13	0.14	0.12	0.11	0.11	0.11	0.14	0.13	0.13	0.14							
24	E. vanbrunti (AF255532)	0.14	0.14	0.14	0.14	0.14	0.14	0.13	0.12	0.13	0.13	0.15	0.15	0.15	0.15	0.13	0.12	0.12	0.12	0.15	0.14	0.14	0.15	0.01						
25	E. vanbrunti (AF255536)	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.11	0.11	0.12	0.13	0.13	0.13	0.14	0.12	0.10	0.11	0.11	0.14	0.13	0.13	0.14	0.01	0.02					
26	E. vanbrunti (AF255538)	0.12	0.12	0.12	0.12	0.12	0.12	0.11	0.11	0.11	0.11	0.13	0.13	0.13	0.13	0.12	0.11	0.10	0.10	0.13	0.13	0.13	0.13	0.00	0.02	0.00				
27	H. crassispina (JN716400)	0.16	0.16	0.16	0.16	0.16	0.16	0.17	0.16	0.17	0.16	0.18	0.18	0.18	0.18	0.20	0.18	0.18	0.18	0.18	0.19	0.19	0.18	0.19	0.20	0.19	0.19			
28	M. nudus (JN716398)	0.20	0.20	0.20	0.20	0.20	0.20	0.21	0.20	0.21	0.21	0.18	0.18	0.18	0.19	0.21	0.21	0.20	0.20	0.18	0.18	0.18	0.18	0.18	0.20	0.18	0.18	0.19		
29	S. purpuratus (NC001453)	0.20	0.20	0.20	0.20	0.20	0.20	0.21	0.20	0.21	0.20	0.23	0.23	0.23	0.23	0.24	0.24	0.23	0.23	0.21	0.22	0.21	0.21	0.23	0.24	0.23	0.23	0.22	0.18	

^aKorean specimens



Fig. 2. Bayesian inference (BI), neighbor-joining (NJ), and maximum-likelihood (ML) trees of the *Echinometra* species inferred from the mitochondrial cytochrome *c* oxidase subunit 1 (COI) partial sequence dataset. Support values for each node are represented by Bayesian posterior probabilities, NJ and ML bootstrap values. Values < "0.70" or "70" appear as hyphens.

bique, Tanzania), Red Sea.

Molecular analysis

The sequences of our Korean *E. mathaei* specimens were compared with GenBank data of six *Echinometra* species such as *E. mathaei*, *E. m. oblonga*, *E. insularis*, *E. lucunter*, *E. vanbrunti*, and *E. viridis* of the family Echinometridae, using *Heliocidaris crassispina*, *Hemicentrotus pulcherrimus*, and *Strongylocentrotus pallidus* of the family Strongylocentrotidae within the same infraorder as outgroups taken from GenBank. After sequence alignment, a portion of the COI gene corresponding to bases 6471-6854 of the *S. purpuratus* complete mitochondrial genome was obtained. Our COI dataset comprised 383 bp of the COI gene.

Genetic pairwise distance (p) values were estimated by the Kimura 2-parameter model and were compared (Table 2). As a result, no differences were found between the two Korean specimens. The average value of Korean *E. mathaei*-GenBank *E. mathaei* was "0.00". This value was much lower than the distance values of *E. mathaei-E. m. oblonga* (p=0.03), *E. mathaei-E. insularis* (p=0.04), *E. mathaei-E. lucunter* (p= 0.12), *E. mathaei-E. vanbrunti* (p=0.12) and *E. mathaei-E.*

viridis (p=0.12).

Phylogenetic trees were estimated by BI, NJ and ML methods. Each species of *Echinometra* established an independent monophyletic clade (Fig. 2). The sequences of Korean *E. mathaei* formed a distinct monophyletic group with the GenBank *E. mathaei*, and these sequences were clearly separated from *E. insularis* and *E. m. oblonga*. Genus *Echinometra* was divided into two groups; Group I=(*E. m. oblonga* (*E. mathaei*, *E. insularis*)) and Group II=(*E. vanbrubti* (*E. lucunter*, *E. viridis*)).

DISCUSSION

Our specimens were identified as *Echinometra mathaei*, which is newly recorded in Korea. To date, 13 echinoid species including this species have been reported from Jeju Island, and 32 echinoid species have been recorded in Korea (Shin and Rho, 1996; Shin, 1998; Shin et al., 2006; Lee and Shin, 2011). *E. mathaei* is represented by great diversity in form of test and spines, as well as in color and form (Mortensen, 1943; Arakaki et al., 1998). Our specimens coincided with these previous morphological descriptions of *E. mathaei*, but the tubefeet spicules differed slightly from those of Japanese specimens. *E. mathaei* has C-shaped and triradiate forms of tubefeet spicules (Arakaki et al., 1998; Arakaki and Uehara, 1999), whereas the tubefeet of our specimens contained only C-shaped spicules, but Japanese specimens contained only one C-shaped type or sometimes two tubefeet types (Arakaki et al., 1998). Because of these morphological variations, some studies have investigated the speciation and interspecific relationships of *Echinometra* species using the mitochondrial COI gene (Palumbi et al., 1997; McCartney et al., 2000; Landry et al., 2003).

The results of the phylogenetic tree (Fig. 2) indicated that the Korean Echinometra specimens clearly established one independent phylogenetic group with those taken from Gen-Bank, and showed no differences in base sequences. These data distinctly support that the Korean Echinometra specimens are E. mathaei. The finding that the genus Echinometra was divided into groups I and II corresponded with the results of previous studies (McCartney et al., 2000; Landry et al., 2003). But, the relationship of group I in the present study was contrary to the results of Landry et al. (2003). The results obtained from 1164 bp of the COI gene dataset analysis using NJ method by Landry et al. (2003) were the same as (E. vanbrunti (E. insularis (E. mathaei, E. m. oblonga))). The results obtained from 930 bp of the COI gene dataset analysis using the NJ method agreed with those of Landry et al. (2003), but the results obtained by the BI and ML methods were the same as those of group I in Fig. 2. Because the results varied according to the analytical methods employed, additional analyses about these relationships are required using other genes.

ACKNOWLEDGMENTS

The authors thank Dr. S.H. Kim (IN THE SEA KOREA Co. Ltd) for providing a specimen. This study was supported by Sahmyook University Research Fund and partially by the Discovery of Korean Indigenous Species Project, NIBR (National Institute of Biological Resources), 2012.

REFERENCES

- Agassiz A, 1863. List of the echinoderms sent to different institutions in exchange for other specimens, with annotations. Bulletin of the Museum of Comparative Zoölogy at Harvard College, 1:17-28.
- Agassiz A, 1872-1874. Revision of the Echini. Memoirs of the Museum of Comparative Zoölogy at Harvard College, 3:1-762.

- Agassiz A, Clark HL, 1907. Preliminary report on the Echini collected, in 1902, among the Hawaiian Islands, by the U.S. Fish Commission steamer "Albatross", in charge of commander Chauncey Thomas, U.S.N., commanding. Bulletin of the Museum of Comparative Zoölogy at Harvard College, 50:231-259.
- Agassiz L, Desor E, 1846. Catalogue raisonné des familles des genres et des espèces de la classe de échinodermes. Annals Science Naturelles, Zoologie, 3:325-374.
- Arakaki Y, Uehara T, 1999. Morphological comparison of black *Echinometra* individuals among those in the Indo-West Pacific. Zoological Science, 16:551-558.
- Arakaki Y, Uehara T, Fagoonee I, 1998. Comparative studies of the genus *Echinometra* from Okinawa and Mauritius. Zoological Science, 15:159-168.
- Blainville HM, 1825. Dictionnaire des sciences naturelles, dans lequel un traité méthodiquement des différences tetres de la nature, considérés soit en eux-memes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retierer la médicine, l'agriculture, le commerce et les arts. Vol. 37. Levrault, Paris, pp. 59-102.
- Blainville HM, 1830. Zoophyte. In: Dictionnaire des Sciences Naturelles. Vol. 60 (Ed., Cuvier F). Levrault, Paris, pp. 1-546.
- Blainville HM, 1834. Manuel d'Actinologie ou de Zoophytologie. Levrault, Paris, pp. 1-644.
- Clark AM, Rowe FWE, 1971. Monograph of shallow-water Indo-West Pacific echinoderms. The British Museum Publication (Natural History), 690:1-238.
- Clark HL, 1908. Some Japanese and East Indian echinoderms. Bulletin of the Museum of Comparative Zoölogy at Harvard College, 52:279-311.
- Clark HL, 1912. Hawaiian and other Pacific echini: the Pedinidae, Phymosomatidae, Stomopneustidae, Echinidae, Temnopleuridae, Strongylocentrotidae, and Echinometridae. Memoirs of the Museum of Comparative Zoölogy at Harvard College, 34:1-383.
- Döderlein L, 1906. Die Echinoiden der deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der Deutschen Tiefsee Expedition auf dem Dampfer "Valdivia" 1898-1899, 5: 63-350.
- Gray JE, 1825. An attempt to divide the Echinida or sea-eggs into natural families. Annals of Philosophy, 26:423-431.
- Guindon S, Gascuel O, 2003. A simple, fast and accurate algorithm to estimate large phylogenies by maximum-likelihood. Systematic Biology, 52:696-704.
- Jacobs HT, Elliott DJ, Math VB, Farquharson A, 1988. Nucleotide sequence and gene organization of sea urchin mitochondrial DNA. Journal of Molecular Biology, 202:185-217.
- Knott KE, Wray GA, 2000. Controversy and consensus in asteroid systematics: new insights to ordinal and familial relationships. American Zoologist, 40:382-392.
- Koehler R, 1914. Echinoderma I. Asteroidea, Ophiuroidea et Echinoidea. In: Beiträge zur Kenntnis der Meeresfauna Westafrikas. Vol. 1 (Ed., Michaelsen W). Friederichsen and Company, Hamburg, pp. 127-303.
- Kroh A, Mooi R, 2012. World Echinoidea database [Internet].

The world register of marine species (WoRMS), Accessed 31 May 2012, http://www.marinespecies.org/echinoidea>.

- Lambert J, 1933. Echinides de Madagascar communiqués par M. H. Besairie. Annales Géologiques du Service des Mines, 3:7-49.
- Landry C, Geyer LB, Arakaki Y, Uehara T, Palumbi SR, 2003. Recent speciation in the Indo-West Pacific: rapid evolution of gamete recognition and sperm morphology in cryptic species of sea urchin. Proceedings of the Royal Society of London Series B-Biological Sciences, 270:1839-1847.
- Lee T, Shin S, 2011. A new record of sea urchin (Echinoidea: Camarodonta: Strongylocentrotidae) based on morphological and molecular analysis in Korea. Korean Journal of Systematic Zoology, 27:213-219.
- Lütken CF, 1864. Bidrag til Kundskab om Echiniderne. Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn, 1863:69-207.
- McCartney MA, Keller G, Lessios HA, 2000. Dispersal barriers in tropical oceans and speciation in Atlantic and eastern Pacific sea urchins of the genus *Echinometra*. Molecular Ecology, 9:1391-1400.
- M'Clelland J, 1840. On *Cyrtoma*, a new genus of fossil Echinida. The Calcutta Journal of Natural History, 1:155-187.
- Mortensen T, 1903. The Danish Ingolf expedition 1895-1896. Vol. 4, No. 2. Echinoidea, Part. 1. Bianco Luno, Copenhagen, pp. 1-200.
- Mortensen T, 1940. Echinoderms from the Iranian Gulf. Asteroidea, Ophiuroidea, and Echinoidea. In: Danish Scientific Investigations in Iran, part 2 (Eds., Jessen K, Spårck R), Einar Munksgaard, Copenhagen, pp. 55-112.
- Mortensen T, 1943. A monograph of Echinoida. Vol. III, 3. Camarodonta. II. Echinoidae, Strongylocentrotidae, Parasaleniidae, Echinometridae. C. A. Reitzel, Copenhagen, pp. 1-446.

- Nisiyama S, 1966. The echinoid fauna from Japan and adjacent regions, Part 1. Palaeontological Society of Japan, Special Papers, 11:1-277.
- Palumbi SR, Grabowsky G, Duda T, Geyer L, Tachino N, 1997. Speciation and population genetic structure in tropical Pacific sea urchins. Evolution, 51:1506-1517.
- Posada D, 2008. jModeltest: phylogenetic model averaging. Molecular Biology and Evolution, 25:1253-1256.
- Ronquist F, Huelsenbeck JP, 2003. Mrbayes: Bayesian phylogenetic inference under mixed models. Bioinformatics, 19: 1572-1574.
- Shin S, 1998. Echinoderms from Geojedo Island and adjacent sea waters, Korea. Korean Journal of Systematics Zoology, 14:193-205.
- Shin S, Pyo J, Kim SH, 2006. A new record of sea urchin (Echinoidea: Echinothurioida) from Jeju Island, Korea. Korean Journal of Systematics Zoology, 22:105-108.
- Shin S, Rho BJ, 1996. Illustrated encyclopedia of fauna and flora of the Korea. Vol. 36. Echinodermata. Ministry of Education, Seoul, pp. 1-780.
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S, 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution, 28:2731-2739.
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG, 1997. The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research, 25:4876-4882.

Received July 2, 2012 Revised July 13, 2012 Accepted July 16, 2012