

New occurrence of fossil lovenioid echinoids from Taiwan with both internal and external moulds

Chia-Hsin HSU¹, Jih-Pai LIN^{2*}

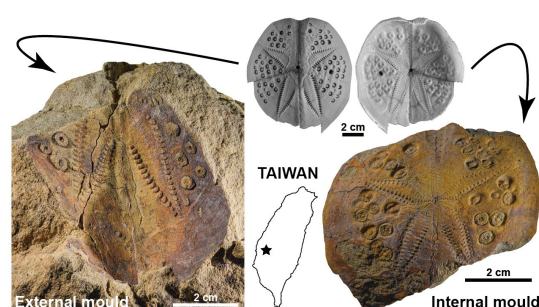
¹*School of Ocean and Earth Science, University of Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, UK*

²*Department of Geosciences, National Taiwan University, 1 Roosevelt Rd Sec 4, Taipei 106319, Taiwan*

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ABSTRACT

Taphonomy plays a crucial role in shaping the fossil record and thereby influencing broader interpretations of evolution, biodiversity and palaeoecology. However, its effects on echinoderm taxonomy are seldom considered. Here, we report new fossil lovenioid echinoids from the Late Miocene of Taiwan, represented by both external and internal moulds that exhibit markedly different morphologies. The external moulds display the typical diagnostic features of the genus *Breynia*, whereas the internal moulds lack the inner fasciole and possess pore pairs fully developed to the apical system, making them resemble *Spatangomorpha*, a fossil genus currently treated as in need of re-description. However, by comparing the fossil internal moulds with the internal surface of skeletons of modern *Breynia* species, we found that their morphologies closely resemble each other, indicating that the fossils are indeed *Breynia* species but reflect the preservation of the internal surface of the skeletons. Our results demonstrated that taxonomically important traits of echinoids such as fascioles and pore pairs may be different in internal mould preservation. This case study highlights that relying solely on preserved internal moulds or steinkerns can lead to taxonomic misidentification of fossil echinoids, which may be generally applicable to other biomineralised fossils.



Keywords: dissolution, fossilisation, spatangoid, steinkern, taphonomy

Introduction

Fossil preservation is inherently biased and non-random, representing the cumulative outcome of a complex series of post-mortem and depositional processes. Over the past decades, palaeontologists have delved deeply into the field of taphonomy to identify the processes and patterns of fossilisation, aiming to better interpret the information preserved in fossil specimens (Hughes, 1995; Martin, 1999).

The taphonomy of echinoids is particularly distinct and complex among skeletonised animals, especially during early biostratinomic stages such as erosion, trans-

port and deposition (Nebelsick and Mancosu, 2021). Firstly, echinoids possess multi-plated calcareous skeletons that can disarticulate to various degrees during taphonomic processes (e.g. Smith, 1984; Donovan and Pawson, 2013; Lee *et al.*, 2019). Secondly, differences in micro-stereomic structures and macro-skeletal architectures result in variable toughness and strength of skeletal plates and their connections (e.g. Smith, 1990, 2005). Thirdly, echinoids inhabiting different benthic environments exhibit markedly different preservation potentials (e.g. Kier, 1977; Greenstein, 1993). These intrinsic and extrinsic factors lead to a highly complex fossil record that is controlled by multiple interacting variables. As a result, large-scale interpretations of palaeobiodiversity dynamics (Smith, 1990; Greenstein, 1992; Smith *et al.*, 2001, 2006; Smith and Benson, 2013; Thompson and Denayer, 2017; Thompson *et al.*, 2025), biogeography (Carter and McKinney, 1992) and palaeoecological pat-

* Corresponding author: Jih-Pai LIN (alexjplin@ntu.edu.tw)



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terns (Ernst, 1969, 1970; Smith *et al.*, 1995; Kroh and Nebelsick, 2003; Smith and Rader, 2009; Thompson *et al.*, 2015; Thompson and Ausich, 2016) often take taphonomic effects into careful consideration.

Although the early biostratinomic processes of echinoid taphonomy have been extensively studied, the later stages, particularly dissolution and early diagenesis, have received much less attention. Because echinoid skeletons are composed of high-Mg calcite, which is more soluble than low-Mg calcite (Brown and Elderfield, 1996; Davis *et al.*, 2000), they are more likely to dissolve and be preserved as moulds, leading to strong differences in preservation potential (Cherns and Wright, 2009).

Furthermore, differences in preservation type can lead to fundamental taxonomic errors. In bivalves and brachiopods, shell ornamentation is often only present on the external surface. When fossils are preserved as internal or external moulds, the resulting morphologies can look very different, although they belong to the same species. A classic example is provided by Crampton (2004), who demonstrated that *Inoceramus ipuanus* Wellman, 1959 (described from a composite external mould of an adult preserved in sandstone), *I. kapuus* Wellman, 1959 (from a high-fidelity but flattened external shell surface in mudstone) and *I. urius* Wellman, 1959 (from an uncrushed internal mould of a juvenile) all represent the same species *Mytiloides ipuanus* (Wellman, 1959). Similar issues have been noted in Palaeozoic praecardioid bivalves (Johnston and Collom, 1998: p. 350), arthropods (e.g. Pulsipher *et al.*, 2022) and echinoids (Müller, 1957; Nebelsick, 2008; Donovan and Lewis, 2011; Tomašových *et al.*, 2024). Overall, how taphonomy affects taxonomy in other taxa and at broader scales remains largely underexplored, likely due to the lack of sufficiently well-preserved fossil datasets.

Here, we describe new fossil lovenioid echinoids from the Late Miocene of Taiwan, represented by both external and internal moulds. These specimens provide examples of distinct internal and external preservation within a single echinoid species. We further discuss their ecology and environments, potential taphonomic pathways and taxonomic implications for related groups, aiming to understand how modes of preservation may have biased the echinoid fossil record.

Geological setting

Taiwan is situated at the suture zone between the Eurasian Plate and the Philippine Sea Plate. Since the onset of active orogeny around 6.5 Ma, rapid uplift has exposed a complete sequence of late Cenozoic marine and terrestrial strata (Lin *et al.*, 2003), yielding diverse fossil faunas (e.g. Senan *et al.*, 2023; Přikryl *et al.*, 2024;

Hsu *et al.*, 2025). Among these, the fossil echinoid fauna stands out as one of the most diverse and iconic groups in Taiwan (e.g. Ho *et al.*, 2022; Hsu *et al.*, 2024; Chen *et al.*, 2025), providing valuable insights into the most recent chapter of echinoid evolutionary history and the development of biodiversity hotspots in the Western Pacific (e.g. Lee *et al.*, 2023; Hsu and Chang, 2025; Chang *et al.*, 2025; Hsu *et al.*, 2025).

All fossil echinoids examined in this study were collected from a large, angular sandstone boulder located beside the Tsengwen Reservoir in southern Taiwan (approximately 23°17'56"N, 120°34'13"E). The Tsengwen Reservoir, the largest lake and reservoir in Taiwan, was constructed in the 1970s. The surrounding region displays a wide range of exposed strata, from the Upper Miocene Chengchikeng Formation to Pleistocene and Holocene deposits, shaped by complex faulting and folding. Nevertheless, a general NE–SW strike trend is observed across most strata, corresponding to the reservoir's overall orientation (Shao and Kao, 2009). The outline of the Tsengwen Reservoir closely mirrors the regional geology. Although the fossils were found in a boulder rather than *in situ*, their lithological characteristics, the collector's field notes and the reservoir's stratigraphic context all suggest that they most likely originated from the Changchikeng Formation (Figure 1), which is characterized by extremely well-cemented sandstone layers as seen in the boulder containing the studied fossils.

Regionally, the Changchikeng Formation is exposed across Chiayi, Tainan and Kaohsiung counties and consists of interbedded dark gray shale and gray sandstone, with muddy sandstone, calcareous sandstone, mudstone and basaltic tuff layers (Shao and Kao, 2009; Chen, 2016). It is interpreted as representing inner offshore environments (Chen, 2016). The formation is about 1200 meters in thickness, conformably overlying the Honghuatzu Formation and underlying the Tangenshan Sandstone (Chen, 2016). The top of the Changchikeng Formation has been dated to the Late Miocene based on calcareous nannofossil *Discoaster quinqueramus* Gartner, 1969, which represents the boundary between NN10 and NN11 nannofossil biozone of Martini (1971) (Chen, 2016).

Material and methods

Six fossil lovenioid echinoids (NTUG300-FU01088, NTUG300-FU01089, NTUG300-FU01090, NTUG300-FU01094, NTUG300-FU01095, NTUG300-FU01097) were examined and described. A description of one fossil pericosmid echinoid found in the same boulder is also included in the supplementary information. All fossils were originally collected by S.-K. Cho, who donated them to the Department of Geosciences, National Taiwan

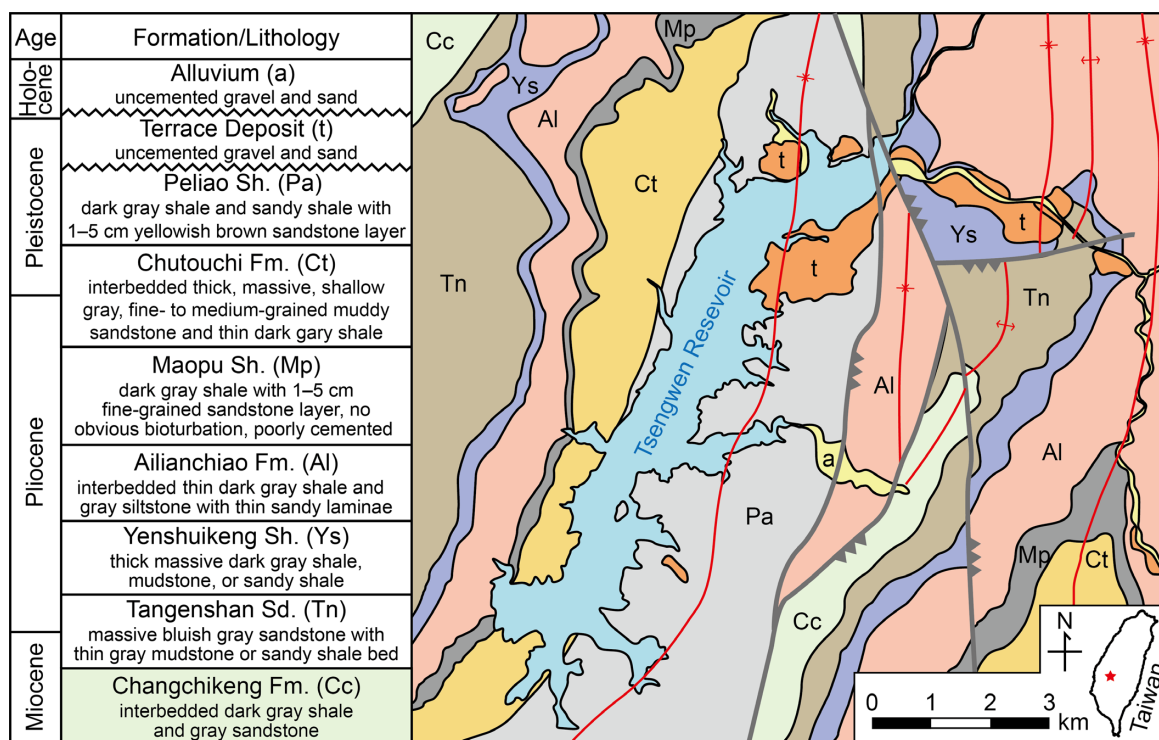


Figure 1. Geological map and stratigraphy of the study area (modified from Sung *et al.*, 2000; Shao and Kao, 2009). Red star represents the fossil locality. Abbreviations: Fm., Formation; Sd., Sandstone; Sh., Shale.

University, Taipei, Taiwan (NTUG). The studied fossils are preserved without calcareous skeletons and consist of six internal moulds and one external mould. To enhance contrast and improve clarity of surface structures, low-angle illumination photography was applied. Additionally, modern specimens of *Breynia elegans* Mortensen, 1948 were studied also for comparison, including a broken specimen (NTUG300-FU01091) and juvenile (NTUG300-FU01092) and adult (NTUG300-FU01093) individuals. Taxonomic nomenclature follows Kroh and Mooi (2025). Morphological descriptions adhere to the terminology of Lewis and Donovan (2007), whereas detailed descriptions of pore pairs and tubercles follow Smith (1980a) and Smith (1980b), respectively. The ambulacral and interambulacral series are numbered according to Lovén's system (Lovén, 1874). All measurements were taken with a digital calliper. All specimens examined in this study are listed in Table S1.

Results

Comparison of fossil moulds with modern test surfaces

The internal and external aboral surfaces of modern skeletons of *Breynia elegans* exhibit distinct differences in several specific traits (Figure 2A, B). In the petals, all

pore pairs on the internal surface are significantly larger than those on the external surface, most notably within the inner fasciole. On the external surface, the pore pairs are markedly reduced in size or even absent (Figure 2A, C, E). In contrast, on the internal surface, although most pores are not open, the sunken pits corresponding to the pore-pair positions remain visible and extend toward the apical system.

For the primary tubercles, the most evident difference lies in their structure and arrangement (Figure 2A, B). On the external surface, a primary tubercle is composed of a convex mamelon, which directly articulates with the spine, a convex boss where the catch apparatus is attached, and a sunken areole for muscle attachment, arranged from the centre to the margin (Figure 2A). However, on the internal surface, markedly different morphologies are observed. The boundary between the mamelon and the boss cannot be clearly distinguished (Figure 2B). The bosses are inflated toward the interior of the test, which makes their area larger on the internal surface than on the external surface (Figure 2B). Likewise, because the areoles are inflated toward the interior of the test, they become enlarged and the tubercles abut one another on the internal surface, whereas they remain separated on the external surface (Figure 2B). Miliary tubercles, though distributed across the aboral external surface, are absent

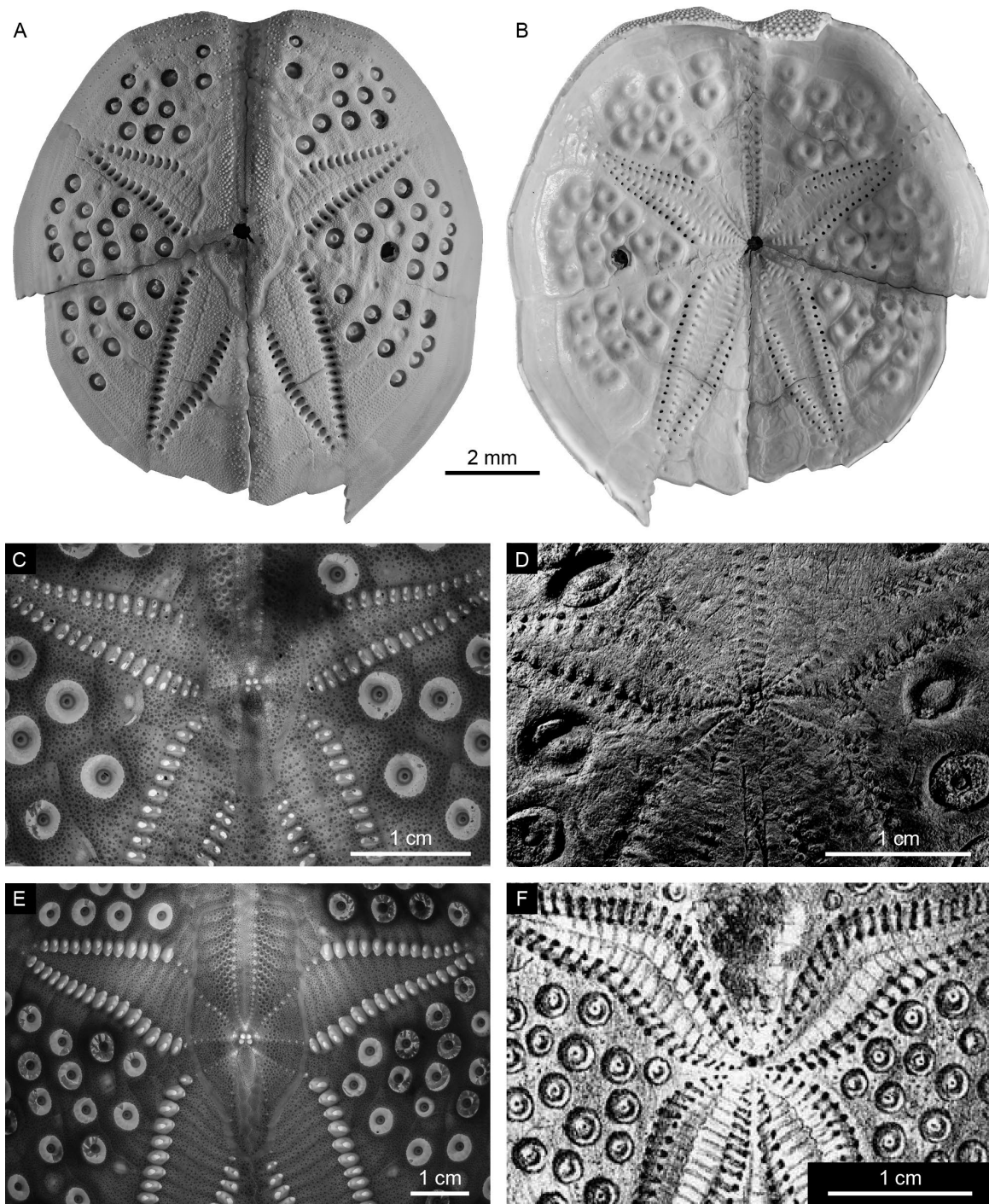


Figure 2. Aboral surface morphology of *Breynia* and *Spatangomorpha*. **A, B**, *Breynia elegans*, external (A) and internal (B) surfaces of extant broken specimen (NTUG300-FU01091); **C**, *B. elegans* (extant, young adult; NTUG300-FU01092); **D**, *Breynia* sp. (fossil, NTUG300-FU01089); **E**, *B. elegans* (extant, large adult; NTUG300-FU01093); **F**, *Spatangomorpha eximia* (fossil, original illustration; modified from Böhm, 1882; Smith and Kroh, 2011). External aboral surfaces of *B. elegans* (A, C, E) show consistent morphology, with inner fasciole and apical pore pairs reduced in size. In contrast, internal aboral surface of *B. elegans* (B) lacks fasciole, with apical pore pairs clearly sunken and distinct, matching fossil steinkern *Breynia* sp. (D) and *S. eximia* (F).

Table 1. Comparison of internal and external moulds of fossil lovenioid echinoids from Taiwan.

Character	Internal mould	External mould
Size of pore pairs	large	small
Adapical pore pairs	extend toward apical system	reduced in size or absent
Aboral pore pairs outside petaloid areas	extend toward test margin	absent
Primary tubercles	enlarged and contacted; mamelon–boss boundary unclear	separated; mamelon–boss boundary clear
Miliary tubercles	absent	present
Fascioles	absent	present

on the inner surface (Figure 2A, B). Fascioles also differ between the two surfaces. The inner fasciole is clearly visible on the external surface in all examined specimens, including both young and large individuals (Figure 2A, C, E), whereas no fasciole pattern or structure can be identified on the internal surface (Figure 2B).

The internal and external mould fossils show similar morphological differences consistent with those observed in the internal and external surfaces of modern specimens, respectively. Internal moulds exhibit fully developed petals adapically (Figures 2D; 3A, G; 4A, D, F, G) and an absence of preserved inner fascioles (Figures 3A; 4A, G). In contrast, external moulds show markedly reduced pore pairs within the inner fasciole, relatively distinct and non-contacting primary tubercles, numerous small pits representing traces of miliary tubercles and well-preserved fasciole structures (Figure 5).

The only structure that is inconsistent between the fossil materials and modern skeletons is the primary tubercle observed in internal moulds. In the examined internal mould fossils, some tubercles show a morphology similar to the internal surface of modern skeletons, with enlarged, contacting tubercles and no clear boundary between mamelons and bosses (Figure 4F–H). However, in some specimens, most tubercles exhibit sunken bosses and convex areoles (Figure 3A, G). In addition, both morphologies may occur within a single specimen (interambulacrum 1 of Figure 4D) and even within a single tubercle (interambulacrum 3 of Figure 3A). Based on observations of this tubercle (interambulacrum 3 of Figure 3A), it is inferred that the unusual morphology, in which the areoles appear convex, most likely results from incomplete separation between the internal moulds and the surrounding sediment (matrix). Parts of the sediment remain adhered to the internal mould, making the areoles appear convex and the bosses relatively sunken.

Overall, by comparing the fossil moulds with the modern skeletons, these results indicate that the morphological differences between internal and external moulds

represent intrinsic structural differences of the test surface. They most likely belong to the same species, as no additional differences beyond those associated with the two surfaces are observed in *Breynia elegans*. Diagnostic features preserved in both internal and external moulds are listed (Table 1).

Systematic palaeontology

Class Echinoidea Schumacher, 1817

Order Spatangoida Agassiz, 1840

Family Loveniidae Lambert, 1905

Genus *Breynia* Desor in Agassiz and Desor, 1847

Type species.—*Spatangus australasiae* Leach, 1815; by original designation (Agassiz and Desor, 1847: p. 12).

Diagnosis.—Loveniid echinoid with frontal sulcus. Anterior and posterior petals confluent; pore pairs significantly reduced in size or disappear within inner fasciole. Adoral anterior ambulacra not constricted. Aboral primary tubercles camellate, confined within peripetalous fasciole. Oral primary tubercles small, non-camellate, restricted to primordial plates of paired interambulacra. Internal, peripetalous and shield-shaped subanal fascioles present. Labrum extending to third ambulacral plate. Sternal plates fully tuberculate, near-straight connection to episternal plates. Six to eight ambulacral plates extending into subanal fasciole (modified from Mortensen, 1951; Kroh, 2007; Smith and Kroh, 2011).

Breynia sp.

Figures 2D, 3–5, S1, S2A–B

Material.—Six fossils from Tsengwen Reservoir, southern Taiwan. Changchikeng Formation, Late Miocene (NTUG300-FU01088, NTUG300-FU01089, NTUG300-FU01090, NTUG300-FU01094, NTUG300-FU01095, NTUG300-FU01097).

Description.—Test medium (test length = 69.2–81.8

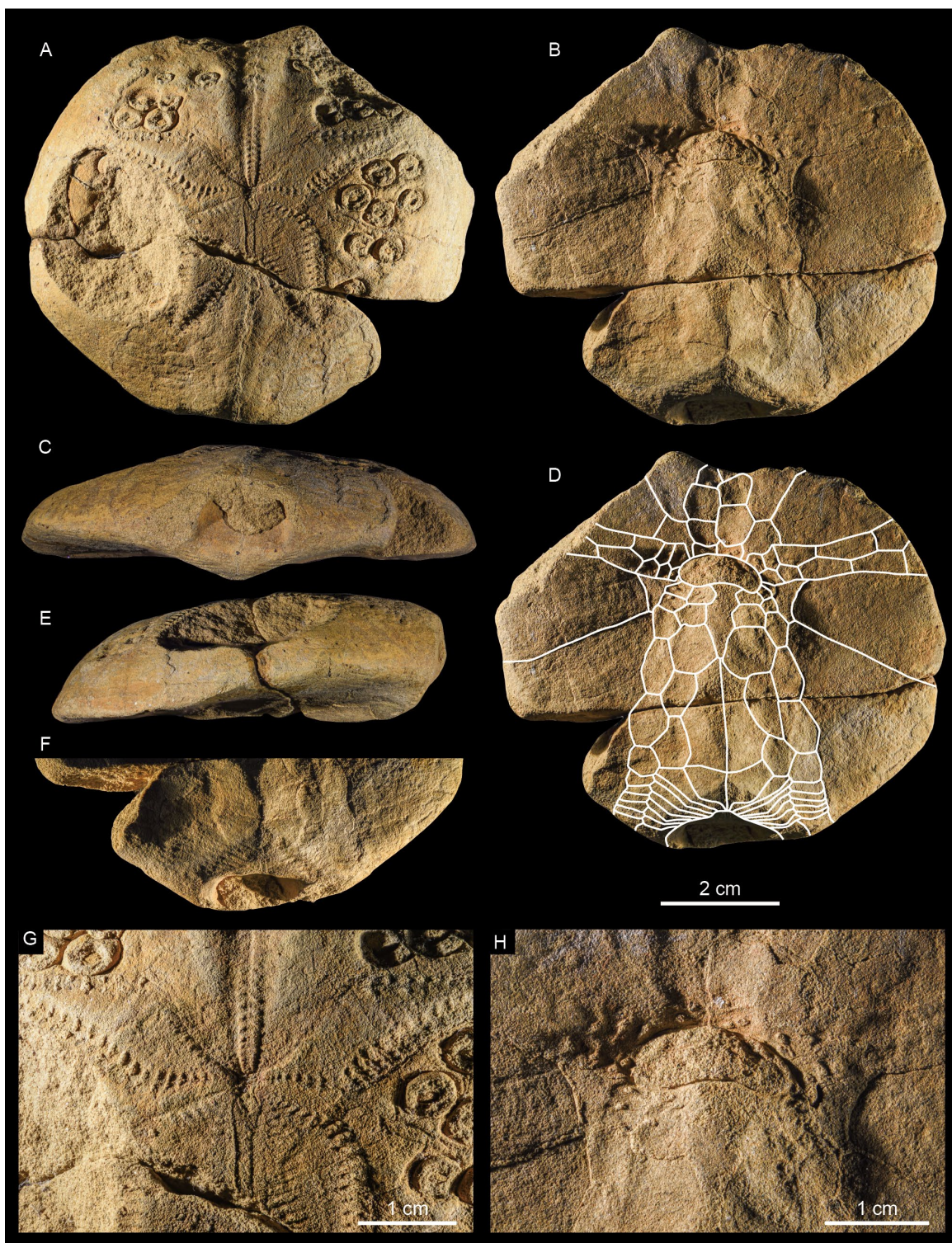


Figure 3. *Breynia* sp. from Tsengwen Reservoir, southern Taiwan. Changchikeng Formation, Late Miocene. Steinkern (NTUG300-FU01088): A, aboral view; B, oral view; C, posterior view; D, oral plating; E, lateral view; F, oblique view; G, apical area; H, peristome.



Figure 4. *Breynia* sp. from Tsengwen Reservoir, southern Taiwan. Changchikeng Formation, Late Miocene. A–E, Steinkern (NTUG300-FU01089): A, aboral view; B, oral view; C, lateral view; D, apical area; E, peristome. F–H, Steinkern (NTUG300-FU01090): F, apical area; G, aboral view; H, lateral view.

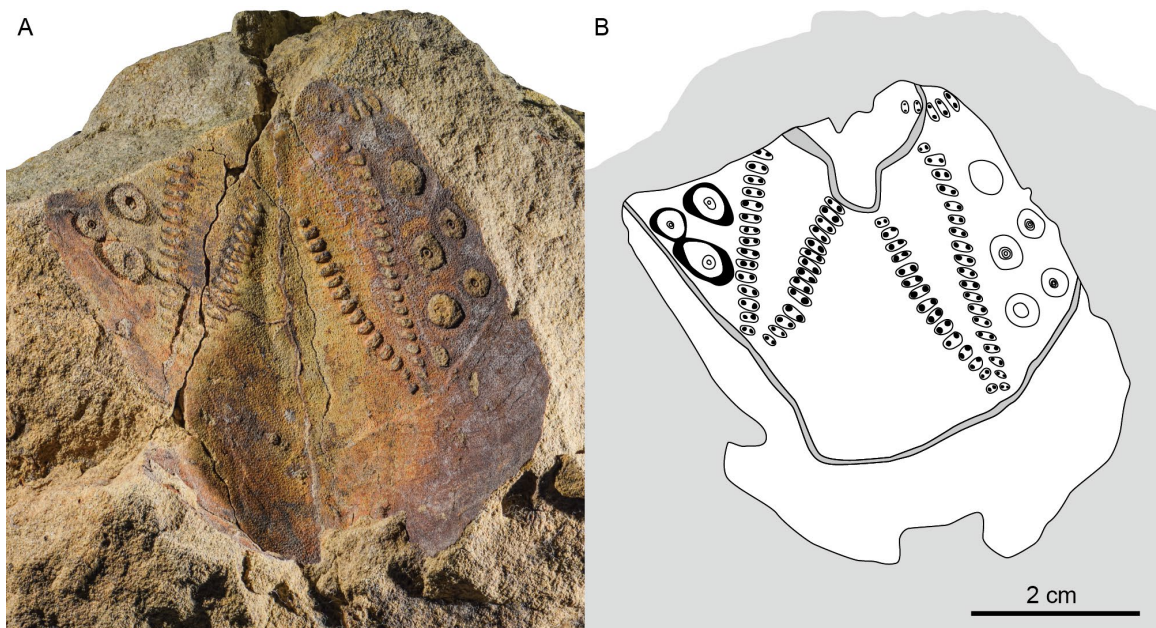


Figure 5. *Breynia* sp. from Tsengwen Reservoir, southern Taiwan. Changchikeng Formation, Late Miocene. External mould (NTUG300-FU01097): **A**, photograph; **B**, illustration.

mm, test width = 57.1–78.4 mm; 70–113% of test length; Table S2), heart-shaped; height low in profile (test height = 26–32% of test length, mean = 29%; Table S2). Maximum width slightly anterior (Figure 3A); maximum height midway between apical system and posterior margin (Figure 3E). Aboral surface flat, not keeled posteriorly (Figure 3C, E); frontal groove shallow, width similar to petal (Figures 3A; 4A, G). Oral surface generally flat, plastron keeled (Figure 3C, E). Posterior margin high and truncated, sunken around periproct (Figure 3C, E, F),

Apical disc aboral and slightly anterior (Figures 3A; 4A, G), with four gonopores (Figure 4A, D). Detailed plating structure unavailable.

Anterior ambulacrum non-petaloid, sunken, with straight, nearly parallel differentiated pores, forming a shallow frontal groove anteriorly from apical disc to peristome (Figures 3A, B; 4A, G).

Ambulacra I, II, IV and V petaloid aborally, lanceolate, flat, with pore pairs sunken separately, extending approximately 70% of the distance between apical disc and margin (Figures 3A; 4A, G); widest point near inner fasciole, where interporiferous zones are two to three times wider than a single pore-pair column (Figure 5). Anterior and posterior petals approximately equal in length (Figure 4A) or anterior petals slightly shorter than posterior petals (Figure 4G). Anterior petals diverge at about 130°, with about 22 double-series pore pairs (Figure 3A, G). Posterior petals diverge at about 60°, with about 27 double-series pore pairs of similar size (Figure 3A, G). Pore pairs

within inner fasciole significantly reduced in size (Figure 5). Interambulacra 1 and 4 amphiplacous adorally (Figure 3D). Adoral ambulacra with sphaeridial pits.

Plastron triangular, widest posteriorly, similar in width to a single adjacent ambulacrum (Figure 3D); mesamphisternous, with nearly symmetrical sternal plates and biserially offset episternal plates (Figure 3D). Labrum elongate, narrow, reaching the third adjoining ambulacral plate, connecting sternal plates (Figure 3D). Sternal plates elongate, sutured to episternal plates near posterior margin (Figure 3D). Seven ambulacral plates extending into subanal fasciole region (Figure 3D, F).

Peristome kidney-shaped, situated about 30% of test length from anterior margin (Figure 3B, D). Periproct oval, located at top of posterior truncated surface (Figure 3C, F).

Inner fasciole lobate posteriorly (Figure 5); peripetalous fasciole rounded (Figure 5); subanal fasciole unpreserved.

Tubercles of two main types: primary and miliary. Aboral primary tubercles camellate, confined within peripetalous fasciole; 7–10 primary tubercles in each interambulacrum 1 and 5 and 5–8 in each interambulacrum 2 and 4 (Figures 3A; 4A, G). Oral primary tubercles small, non-camellate, restricted to primordial plates of paired interambulacra. Aboral miliary tubercles nearly homogeneous and dense, covering the entire surface (Figure 5A). Oral miliary tubercles unpreserved (Figures 3F, S1).

Remarks.—All examined specimens (except for one; Figure S2C, D) are assigned to the genus *Breynia* mainly based on their overall outline, petal morphology, tubercle arrangement and fasciole pattern, which clearly distinguish them from the similar genera *Lovenia* and *Echinocardium*. The fossils differ from *Lovenia* in possessing a peripetalous fasciole that encloses all camellate aboral primary tubercles and from *Echinocardium* in having the same fasciole and aboral primary tubercle patterns together with a narrow and elongate labrum (Shigei, 1986).

At the species level, confident identification is hindered by the high degree of ontogenetic and intraspecific variation within *Breynia* (McNamara, 1982) and the limited number of available fossil specimens. Currently, five extant and four to nine fossil species are recognised within *Breynia* (Smith and Kroh, 2011; Kroh and Mooi, 2025), all restricted to the Indo–West Pacific region (Smith and Kroh, 2011; Kroh and Mooi, 2025). In Taiwan, *B. elegans* is the only extant species recorded (Lee, 2020). However, the examined fossils differ from *B. elegans* in having wider petals, anterior and posterior petals of equal length and a more rounded posterior margin.

Other fossil species previously reported from Taiwan include *B. carinata* d'Archaic and Haime, 1853 from the Miocene of northern and central Taiwan (Hayasaka, 1948; Cheng and Wang, 1981; Huang, 2011), *Breynia* sp. from southern Taiwan (Huang, 2015) and *B. cordata* Hayasaka, 1947 from the Pleistocene of northern Taiwan (Hayasaka, 1947; Huang, 2011). *B. testudinaria* Hayasaka, 1947 is not considered here, as it is most likely a synonym of *B. cordata* (Huang, 2011; Chang, pers. comm.). Because these species were described from few, often poorly preserved, generally larger specimens (>10 cm test length), ontogenetic and intraspecific variation between them and the present material cannot be thoroughly evaluated. Accordingly, the studied fossils are conservatively referred to the genus level. Nevertheless, they most closely resemble *B. cordata* in having wide petals, anterior and posterior petals of equal length and a slightly overhung periproct.

Discussion

Ecological implications

The lifestyle and habitat of organisms are closely correlated with the final morphologies of fossils preserved in rocks. The majority of spatangoid echinoids are known for their infaunal lifestyle, with overall morphologies corresponding to different burrowing mechanisms, available burrowing depths and preferred sediment grain sizes (Kanazawa, 1992; Saitoh and Kanazawa, 2012, 2019). Flat spatangoids burrow by pushing excavated sediment to the posterior side of the test, live close to the sediment

surface and typically as sand dwellers; wedge-shaped types move through sediment by thrusting into it and rocking their anterior end up and down, which is effective in soft muddy environments; globular forms benefit deep-burrowing sand dwellers by helping support the burrow walls (Kanazawa, 1992).

The typical flat profile morphology of *Breynia* sp. in this study indicates that they were likely shallow-burrowing sand dwellers, as seen in modern *Breynia* species occurring at depths ranging from the intertidal zone to 140 m, and found buried in sand up to 8 cm below the sediment surface (McNamara, 1982; Keesing and Irvine, 2013).

On the other hand, the host rock lithology of these fossils is also consistent with the sand-dwelling ecology of *Breynia*. The medium-grained, bioturbated, brown massive sandstone most likely indicates relatively shallow water above the storm wave base in Taiwan (Chen, 2016). With potentially short post-mortem transport (see discussion below), this shallow water, sandy environment is likely where they lived, which has also been observed in other *Breynia* fossil assemblages (Chen *et al.*, 2025).

Death to burial

Deaths of echinoids may result from predation, environmental events or natural senescence, each leaving slightly different signatures in the fossil record. Predation-mediated deaths are characterised by damaged skeletal traces such as drill holes, crushing or marginal breakage, caused by various predators including fishes, birds, turtles, mammals, decapods and cassid gastropods (Petsios *et al.*, 2023). Event-mediated deaths in spatangoid echinoids may occur when individuals are smothered by a thick layer of sediment during high-energy storm events (Schäfer, 1962, 1972) or killed by episodes of low oxygenation, which strongly affect these infaunal echinoids. The former typically results in *in situ* preservation without concentration but with relatively complete tests and spines. The latter (anoxia-related death) resembles senescence-related mortality in taphonomic structures (Kudrewicz, 1992). During near-death conditions, spatangoid echinoids often move toward the sediment surface before dying (Nebelsick *et al.*, 1997), which may explain the occurrence of often concentrated complete tests in similar size, suggesting single populations or similar ages. In our examined fossils, the absence of drill holes, crushing and marginal damage, coupled with their relatively complete preservation and concentration within a single boulder, indicates that death most likely resulted from low-oxygen events or senescence.

After death, the early post-mortem taphonomic stage of echinoids is mainly controlled by their multi-plated calcareous skeleton, micro-stereomic structure, macro-skeletal architecture and the surrounding environmental

conditions (Nebelsick and Mancosu, 2021). These factors control processes from disarticulation, fragmentation, transportation, burial, infilling and dissolution to diagenesis. Disarticulation in spatangoid echinoids is typically driven by soft tissue decay and the associated loss of spines. Most spines are lost within about a week (Nebelsick *et al.*, 1997), although the timing varies between species, as some spines remain firmly attached even after prolonged exposure and transport (Radwański and Wysocka, 2001; Nebelsick and Kroh, 2002). The disarticulation rate of the spines is also strongly controlled by temperature, with lower temperatures significantly delaying the disarticulation process (Banno, 2008; Banno *et al.*, 2010). In the fossils examined here, the absence of preserved spines or spine imprints, as well as their absence in surrounding sediment, suggests that these echinoids were not buried immediately after death but were exposed for a period long enough to lose their spines; however, the exact duration depends on water temperature.

Fragmentation, transportation and burial are closely interconnected. Once spatangoid echinoids are exposed at the sediment surface, factors such as exposure duration, temperature and hydrodynamic energy become key determinants of taphonomic changes. Longer exposure, higher temperature and stronger currents typically result in greater abrasion and fragmentation of the tests (Kidwell and Baumiller, 1990; Nebelsick and Mancosu, 2021). Additionally, prolonged exposure may also promote encrustation and bioerosion (Nebelsick and Mancosu, 2021). Although most examined specimens are preserved as internal moulds, making detailed assessment of abrasion, encrustation or bioerosion unavailable, their relative completeness and low degree of fragmentation clearly indicate a short exposure time, relatively low ambient temperature and low flow energy prior to burial.

Infilling, dissolution, diagenesis and fossil preservation

Across diverse marine faunas, it has been estimated that about 70–80% of organisms are not normally fossilised (Lawrence, 1968; Allison and Briggs, 1991a, b). These taxa can only be found in Konservat-Lagerstätten with exceptional taphonomic conditions (Seilacher, 1970). Among the remaining taxa, which are mostly skeletonised organisms preserved in Konzentrat-Lagerstätten formed by sedimentological and biological concentration processes (Seilacher, 1970), multiple complex post-mortem processes may still alter their original skeletons. As a result, fossils are often preserved in different taphonomic forms rather than as the original skeletal remains (e.g. Seilacher, 1970, 1990; Seilacher *et al.*, 1985).

In marine calcareous skeletons, moulds are a common mode of preservation. This is because carbonate miner-

als, particularly high-Mg calcite and aragonite, easily dissolve when the decay of organic matter generates acidic and undersaturated microenvironments (Fairbridge, 1979; Martin, 1999). Once the skeleton dissolves, only the sediment formerly in contact with shell remains as an impression. These impressions finally form external and internal mould fossils (or steinkerns), as observed in the examined fossil echinoids.

These moulds, especially steinkerns, vary in form depending on the degree of abrasion, sediment infilling and burial before diagenesis (e.g. Seilacher, 1971) and on dissolution, compaction and cementation during diagenesis (e.g. Seilacher *et al.*, 1976). Two main modes can be recognised in echinoid steinkerns, reflecting different sediment infilling histories. The first type consists of steinkerns composed of sediment identical to that of the surrounding matrix, which indicates that the tests were completely infilled before or during burial (e.g. Machalski and Jagt, 2018, text-figs. 3, 4). The second type consists of precipitated materials such as flint, which is commonly seen chalk echinoids (e.g. Krüger, 2002, fig. 1; Donovan *et al.*, 2014, fig. 2). These examples represent empty tests that were not infilled by sediment but were later mineralised before dissolution during diagenesis. Partially infilled tests with geopetal-like preservation may also occur (e.g. Müller *et al.*, 2023, figs. 2, 6), although such examples are rare in steinkern and harder to be preserved due to test implosion (Müller, 1957; Nebelsick, 1999; Donovan and Clements, 2002).

In the examined material, all steinkerns are composed of medium-grained brown sandstone consistent with the host rock. This indicates that the tests were completely infilled by surrounding sediment before or during burial. Only slight deformation and rupture is observed (Figures 4A, G; 5), suggesting that sediment entered the test through the peristome and periproct after the decay of the peristomial membrane and disarticulation of the periproctal plates. The infilling is remarkably complete, accurately replicating the internal skeletal surface of echinoid tests. Subsequently, the relatively unstable high-Mg calcite skeleton dissolved and slight tectonic compression happened during early and/or late diagenesis (Fairbridge, 1979; Martin, 1999), leaving external and internal moulds that preserve the outer and inner skeletal surfaces, respectively.

Status of genus *Spatangomorpha*

The genus *Spatangomorpha* Böhm, 1882 is a questionable taxon with an extremely close relationship to *Breynia*. It was established based on two specimens from the Miocene of Java, Indonesia, with only the illustration of a single specimen available from the original publication (Figure S3). Böhm (1882) initially distinguished

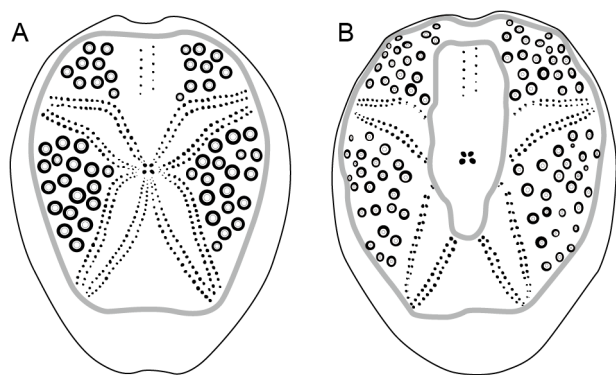


Figure 6. Aboral morphological comparisons between the genera (A) *Spatangomorpha* (modified from Böhm, 1882) and (B) *Breynia* (modified from Kroh, 2007).

Spatangomorpha from other lovenioid genera by its posterior ambulacra, which meet at the oral midline and separate the labrum from the sternal plates. However, this character has proven unreliable, as several fossil species of *Breynia* also exhibit this condition (e.g. *B. vredenburghi* Anderson, 1907), and similar variation occurs within extant Australian species *B. desorii* Gray, 1851 (McNamara, 1982).

Mortensen (1951) later re-examined the illustrations of the type species *Spatangomorpha eximia* Böhm, 1882 and proposed several additional diagnostic features not noted by Böhm, including a subanal fasciole enclosing more than eight ambulacral plates and the absence of an inner fasciole, with the upper ends of the petals unreduced. The latter feature was emphasised as a distinction from *Breynia*, which typically has an inner fasciole and petals reduced near the apical system (Figure 6). Nevertheless, *Spatangomorpha* is often considered synonymous with *Breynia*, as the two share nearly all diagnostic features (Smith and Kroh, 2011; Kroh and Mooi, 2025). The supposed absence of an inner fasciole and the presence of fully developed pore pairs extending toward the apical system are regarded as illustration artefacts (Smith and Kroh, 2011), and the genus is currently treated as a nomen dubium pending re-description (Kroh and Mooi, 2025).

Although no type material is known to exist, the differences between *Spatangomorpha* and *Breynia* inferred from Böhm's original figures are strikingly similar to those observed between internal and external moulds in the material described herein. Notably, Böhm (1882) did not specify the preservation state of the examined fossils, and although both peripetalous and subanal fascioles were mentioned in the description, neither feature is clearly visible in the figures. These observations suggest that the apparent absence of the inner fasciole and

the fully developed pore pairs toward the apical system likely result from differential preservation, and therefore the two genera are probably synonymous if the former was indeed based on internal moulds.

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Supplementary materials

Figure S1, oblique views of fossil steinkern (NTUG300-FU01088) (A) and modern skeleton (NTUG300-FU01092) (B) of *Breynia*. Subanal fasciole absent in internal mould but clearly visible in modern skeleton.

Figure S2, additional fossil spatangoid echinoids from Tsengwen Reservoir, southern Taiwan. Changchikeng Formation, Late Miocene. A, *Breynia* sp., steinkern (NTUG300-FU01094): aboral fragments; B, *Breynia* sp., steinkern (NTUG300-FU01095); C, D, Pericostmidæ indet., steinkern (NTUG300-FU01096): aboral view (C), oral view (D).

Figure S3, original figures of *Spatangomorpha eximia* from Böhm (1882): A, aboral view; B, oral view; C, lateral view; D, posterior view; E, plating pattern.

Table S1, list of specimens used in this study.

Table S2, biometric measurements of examined fossil *Breynia* sp.

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Author contributions

C.-H. H. initiated the study, was primarily responsible for the taxonomic and taphonomic aspects, and completed the first draft of the manuscript. J.-P. L. designed and organised the study. All authors reviewed and contributed to the writing of the paper.