Terr. Atmos. Ocean. Sci., Vol. 32, No. 6, Part II, 1069-1080, December 2021 doi: 10.3319/TAO.2021.12.21.01

Restudy of fossil specimens of *Sinaechinocyamus* (Echinoidea; Scutelloida) with new occurrences from Taiwan

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Article history:

Received 19 April 2021
Revised 12 December 2021
Accepted 21 December 2021

Keywords:

Taxonomy, Scutelloida, Echinodermata, Paleontology, Cenozoic

Citation:

Chu, W.-C. and L.-Y. Chang, 2021: Restudy of fossil specimens of *Sinaechinocyamus* (Echinoidea; Scutelloida) with new occurrences from Taiwan. Terr. Atmos. Ocean. Sci., 32, 1069-1080, doi: 10.3319/TAO.2021.12.21.01

ABSTRACT

Sinaechinocyamus is a small echinoid genus that belongs to Scutelloida. From the perspective of fossil evidence, *Sinaechinocyamus* may have first appeared in the northern part of Taiwan since the late Miocene and gradually distributed to southern Taiwan in the late Pliocene. The extant population of *Sinaechinocyamus mai* distributes in the coastal area from Hsinchu to Tainan in Taiwan. In previous research, three fossil *Sinaechinocyamus* species in Taiwan were described. In this study, a total of 321 fossil and extant specimens of *Sinaechinocyamus* spp. were collected from 9 sites. Subsequent morphological analyses were conducted to reclassify the specimens, which confirmed that the morphological differences of fossil data fell within the range of extant *S. mai*. Therefore, these fossils specimens of *Sinaechinocyamus* spp. found in Taiwan should be classified as *S. mai*.

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1. INTRODUCTION

Based on the sediments sampled in the northern Yellow Sea at a depth of 72 m, Liao (1979) identified some small clypeasteroids and named *Sinaechinocyamus planus* with an indeterminate higher systematic ranking. In Taiwan Strait, Wang (1984) discovered similar clypeasteroids independently. He collected live specimens from the Taiwan Strait near Miaoli County, Taichung County, and Yunlin County of western Taiwan and described them as *Taiwanaster mai* Wang 1984, and placed it under its own family Taiwanasteridae Wang 1984. He also named the two similar fossils found in Bitoujiao and Gutingkeng in Taiwan as *T. pitouensis* and *T. gutingkengensis*. Mooi (1990) compared the two genera and synonymized them into one valid genus *Sinaechinocyamus* and two species: *S. planus* and *S. mai*. In summary, there are currently four published species of this genus, including two extant species and two fossil species (with † mark): *Sinaechinocyamus planus* Liao 1979; *Sinaechinocyamus mai* (Wang 1984); *Sinaechinocyamus pitouensis* (Wang 1984)†; *Sinaechinocyamus gutingkengensis* (Wang 1984)†. The phylogenetic relationship among irregular echinoids is a field under active investigation. According to recent morphological and molecular studies, *Sinaechinocyamus* is now placed in Order Scutelloida (Mongiardino Koch et al. 2018; Kroh 2020; Lin et al. 2020; Mongiardino Koch and Thompson 2021).

Subsequent studies focused on the ontogeny of extant *S. mai*. Chen and Chen (1993) reported that the spawning season of *S. mai* is between October and November, and it metamorphoses into planktotrophic larvae nine days after fertilization. The natural population density of *S. mai* has an inverse relationship to the body length (Chen and Chen 1994). They also noted that the juveniles of *S. mai* tend to contain a higher weight percentage of sand than adults. The majority of sand in the diverticulum belongs to the size class ranging from 0.075 to 0.125 mm (Chen and Chen 1994). The closest taxonomic relative of *S. mai* is *Scaphechinus mirabilis* (Mooi 1990), whose extant population inhabits the Northwest Pacific with only fossil specimens found in

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Taiwan. (e.g., Lin et al. 2021; and references therein) By comparing and contrasting the ontogeny and growth rates of the two species, Chen and Chao (1997) demonstrated that the growth rate of *S. mai* is about 19% the rate of *S. mirabilis*. *S. mai* reaches sexual maturity at two years with a maximum size of 10.9 mm. Based on the analysis of growth curve patterns, Chen and Chao (1997) concluded that neoteny by growth rate reduction was the main driver for miniaturization in *S. mai*.

Based on the author's field investigations and reports from amateur collectors, the fossil localities of *Sinaechinocyamus* in Taiwan have been increasingly abundant in recent years (Lin and Chien 2022). At least ten fossil sites (eight of them are visited, and new fossils are collected by the author; Fig. 1) yield complete specimens of *Sinaechinocyamus*. This study aims to compare and contrast samples from eight fossil and one modern localities with morphological analysis and subsequently proposes the number of species present in the studied specimens.

2. MATERIALS AND METHODS

2.1 Samples Sites

The *Sinaechinocyamus* fossils were investigated and collected from 8 locations in this study (Fig. 1), including seven localities in the Taiwan Main Island and one site from Pescadores Islands. These sites are described further below.

2.1.1 Bitoujiao (Site 1 in Fig. 1)

Fossil specimens were found on the middle part of the Erhchiu Member of the Kueichuling Formation (early Pliocene). The lithology of Erhchiu Member is thick muddy sandstone occasionally intercalated with thin shale. The sandstone has fine to very coarse grains, locally with fine gravels, and sedimentary structures such as cross-bedding and nodules (Huang and Liu 1988; Yu and Teng 1996). There are a few fossil fragments of mollusks and echinoids at the layer of specimen collected. Several layers of sandstones

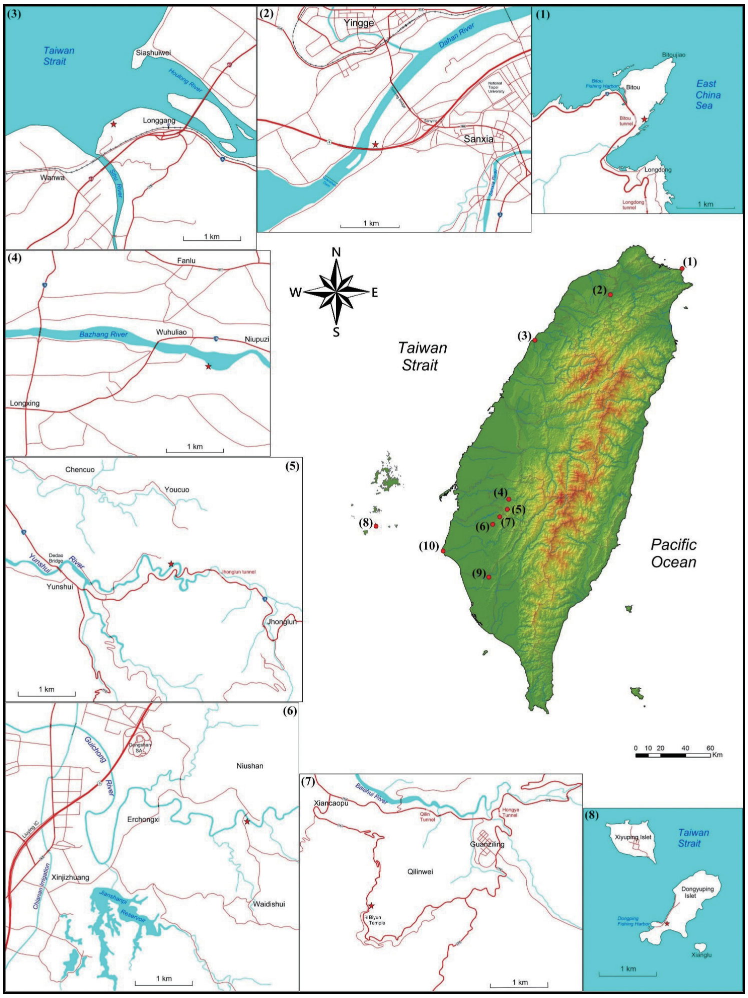


Fig. 1. Map showing sample localities (red dots in index map and red stars in each locality map) of *Sinaechinocyamus* in this study, where (1) Bitoujiao, (2) Sanying Bridge, (3) Longgang, (4) Niupu, (5) Jhonglung, (6) Niushan, (7) Guanzjling, (8) Dongyuping, (9) Gutingkeng, (10) Zengwenxikou.

with flat cross-bedding and herringbone cross-bedding are exposed in the upper part. Specimens were studied on-site because that fossil-bearing sandstones were cemented very well and cannot be collected without damaging the fossil.

2.1.2 Sanying Bridge (Site 2 in Fig. 1)

Specimens were collected from the Tapu Member of the Kueichuling Formation. The lithology of Tapu Member is composed of grayish, thick, massive fine to medium-grained sandstone, occasionally with thin shale lens and coal traces (Huang and Liu 1988; Lin and Chang 2014). The lithology of the fossil-bearing strata is blue-gray muddy sandstone, containing many fossil fragments, most of which are very weathered. On this site, 29 complete specimens were collected for analysis.

2.1.3 Longgang (Site 3 in Fig. 1)

Fossils were collected from the Toukoshan Formation (Chang 1990). The thickness of the section exposed at the site is approximately 90 m. The upper part is about 80 m of interbedded brown-yellow sandstone and blue-gray siltstone to mudstone. There is a 10 cm thick layer containing aggregates of *Pecten* (Bivalvia; Pectinida) on the top of the sandstone-shale interbedded section, which is laterally continuous and well-cemented. Some echinoid fossils in the lower section near the bottom like *Astriclypeus*, *Sinaechinocyamus*, *Fibularia*, and *Breynia* have been reported. Based on the relative age dating with biostratigraphy based on calcareous nanofossils and foraminiferan fossils, the geological age of this section is about 1.03 - 0.46 Ma, which corresponds to the middle and upper part of the Toukoshan Formation (Lee 2000). On this site, 110 specimens were collected, and 57 complete ones were included for statistical analyses.

2.1.4 Niupu (Site 4 in Fig. 1)

Fossils were collected from the lower part of the Kanshialiao Formation. The lithology of the Kanshialiao Formation is dominated by mudstone and sandy shale. The sedimentary environment of the Kanshialiao Formation belongs to the shoreface (Chang 2008). On this site, 42 complete specimens were collected for analysis.

2.1.5 Jhonglun (Site 5 in Fig. 1)

Fossils were collected from the lower part of the Yunshuichi Formation. The lithology of the Yunshuichi Formation is dominated by shale with sandy shale (Shao and Kao 2009). The specimens collected from a well cemented fine sandstone are associated with other kinds of fossil fragments. Since the unit is well cemented and few specimens could be collected, material from this unit is not included for statistical analyses.

2.1.6 Niushan (Site 6 in Fig. 1)

Specimens were collected from the lower part of the Liuchungchi Formation. The lithology of the Liuchungchi Formation is dominated by muddy silt (Chang 2008). Fossils are mainly found in a calcareous muddy sandstone, and some *Laganum* (Echinoidea; Clypeasteroida) fossils can be found in the same place. The collected sample size is too small to be included for statistical analyses.

2.1.7 Guanziling (Site 7 in Fig. 1)

Specimens were collected from the upper part of the Yunshuichi Formation (Chang 2008). A bioclastic sandstone can be found in the outcrop, containing fossil fragments of *Sinaechinocyamus*, bivalves, gastropods, corals, and small gravels. Based on the fossil assemblage, it can be inferred that the *Sinaechinocyamus* fossils did not get preserved *in situ* but were transported to the depositional site (Chu 2003).

2.1.8 Dongyuping (Site 8 in Fig. 1)

Specimens were collected from Dongyuping Islet in Wangan Township, Penghu County from a yellow-brown, poorly cemented sandstone. This sandstone is characterized by large cross-beds and ferriferous, well-cemented sand grains. The upper boundary of the sandstone is not exposed, and the lower boundary is a nonconformity associated with the basalt layer. According to the geologic map (Yen and Lee 2017), collected specimens are estimated to belong to the Holocene beach deposits (Yen and Lee 2017). Since the apical system of most specimens is damaged, key morphologic features cannot be determined and measured.

2.1.9 Gutingkeng (Site 9 in Fig. 1)

Wang (1984) reported a new species from the Gutingkeng Formation. However, the author was unable to re-locate the fossil site.

2.1.10 Zengwenxikou (Site 10 in Fig. 1)

Specimens of extant species *S. mai* were collected from the beach sediment of intertidal zone from Zengwenxikou in Cigu District, Tainan City (Chu 2003). A total of 62 complete samples was included in this study.

2.2 Statistical Analysis

The morphological measurement of *Sinaechinocyamus* basically refers to the method carried out for *Scaphechinus* *mirabilis* (Wang et al. 1984). In this study, test length (L), test width (W), and test height (H) of each specimen were measured (Fig. 2). The test length is the largest distance from the front to the rear of the test, the test width is the widest distance from left to right, and the test height is the distance from the bottom of the oral surface to the top of the aboral surface. A vernier scale was used as a measuring tool with an accuracy of 0.05 mm. Linear regression plots are included in the Appendixes Figs. A1 - A4.

Analysis of variance (ANOVA) with *post hoc* Student's t-tests for intergroup statistical testing and subsequent visualization were conducted through Prism 8.4.0 (GraphPad). Bonferroni correction was used for multiple comparison p-value corrections. The significance threshold for the corrected p-value was 0.05. Principle component analysis (PCA) was conducted through R 4.1.0 with homemade script utilization of *stats* package 4.1.0 and *ggplot2* 3.3.5 and *ggfortify* 0.4.13 for visualization.

Among 231 samples analyzed, 127 fossil samples collected from Sanying Bridge, Longgang, and Niupu were new. Fossil specimens (n = 42) collected from Guanziling in Tainan and the extant specimens (n = 62) collected from Zengwenxikou reported in Chu (2003) were also included in the analysis.

3. SYSTEMATICS

Class Echinoidea Leske 1778
Order Scutelloida Mongiardino Koch et al. 2018
Infraorder Scutelliformes Haeckel 1896
Family Taiwansteridae Wang 1984
Genus *Sinaechinocyamus* Liao 1979
Sinaechinocyamus mai (Wang 1984)

Description (modified from Wang 1984): Test is slightly transversely elongated. The greatest width occurs posterior to the apical system, test more or less inflated with the greatest height at the apical system. The oral surface is slightly concave with a low and wide keel between the peristome and posterior test margin. The apical system is distant from the center of apical system, approximately two-fifths of test length near anterior margin. Adult contains four large genital pores. Petals are wide and slightly restricted and diverge out distally. Each petal consists of 9 to 11 pairs of ambulacral pores. On oral surface, food grooves are absent. Peristome is centered on oral surface, and periproct is supramarginal on aboral surface. Internally, five pairs of simple radial supports are present around interambulacral. On aboral surface of holotype, 13 to 14 plates are present on ambulacra I and V, 13 plates in ambulacral II and IV, 12 plates in ambulacral III, and 5 to 8 plates in each interambulacral region. On oral surface of the holotype, 3 to 4 plates are present in each ambulacral and 2 to 3 plates are present in each interambulacral region. The first post-basicoronal ambulacral plates are greatly enlarged.

Remarks: Mooi (1990) compared the extant species of *S. planus* and *S. mai*, and found that they are very similar in size and shape. The difference lies in the ratio of test width to length, in which the W/L ratio is about 0.909 in *S. planus* and about 1.052 in *S. mai*.

4. RESULTS

4.1 Description of the Fossil Specimens

New fossil specimens of *Sinaechinocyamus* collected at 8 localities (Figs. 3-1 - 3-7) are all similar to modern specimens of *S. mai* (Figs. 3-8, 3-9) in size and shape. On average, a test is small, with 5 pairs of petals and 4 genital pores on the aboral surface. The peristome is about central in position in the oral surface, and food grooves are absent. The periproct is supramarginal in the aboral surface. Unlike the modern specimens with clear plate boundaries (Chen and Chen 1994), plate boundaries are difficult to identify on the fossil samples. Observe some broken specimens (Fig. 4), the inner support structures are simple five pairs, located on

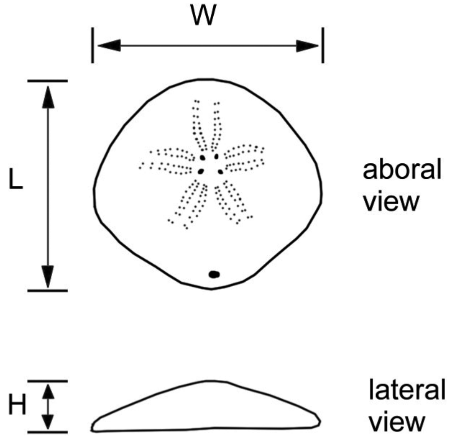


Fig. 2. Schematic diagram of *Sinaechinocyamus* for measurements used in this study.

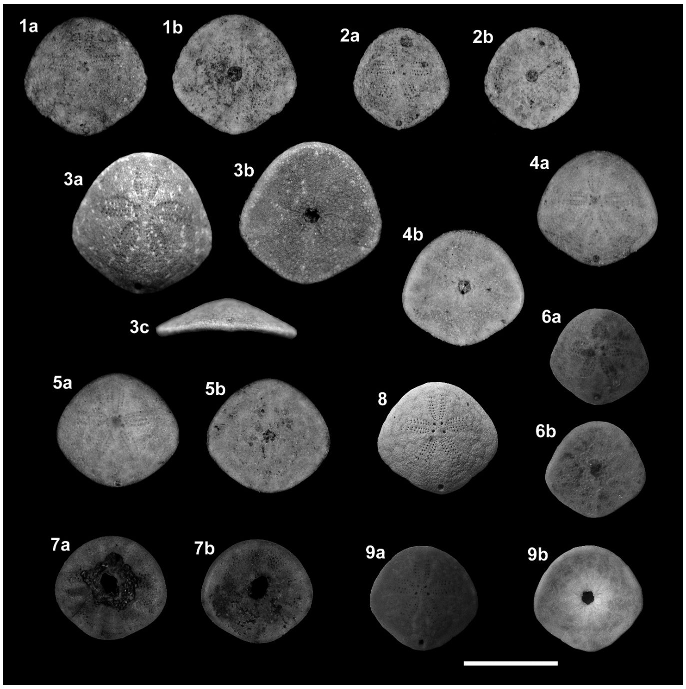


Fig. 3. Specimens of *Sinaechinocyamus* from different localities. 1 and 2: Sanying Bridge specimens, 3: Longgang specimen, 4: Niupu specimen, 5: Jhonglung specimen, 6: Guanzjling specimen, 7: Dongyuping specimen, 8 and 9: Zengwenxikou specimens. In every location, a: aboral view, b: oral view, c: posterior lateral view. Scale bar = 5 mm.

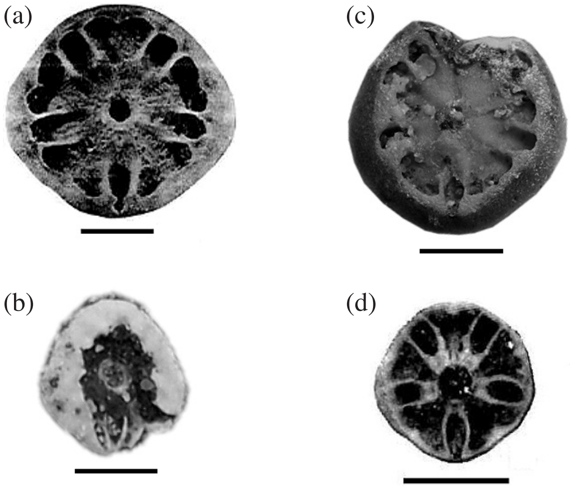


Fig. 4. Inner supporting structures of *Sinaechinocyamus*. (a) Recent specimen (modified from Wang 1984), (b) Bitoujiao specimen, (c) Longgang specimen, (d) Guanziling specimen. Scale bars = 3 mm.

the interambulacral zone. The inner support structures of the specimens from Longgang are extending from the test edge to about 1/2 of the radius. The inner support structures of the specimens from Guanziling are extending from the test edge to the peristome. The inner support structures of the specimen from Bitoujiao are extending to half of the radius, but the inner support structures of the specimen from the same place mentioned in Wang (1984) are extending from the test edge to the peristome.

4.2 Geological Ages of *Sinaechinocyamus* Fossils

Summarized the strata of the specimens collected (Fig. 5), the oldest production strata is Late Miocene Tapu Member of the Kueichulin Formation in north Taiwan (Sanying Bridge) to the Holocene beach sediments (Dongyuping). Based on the occurrence of fossils, most of them were collected with fossil debris. Therefore, they are estimated to be transported and re-stacked rather than deposited *in situ*, which cannot reveal the original living environment.

4.3 Statistical Analysis

The length (L), width (W), and height (H) of both fossil and extant *S. mai* from the five localities were included in the analysis. The violin plots of the distribution of individual parameters and inter-localities Student's t-test were shown in Fig. 6. In terms of length and width, the specimens from the Longgan site were significantly longer and wider than the counterparts from other localities. On the other hand, the height of *S. mai* specimens from different sites showed generally no significant outlier. Based on the methodology used by Wang (1984) and Mooi (1990), the ratio of width to length (W/L) and height to length (H/L) were calculated as well to account for the general body size difference among samples and localities. The results were shown in Fig. 7. The specimens from Longgang presented with W/L ratio significantly lower than the counterparts from other localities. On the other hand, the samples from Guanziling had higher H/L than other groups.

To summarize the three parameters used in this study, principal component analysis (PCA) was utilized to reduce the order. The results were shown in Fig. 8. The principal component 1 (PC1) explained up to 96.4% of data variation, which was in congruence with the results shown in the supplementary figure as the length, width, and height were all highly correlated with each other. As demonstrated by the cluster analysis, the 95% confidence clusters based on localities were highly overlapping, suggesting no distinct difference among the specimens from different collection sites in terms of overall external morphology. Furthermore, when comparing the pooled fossil specimens form the four

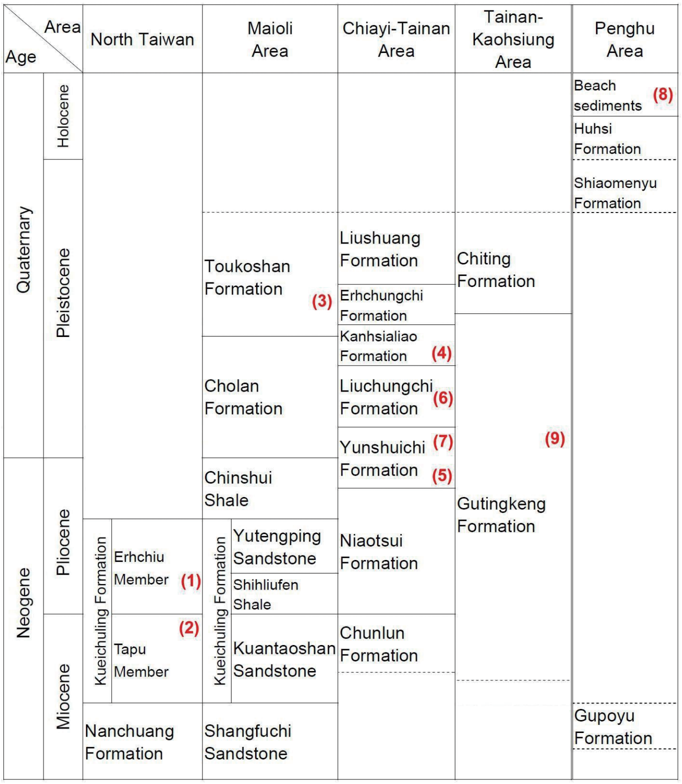
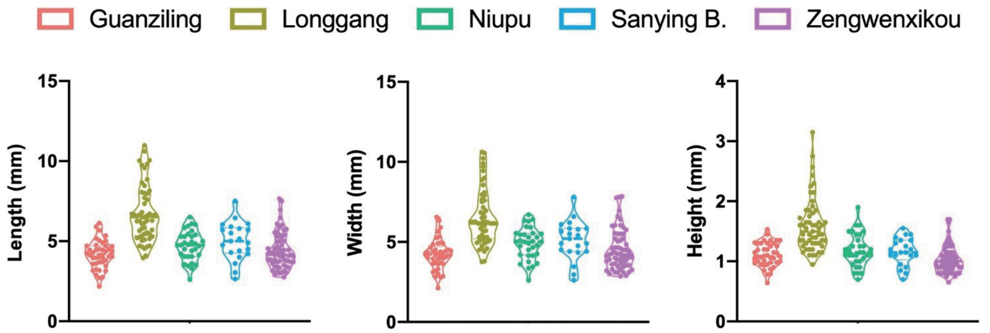


Fig. 5. Comparison of fossil collection strata. Localities are numbered and listed in Fig. 1 (modifying from Huang and Liu 1988; Chang 1990, 2008; Ho 1994; Shao and Kao 2009; Lin 2013; Lin and Chang 2014; Chen 2016; Yen and Lee 2017).

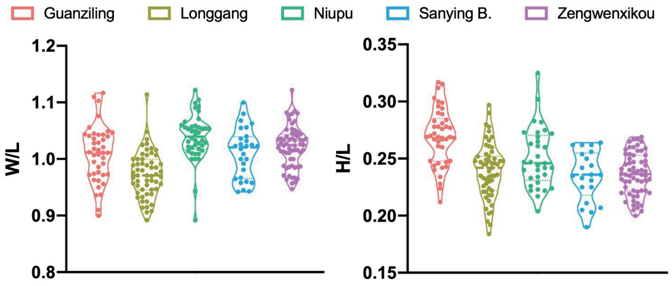


Corrected p-value	G	L	N	S
L	<0.001			
N	0.273	<0.001		
S	0.030	<0.001	>0.999	
Z	>0.999	<0.001	>0.999	0.273

Corrected p-value	G	L	N	S
L	<0.001			
N	0.056	<0.001		
S	0.017	<0.001	>0.999	
Z	>0.999	<0.001	>0.999	0.314

Corrected p-value	G	L	N	S
L	0.239			
N	>0.999	0.728		
S	>0.999	>0.999	>0.999	
Z	>0.999	0.039	>0.999	>0.999

Fig. 6. The violin plots of the length, width, and height of collected *Sinaechinocyamus* spp. specimens from four fossil and one extant localities. The table below shows the p-value of *post hoc* inter-group Student's t-test with Bonferroni correction.



Corrected p-value	G	L	N	S
L	<0.001			
N	0.018	<0.001		
S	>0.999	0.002	0.063	
Z	>0.999	<0.001	0.462	>0.999

Corrected p-value	G	L	N	S
L	<0.001			
N	0.006	0.259		
S	<0.001	>0.999	0.144	
Z	<0.001	>0.999	0.048	>0.999

Fig. 7. The violin plots of the width to length ratio (W/L) and height to length ratio (H/L) of collected *Sinaechinocyamus* spp. specimens from four fossil and one extant localities. The table below shows the p-value of *post hoc* inter-group Student's t-test with Bonferroni correction.

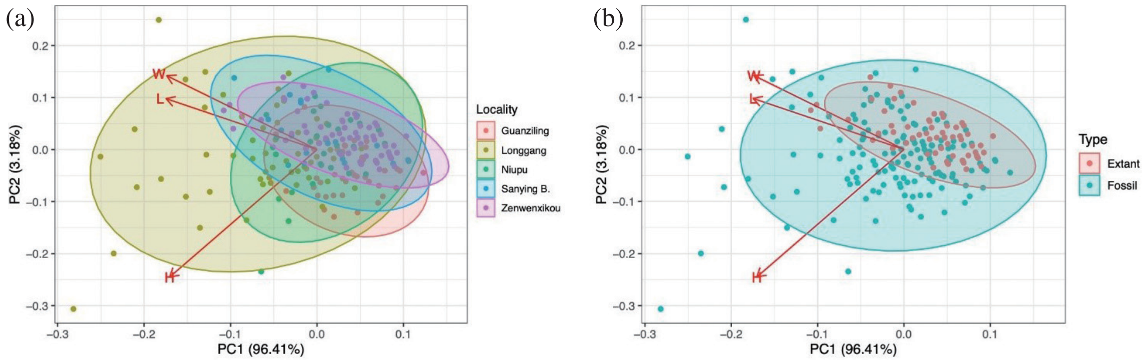


Fig. 8. The principal component analysis (PCA) of collected specimens of *Sinaechinocyamus* spp. based on the three measured morphological aspects (width, length, and height). (a) Grouping based on locality; (b) Grouping based on the specimen type (extant or fossil).

sites (Sanying Bridge, Longgang, Niupu, and Guanziling) with extant samples (Zengwenxikou), the clusters were totally overlapping, indicating the fossil *Sinaechinocyamus* sp. specimens in this study were within the morphological distribution of extant *S. mai*, and should be classified as *S. mai* accordingly.

5. DISCUSSION

Under close examination, morphologic features, such as outline, petals and plate arrangement, of *Sinaechinocyamus* specimens from various places of Taiwan are very similar. The obvious difference is the extension of the inner support structures. The inner support structures of the extant *Sinaechinocyamus* species consist of five pairs, extending from the test margin to approximately 3/5 of the radius. The inner support structure of the specimens from Longgang on average extends from the test margin to approximately 1/2 of the radius. The inner support structure of the specimens from Guanziling extends from the test margin to the peristome. The inner support structure of the specimen from Bitoujiao illustrated in Wang (1984) extends from the test margin to peristome. However, by revisiting the fossil sites and collected new samples, some specimens only extend to half of the radius (Fig. 4). In addition, most of the small specimens (< 5 mm in length) have the inner support structure extending from the test margin to the peristome, while this feature does not present in larger specimens. Thus, such change may reflect an ontogenetic feature.

Currently, there are three species reported from Taiwan. According to Wang (1984), *S. mai* has interambulacral plates discontinuous on oral surface; *S. pitouensis*† has interambulacral (1b), (4a), and (5) plates discontinuous on oral surface; *S. gutingkengensis*† has all interambulacral plates continuous on oral surface. Wang (1984) hypothesized that the evolutionary trend of the interambulacral plate on the oral surface should be first appeared as completely continuous to partially continuous, and then to all discontinuous. Chen and Chao (1997) compared the growth process of the extant *S. mai* with *Scaphechinus mirabilis* and suggested that the interambulacral plates on the oral surface are all continuous in juveniles and become discontinuous in adults. Moreover, illustrated specimens of the fossil species *S. pitouensis*† and *S. gutingkengensis*† studied by Wang (1984) were smaller than the extant specimens of *S. mai*. In addition, the W/L of the extant *S. mai* observed by Mooi (1990) is about 1.052, whereas that of the extant specimens collected from Zengwenxikou section reported in Chu (2003) is about 1.107. Thus, there are at least 5% variations of W/L ratios among modern populations.

By combining all fossil data from four localities and modern samples from one locality, the W/L ratios between populations and overall population are very similar (Appendix Fig. A3). The H/L ratios exhibit similar results (Appendix Fig. A4). In particular, data representing individuals smaller than 7 mm are very concentrated for both L vs. W plot (Appendix Fig. A3) and L vs. H plot (Appendix Fig. A4). In summary, among 231 samples analyzed, fossil and living samples are indistinguishable. They should all be identified as *S. mai*.

6. CONCLUSION

In summary, fossil occurrences of *Sinaechinocyamus* in Taiwan range from Tapu Member of Kueichulin Formation (late Miocene) to Toukoshan Formation (Pleistocene). Based on the fossil records, *Sinaechinocyamus* first appeared in the northern part of Taiwan during the late Miocene and migrated southward by the late Pliocene.

The interior support structure within the test of *Sinaechinocyamus* changes ontogenetically. The continuity of the interambulacral on the oral surface changes at different growth stages. Interambulacral plates are mostly continuous in juveniles and become mostly discontinuous in adults. Thus, the species characters diagnosed by Wang (1984) are not supported by the present study.

Among the fossil localities, the overall difference between the maximum and minimum W/L ratios is approximately 11.3%, and there is no obvious difference between the samples and within the sample (Figs. 6 - 7). More specifically, fossil data and modern samples of *S. mai* are indistinguishable (Fig. 8). Thus, all fossil samples reported here should be treated as *S. mai*.

Acknowledgements Special thanks to the editor-in-chief of *TAO* for the opportunity summarizing my work resulting from the field surveys for the past decade. Thanks to Kae-Shyuan Shieh and two anonymous reviewers for reviewing and commenting on the earlier drafts.

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APPENDIX

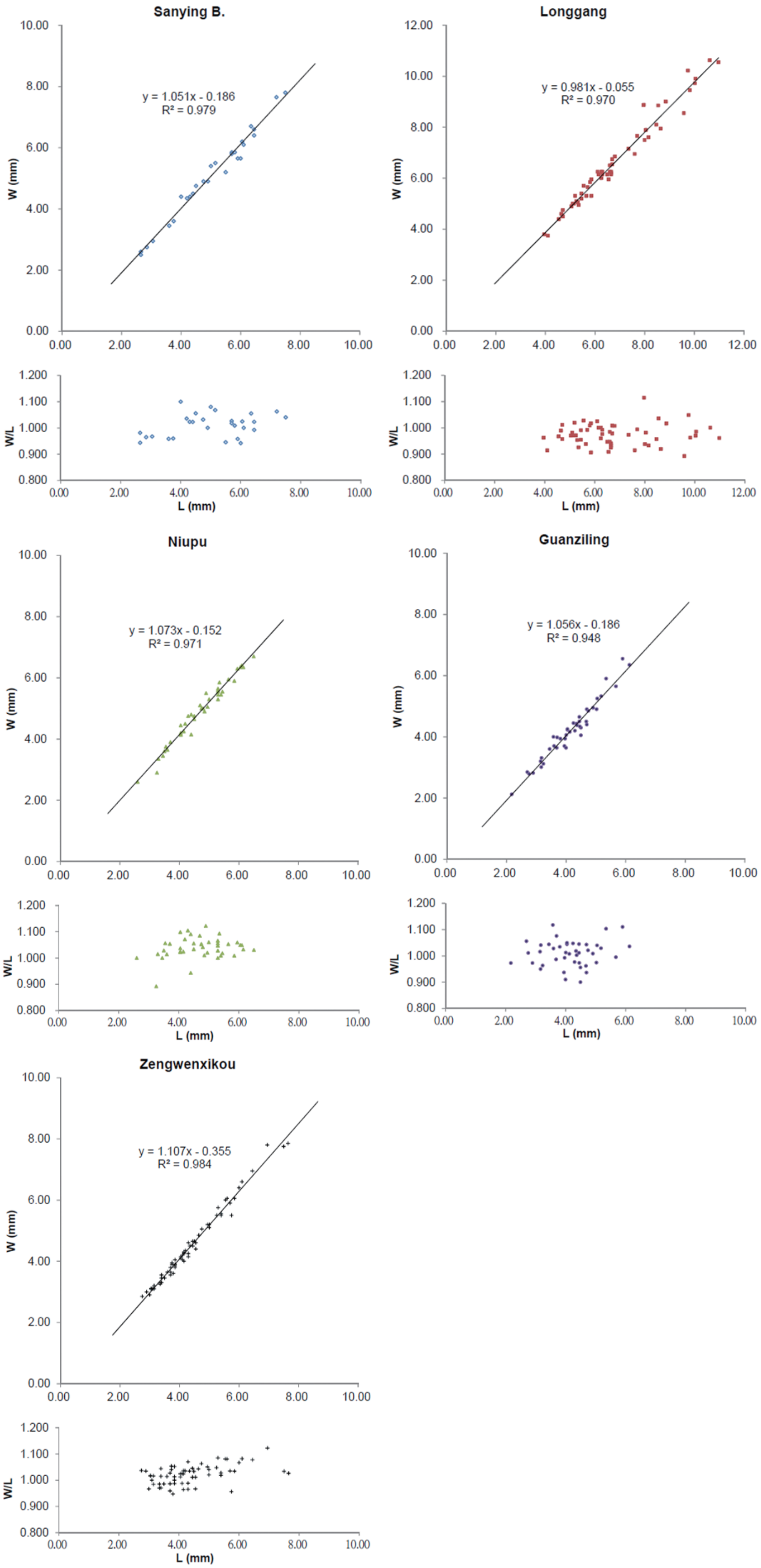

Fig. A1. Results of L vs. W (above) and L vs. W/L (below) bivariate plots of fossil data from each locality.

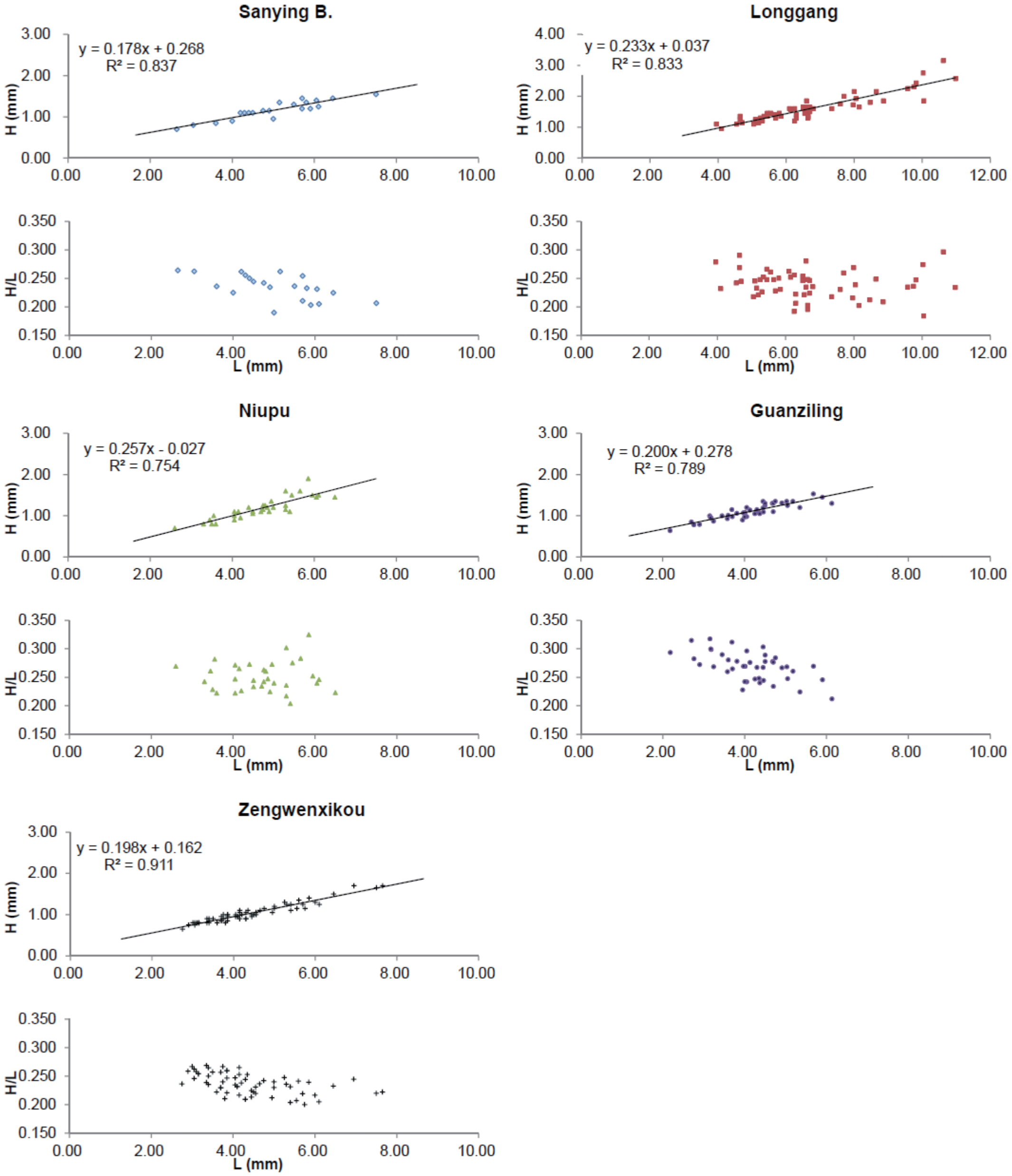

Fig. A2. Results of L vs. H (above) and L vs. H/L (below) bivariate plots of fossil data from each locality.

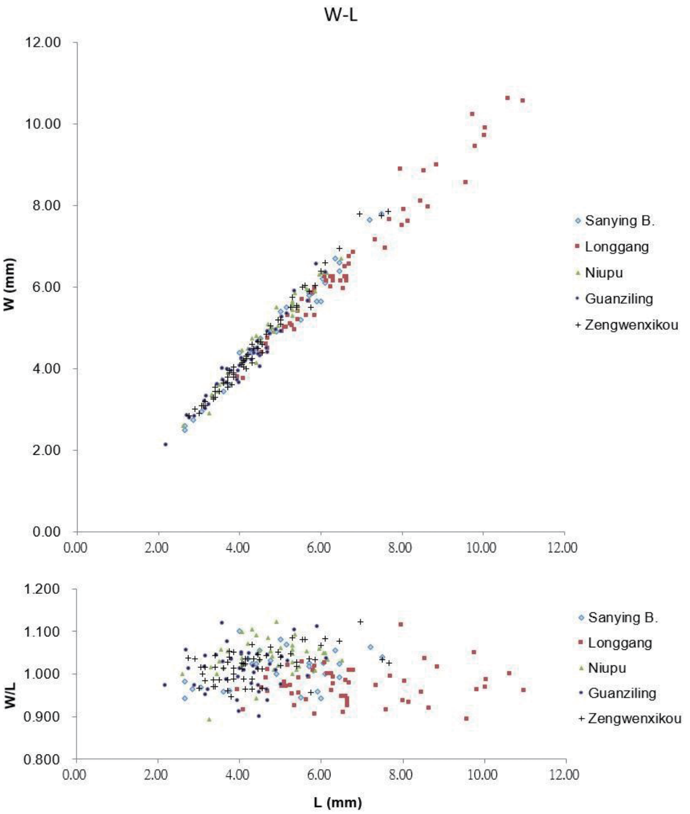

Fig. A3. L vs. W bivariate plot for all data (n = 231).

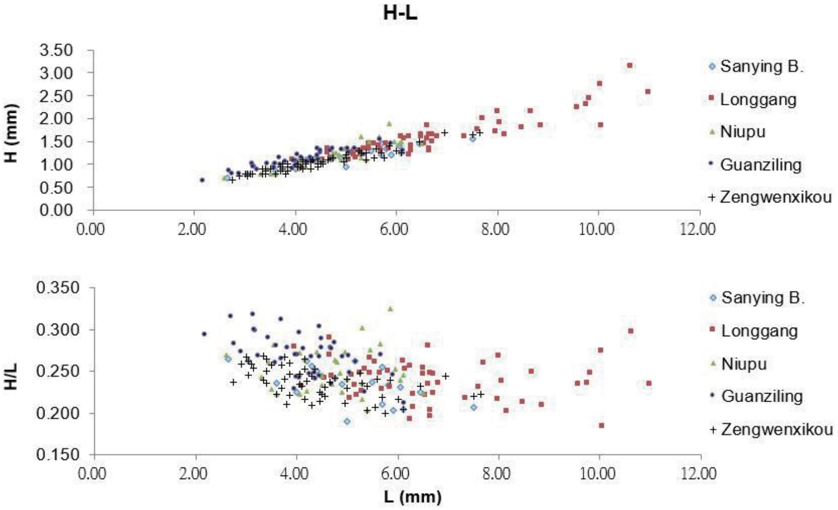

Fig. A4. L vs. H bivariate plot for all data (n = 231).