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Chia-Hsin HSU, Diana OSIPOVA & Chien-Hsiang LIN

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# Fossil freshwater mollusks from the Early Pleistocene (Calabrian) of northern Taiwan

**Chia-Hsin HSU**
Department of Geosciences, National Taiwan University,
no. 1, Roosevelt Road, Sec. 4, Taipei 106319 (Taiwan)
b09204010@ntu.edu.tw

**Diana OSIPOVA**
**Chien-Hsiang LIN**
Biodiversity Research Center, Academia Sinica,
no. 128, Academia Road, Sec. 2, Nankang, Taipei 11529 (Taiwan)
osipova.ds@outlook.com
chlin.otolith@gmail.com (corresponding author)

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ABSTRACT

Despite the extensive fossil mollusk records in Taiwan, over 99% are marine species. Among the few freshwater deposits, the Tananwan Formation (1.46-1.24 Ma) in northern Taiwan has been recognized as one of the most prolific fossiliferous strata. In a 1-meter thick fossiliferous mudstone layer within the formation, we identified five molluscan taxa. The assemblage is primarily dominated by *Sinotaia quadrata* (Benson, 1842) and the less common *Melanoides* aff. *tuberculata*, which corresponds to the current freshwater ecosystem in northern Taiwan. This study presents detailed descriptions and images of fossil freshwater molluscan assemblage from Taiwan, providing insights into the origins of contemporary freshwater biodiversity in the subtropical West Pacific. Additionally, in several fossil *S. quadrata* specimens, juvenile shells were found within female shells, marking the second known case of child-carrying in fossil viviparids.

KEY WORDS
Taiwan,
Early Pleistocene,
freshwater snails,
viviparid,
biogeography,
paleoenvironment.

RÉSUMÉ

*Mollusques fossiles d'eau douce du Pléistocène inférieur (Calabrien) du nord de Taïwan.*

Malgré l'abondance des mollusques fossiles à Taïwan, plus de 99 % d'entre eux sont des espèces marines. Parmi les rares dépôts d'eau douce, la formation Tananwan (1,46-1,24 Ma), dans le nord de Taïwan, est reconnue comme l'une des unités fossilifères. Dans une couche de mudstone fossilifère d'un mètre d'épaisseur au sein de la formation, nous avons identifié cinq espèces de mollusques. L'assemblage, principalement dominé par les espèces *Sinotaia quadrata* (Benson, 1842) et, moins communément, *Melanoides* aff. *tuberculata*, correspond à l'écosystème d'eau douce actuel du nord de Taïwan. Cette étude présente des descriptions détaillées et des images d'assemblages de mollusques d'eau douce fossiles à Taïwan, permettant ainsi de mieux comprendre les origines de la biodiversité contemporaine des eaux douces du Pacifique ouest subtropical. En outre, dans plusieurs spécimens fossiles de *S. quadrata*, des coquilles juvéniles ont été trouvées à l'intérieur de coquilles femelles, ce qui constitue le second cas connu de portage de juvéniles chez les viviparidés fossiles.

MOTS CLÉS
Taïwan,
Pléistocène inférieur,
Escargots d'eau douce,
vivipare,
biogéographie,
paléoenvironnement.

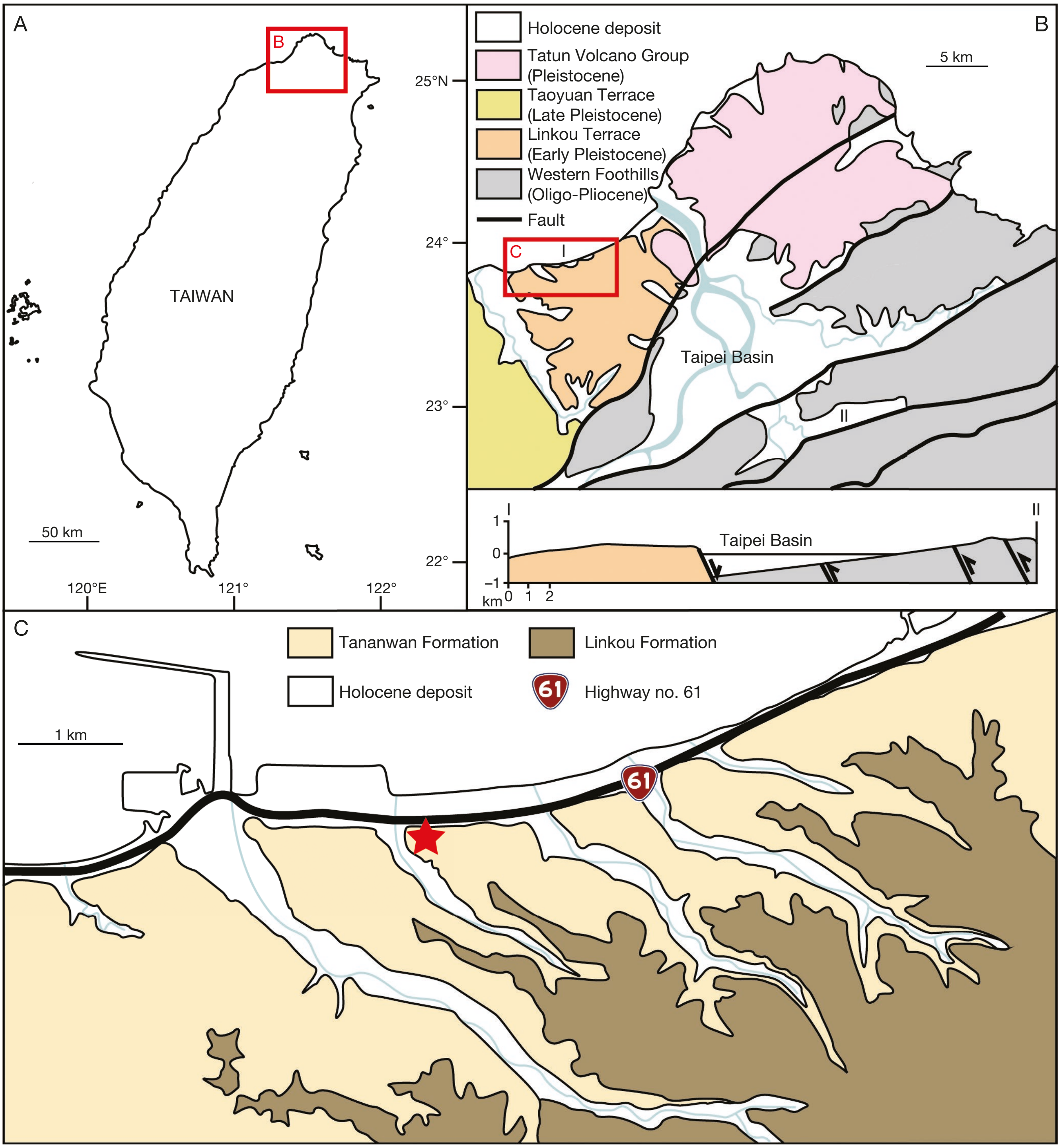

FIG. 1. — Locality and geological background of sampling site: **A**, study area; **B**, general geological background and sections of Taipei Basin (modified from Teng 2007); **C**, geological map of sampling site (modified from Lin 1981). Red star represents the sampling site. Map: Chia-Hsin Hsu.

# INTRODUCTION

Molluscan fossils are among the most abundant biological remains in the sedimentary archives of Taiwan. More than 1000 species belonging to at least 430 genera have been recorded, ranging from the Oligocene to the Quaternary (e.g., Hu & Tao 2003; Senan *et al.* 2023). Most of them co-occur with corals (e.g., Ribas-Deulofeu *et al.* 2021), echinoids (e.g., Hsu *et al.* 2024; Chen *et al.* 2025), fish (e.g., Lin *et al.* 2021; Lin & Chien 2022; Přikryl *et al.* 2024), and crabs (e.g., Hu & Tao 1996). Despite the abundant fossil mollusk records in Taiwan, more than 99% are recognized as marine species (Hu & Tao 2003), with fewer than 20 freshwater mollusk species sporadically reported (Hu & Tao 1991; Hu 1992a; Hu & Wang 1995; Lee 2000).

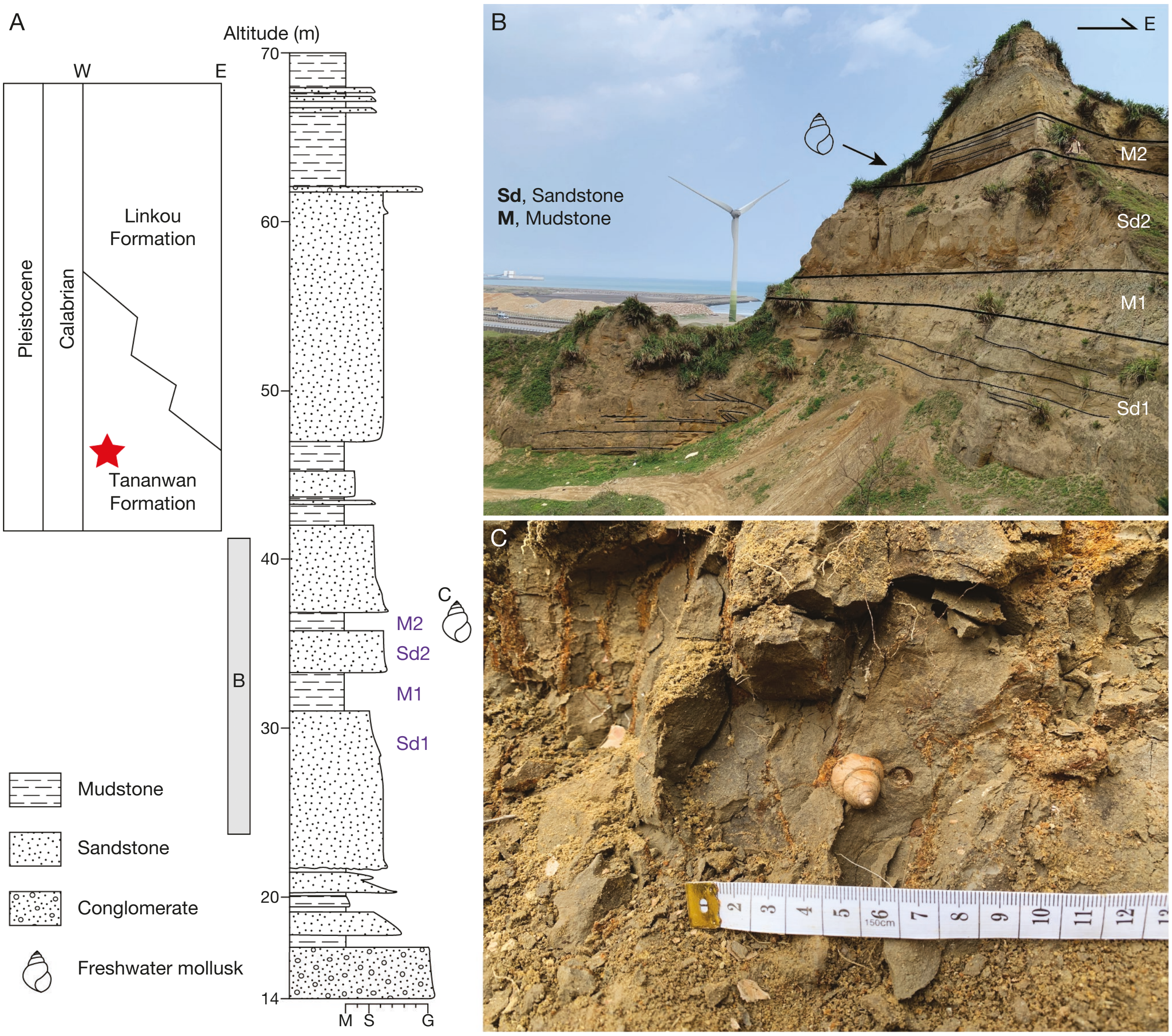

Fig. 2. — Geological column and field observations on the Tananwan Formation, Linkou Plateau, northwestern Taiwan: **A**, geological column of the sampling outcrop (modified from Chuang *et al.* 2012), red star represents the relative time scale of the outcrop; **B**, sampling outcrop, black arrow indicates the fossil beds; **C**, field photos of fossils and the bedrock. Photos and drawing: Chia-Hsin Hsu.

The difference between marine and freshwater fossil records can potentially be attributed to the relatively young geological history of Taiwan. The ongoing orogeny of Taiwan started around the Miocene and Pliocene transition (Lin *et al.* 2003), and most of the typical terrestrial strata were deposited later than the Pleistocene (Chen 2016), making freshwater mollusk faunas in Taiwan extremely rare. Moreover, within terrestrial fossiliferous strata, vertebrate fossils have received more attention (e.g., the Chochen Vertebrate Fauna; Wei 2007), resulting in relatively limited research on freshwater mollusks.

The Tananwan Formation, which contains both marine and terrestrial fossiliferous deposits, possesses one of the best-preserved freshwater mollusk assemblages. Lee (2000) first reported eight species from five families of freshwater mollusk (i.e., Bithyniidae Gray, 1857, Semisulcospiridae Morrison, 1952, Viviparidae Gray, 1847, Lymnaeidae Rafinesque, 1815, and Planorbidae Rafinesque, 1815), although without specimen figures or descriptions. Chuang *et al.* (2012) mentioned this assemblage but provided no further taxonomical analysis. As for other fossils found in the Tananwan Formation, Yokoyama (1928) reported 17 marine mollusk species from the formation in his general report on Taiwanese mollusk fossils. Vertebrate fossils have also been found on the tidal plain of the coastal Linkou Plateau, recognized as belonging to the Tananwan Formation (Shieh 2007). Here, we describe the taxonomic composition of an Early Pleistocene freshwater mollusk assemblage from the Tananwan Formation, providing a framework for understanding the regional freshwater biogeography during the Pleistocene.

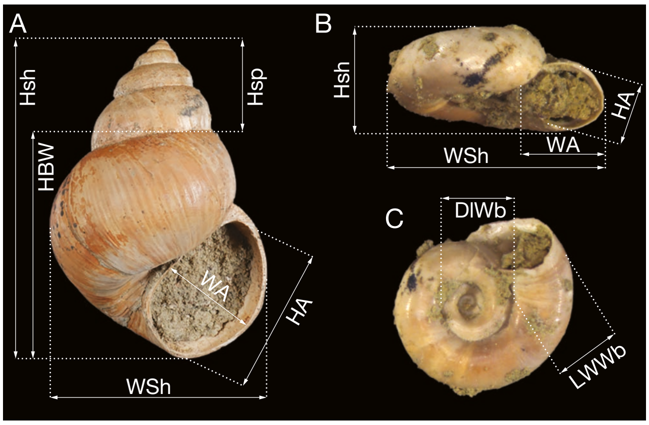

Fig. 3. — Diagram of freshwater mollusks for measurements used in this study: **A**, apertural view of viviparid shell; **B**, apertural view of planorbid shell; **C**, apical view of planorbid shell. Photos: Diana Osipova.

## GEOLOGICAL BACKGROUND

Fossils were collected from the Tananwan Formation (25°07'13.1"N, 121°19'11.7"E; Figs 1, 2), a sedimentary unit regionally exposed only on the Linkou Plateau in northwestern Taiwan. This formation is characterized by its horizontal strata, consisting of loosely cemented sandstones and mudstones intercalated with thin conglomerate beds (Horng 2014). The Tananwan Formation is indented and overlain by the Linkou Formation, which is composed of massive conglomerate (Chen 2016). Both formations are interpreted as part of a west-flowing paleo-fan-delta system, known as the Linkou Fan-Delta, supported by paleocurrent analysis and geological structures (Chen & Teng 1990; Chuang *et al.* 2012). The sedimentary environments of the Linkou Formation and the Tananwan Formation are therefore recognized as alluvial fan and river to shallow marine, respectively (Chen & Teng 1990; Chuang *et al.* 2012). On the other hand, the age of the Tananwan Formation has been debated for a long time. A recent comprehensive study suggests that the formation was deposited between 1.46 and 1.24 Ma (Early Pleistocene Calabrian Stage), based on magnetostratigraphy and the occurrence of large-sized *Gephyrocapsa* spp., correlated with well-studied continuous sections of the Gutingkeng Formation in southern Taiwan (Horng 2014). We tentatively followed this age estimation due to its comprehensive sampling and the combination of magnetostratigraphy and biostratigraphy in the analysis.

## MATERIAL AND METHODS

Mollusk fossil specimens were hand-picked directly in the field (25°07'13.1"N, 121°19'11.7"E; Fig. 1) between 2023 and 2024, without the use of sieving. All specimens are from the one-meter-thick mudstone layer pointed out by the arrow in Fig. 2. No other obvious fossils have been found in the other layers exposed at this outcrop. Fragile specimens were reinforced with super glue before being extracted from bedrock using a steel needle. After brief preparation, the specimens were dried overnight in a 40°C oven to remove moisture from the muddy bedrock. Complete specimens were then described, measured (Fig. 3), and photographed. All descriptions and measurements were conducted only on specimens without obvious taphonomic deformation. Specimens of viviparids and thiarids were measured for six parameters (Fig. 3A): width of shell (WSh), height of shell (HSh), height of spire (HSp), height of basal whorl (HBW), height (HA) and width of aperture (WA). Two additional measurements (Fig. 3C) were done for planorbid shells: the diameter of inner whorls from the basal surface (DIWb) and the last whorl width from the basal surface (LWWb). All specimens are deposited in the Biodiversity Research Museum, Academia Sinica, Taiwan (BRMAS) under the code ASIZF.

### Abbreviations

| | |
|---|---|
| DIWb | diameter of inner whorls from the basal surface; |
| HA | height of aperture; |
| HBW | height of basal whorl; |
| HSh | height of shell; |
| HSp | height of spire; |
| LWWb | last whorl; |
| WA | width of aperture; |
| WSh | width of shell. |

## SYSTEMATIC PALAEONTOLOGY

Class GASTROPODA Cuvier, 1795
Order ARCHITAENIOGLOSSA Haller, 1892
Superfamily Viviparoidea Gray, 1847
Family Viviparidae Gray, 1847
Subfamily Bellamyinae Rohrbach, 1937

Genus *Sinotaia* Haas, 1939

Type species. — *Paludina quadrata* Benson, 1842, by original designation.

### ***Sinotaia quadrata*** (Benson, 1842)
(Figs 4, 5)

*Paludina quadrata* Benson, 1842: 487.

*Paludina purificata* Heude, 1890: 176, pl. 40, fig. 4, 4a.

*Viviparus* (*chinensis* var?) *formosensis* Kobelt, 1909: 413, pl. 77, figs 6-7.

*Vivipara quadrata* – Odhner 1930: 27.

*Vivipara* cf. *lecythoides* – Hsu 1935: 32, pl. 3, figs 2a-b, 3-5.

*Vivipara dispiralis* – Hsu 1935: 33, pl. 3, figs 6a-b, 7a-b, pl. 4, fig. 10.

†*Bithinia viviparoides* Hsu, 1936: 32, pl. 2, figs 19a-b, 20.

*Viviparus quadratus turritus* Yen, 1939: 36, pl. 3, fig. 8.

*Viviparus quadratus limnophilus* – Yen 1939: 192; 1943: 284.

*Viviparus quadratus* – Kuroda 1941: 82. — Yen 1941: 191; 1943: 284.

*Bellamya purificata* – Yen 1943: 126.

*Sinotaia quadrata* – Pace 1973: 30, pl. 5, fig. 2.

(For an extensive synonymy list of *S. quadrata* in East Asian, refer to Ye 2020)

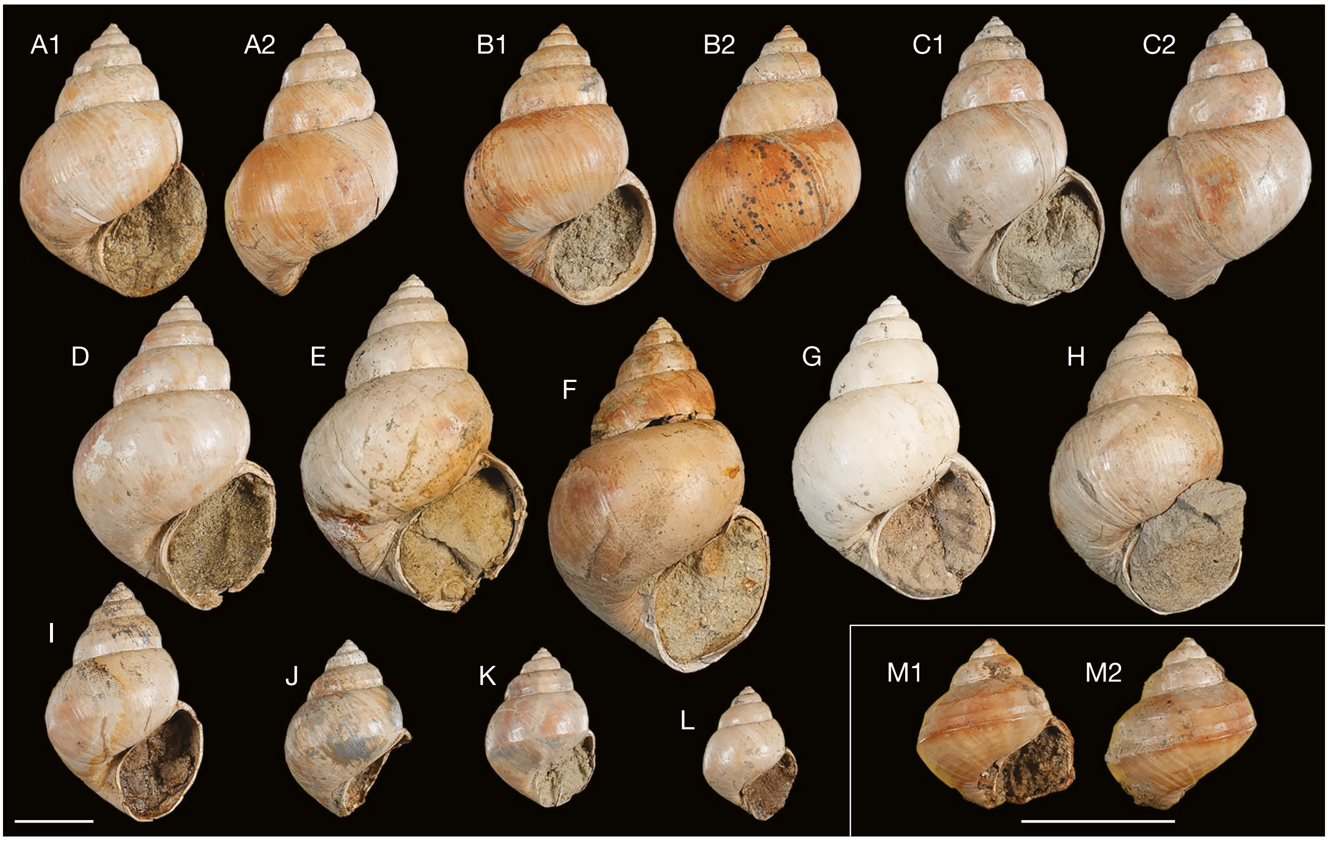

Fig. 4. — *Sinotaia quadrata* (Benson, 1842) from the Lower Pleistocene Tananwan Formation, Shuiniukeng, northern Taiwan: **A**-**M**, ASIZF0100893 to ASIZF0100905, respectively. Scale bars: 10 mm. Photos: Diana Osipova.

Material examined. — **Taiwan** • 37 specimens; Shuiniukeng (= Water Buffalo Valley), New Taipei City; Tananwan Formation; Early Pleistocene, Calabrian; ASIZF0100893-ASIZF0100912, ASIZF0100923-ASIZF0100939.

### Description

Shell turbiniform, elongate subconical, appears thin, but not fragile. Medium to large in size, with HSh and WSh of adult shell ranging from 25-40 mm and 15-25 mm, respectively. HBW of adult shell about 70% of HSh. HA longer than WA. Shell solid, whorls profile rounded with distinct periphery, sutures impressed but shallow on early whorls, and deep suture of the body whorl. Surface shiny with weak growth lines, with 1-3 loose spiral keels (better visible on the last whorl), not evident in some specimens. Spire rather short, rounded, consists of 4-5 whorls that enlarged slowly; ratio of 1:1.5 to body whorl. Aperture subovate, broad, and prosocline, well angled posteriorly. Umbilicus small and narrow. Subadult shells (Fig. 4M) with pronounced 2-3 spiral keels that become less prominent with age. Juvenile shell (Fig. 5B-E) conical, turbiniform, early protoconch of 3 whorls with evident 2-3 ridges.

### Remarks

Viviparid snails exhibit modest sexual dimorphism within species, due to their ovoviviparous reproductive strategy (Minton & Wang 2011). Additionally, shell shape variation, partly influenced by environmental factors, sometimes leads to slight morphological differences between closely related species (Chiu *et al.* 2002). For instance, *Sinotaia quadrata histrica* (Gould, 1859) inhabiting lagoonal environments develops thicker, more elongated shells with narrower apertures comparing to those found outside the lagoon (Kagawa *et al.* 2019). A similar case involves the often co-occurring invasive *Cipangopaludina chinensis* (Gray, 1833) and *C. japonica* (Martens, 1861) in the United States, which are morphologically indistinguishable, likely due to their shared habitats (Van Bocxlaer & Strong 2016). These phenotypic variations make species identification in viviparids challenging if relying solely on shell morphology. Moreover, the taxonomic uncertainty surrounding viviparid species has persisted since the 19th century and remains unresolved (Van Bocxlaer & Strong 2019; Ye 2020; Stelbrink *et al.* 2020).

In this study, the juvenile specimens played a crucial role in identifying *S. quadrata*. Juvenile shells from the Tananwan Formation closely resemble the outline and microsculpture of extant juvenile shells of *S. quadrata* (Fig. S1A, B). Compared to *C. chinensis* juveniles (Fig. S1C), the Tananwan juveniles have a less angular outline and the widest point positioned closer to the anterior. They also differ from *C. japonica* juveniles (Fig. S1D) in having a larger spire whorl angle, resulting in a distinct outline. While typical adult shells of these species differ significantly from our specimens (Fig. S1E-H), the Tananwan specimens

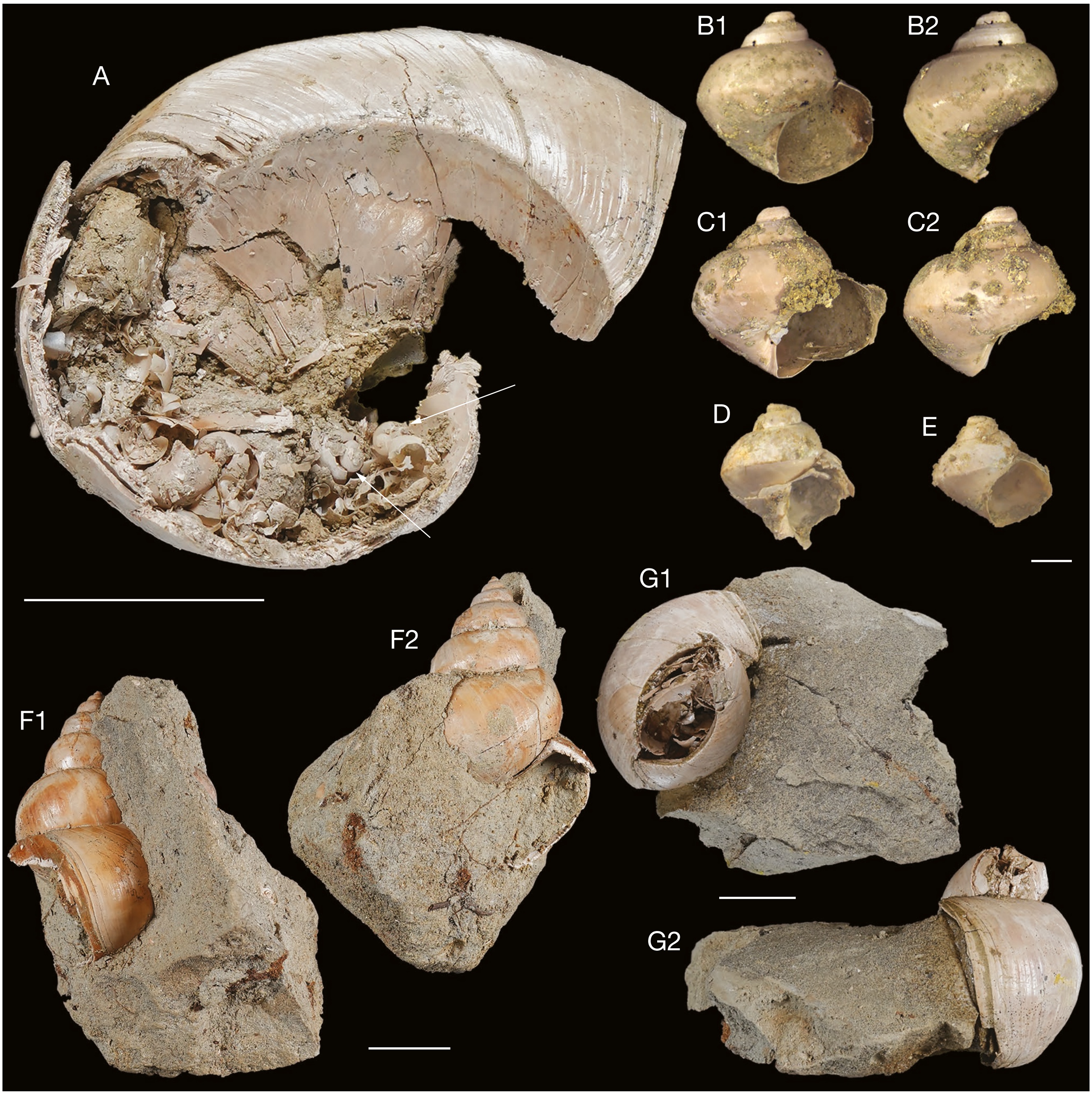

Fig. 5. — *Sinotaia quadrata* (Benson, 1842) from the Lower Pleistocene Tananwan Formation, Shuiniukeng, northern Taiwan: **A**, specimen with intact juvenile shells (pointed out by arrows) (ASIZF0100906); **B**-**E**, juvenile shells (ASIZF0100907 to ASIZF0100910) extracted from ASIZF0100906; **F**, non-deformed specimen with bedrock (ASIZF0100911); **G**, deformed specimen with bedrock (ASIZF0100912). Scale bars: A, F, G, 10 mm; B-E, 1 mm. Photos: Diana Osipova.

share similarity with some of the morphotypes of those species (Fig. S1I-L), though the Tananwan adults are smaller than *C. chinensis* and *C. japonica*. Thus, based on both juvenile and adult shell morphology, our specimens are most likely belong to *S. quadrata*. This species has a wide distribution in East Asia, with records from China (Yen 1943), Korea (Lee 2009), and Japan (Hirano *et al.* 2015; Saito & Kagawa 2020). In Taiwan, this species was first reported as *Viviparus angularis* (Müller, 1774), followed by more recent studies (Pace 1973; Chiu *et al.* 2002). Chen (2011) summarized at least 12 varieties of shell morphotypes of *S. quadrata* across Taiwan. In addition, the subspecies *S. quadrata heudei* (Dautzenberg & Fischer 1905) is distinguished by its smaller shell with three well-defined spiral keels (Chen 2011). However, this subspecies has been recognized as synonym of the *S. quadrata* (Qian *et al.* 2014; Ye 2020).

Fossil occurrences of *S. quadrata* are known from Pleistocene deposits in Asia (Taiwan Malacofauna Database 2013; Ye *et al.* 2020). Yen (1943) referred to this species as *Viviparus quadratus* Benson, 1843 from the Para-loess Formation (possibly Late Pleistocene) in the Yangtze Valley. This species

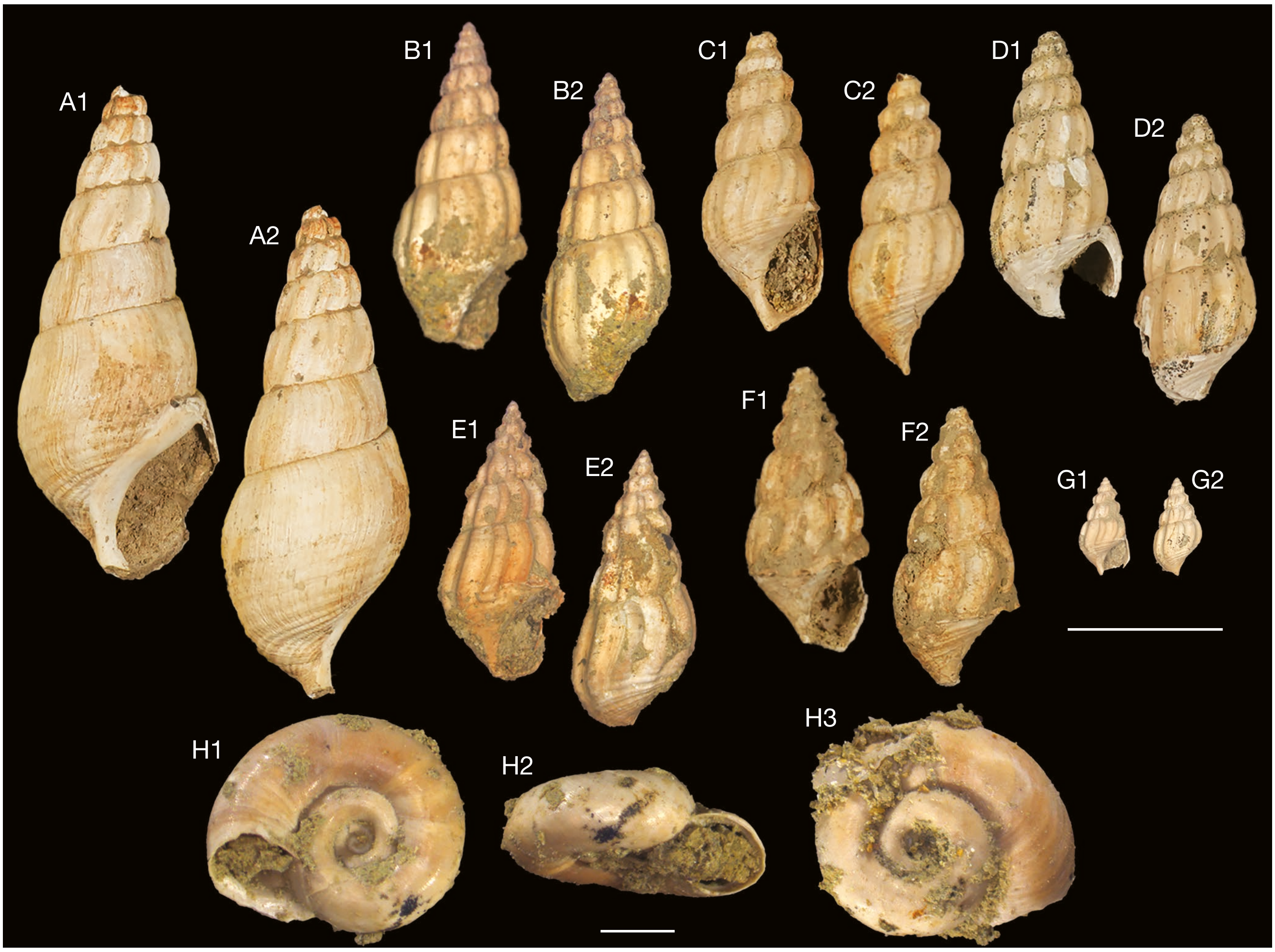

FIG. 6. — *Melanoides* aff. *tuberculata* (**A**-**G**) and *Gyraulus* sp. (**H**) from the Lower Pleistocene Tananwan Formation, Shuiniukeng, northern Taiwan: **A**-**G**, ASIZF0100913 to ASIZF0100919, respectively; **H**, ASIZF0100920. Scale bars: A-G, 10 mm; H, 1 mm. Photos: Diana Osipova.

has also been identified in the Upper Pleistocene deposits in Maping (Liuchow), Kwangsi, and Maoshan, Chuyung, Kiangsu (Yen 1943), as well as from Toning and Hainan (Odhner 1930). Yen (1943) synonymized †*Bithinia viviparoides* Hsu, 1936 from the Siashu Formation (Late Pleistocene), Nanking, China (Hsu 1936), with *S. quadrata*. Additionally, *Viviparus quadratus limnophilus* Mabille, 1886, which Yen (1943) synonymized with *Vivipara dispiralis* Heude 1890, was recorded from the post-Pleistocene period in Kweilin, Kwangsi (Hsu 1935).

### Order CAENOGASTROPODA *incertae sedis*
### Superfamily CERITHIOIDEA Fleming, 1822
### Family THIARIDAE Gill, 1871 (1823)
### Subfamily THIARINAE Gill, 1871 (1823)

### Genus *Melanoides* Olivier, 1804

TYPE SPECIES. — *Melanoides fasciolata* Olivier, 1804, by monotypy.

### *Melanoides* aff. *tuberculata*
(Fig. 6A-G)

MATERIAL EXAMINED. — **Taiwan** • 8 specimens; Shuiniukeng (= Water Buffalo Valley), New Taipei City; Tananwan Formation; Early Pleistocene, Calabrian; ASIZF0100913-ASIZF0100919, ASIZF0100940.

#### DESCRIPTION

Shell turriculate, thick, elongated, with HSh being greater than twice of WSh. HBW and HSp of adult shell about 60% and 40% of HSh respectively. HA longer than WA. Surface smooth on last two whorls, but adapical whorls covered with widely spaced, prosocline collabral undulations. Spiral threads on abapical part of the base. Spire tall, comprising ⅔ of the shell. Suture shallow, but impressed in adapical whorls, last two whorls with slight shoulder at shallow suture. Whorls 7-8 in number (early whorls missing), increasing in diameter slowly, profile flattened. Aperture ovate, but not well preserved in all specimens.

TABLE 1. — Shell measurements (in mm) of fossil freshwater mollusks. Measurements are indicated as: mean (range).

| | ***Sinotaia quadrata* (Benson, 1842)** | | ***Melanoides* aff. *tuberculata*** | ***Gyraulus* sp.** |
|---|---|---|---|---|
| | **Adult** | **Juvenile** | | |
| N | 25 | 5 | 8 | 1 |
| Wsh | 15.90 (8.61-25.78) | 3.48 (2.74-4.33) | 6.14 (3.11-12.17) | 3.51 |
| Hsp | 8.07 (3.30-15.05) | 0.56 (0.37-0.69) | 7.04 (2.48-13.39) | – |
| Hsh | 23.46 (13.01-39.45) | 3.50 (2.89-4.20) | 12.96 (1.90-30.94) | 1.1 |
| HBW | 17.17 (6.85-28.36) | 2.91 (2.43-3.40) | 8.53 (3.50-17.88) | – |
| HA | 13.52 (7.64-20.48) | 2.29 (1.81-2.85) | 7.45 (4.81-12.73) | 0.84 |
| WA | 10.15 (5.77-15.15) | 1.62 (1.08-1.91) | 3.97 (2.90-5.04) | 1.05 |
| DIWb | – | – | – | 1.37 |
| LWWb | – | – | – | 1.2 |

### REMARKS

Thiaridae species exhibit considerable polymorphism in shell ornamentation, which allows them to adapt to diverse environments across their range. In some lineages, predominantly parthenogenetic reproduction results in minimal intrapopulation variability in key morphological traits, allowing for regional morphological comparisons and identification (Samadi *et al.* 2000).

The studied specimens closely resemble extant *Melanoides tuberculata* (Müller, 1774) populations in Taiwan (Chiu 2006; Chen 2011). These shells are characterized by the general shell outline and the presence of wavy longitudinal ribs on each whorl, which become less distinct towards the body whorl. They also differ from other Taiwanese thiarids. Specifically, *Stenomelania costellaris* (Lea & Lea, 1851) has more distinct sutures and smaller shells; *S. plicaria* (Born, 1778) exhibits smoother and higher shells; *S. torulosa* (Bruguière, 1789) displays thick longitudinal ribs with spiral grooves. However, due to the strong morphological variations within Thiaridae species, fragmentation of the specimens, and the lack of criteria for observing adult shell characteristics, we identified the specimens as *Melanoides* aff. *tuberculata*.

*Melanoides tuberculata* has been reported from various localities across East Asia. In Taiwan, it was first described *M. formosensis* as a new species alongside *M. tuberculata*, while it has been suggested that *M. formosensis* may be a morphotype or a subspecies of *M. tuberculata* (Pace 1973). Chen (2011) documented possible shell morphological variations throughout Taiwan, demonstrating that such variability can be observed even among individuals from the same locality.

Fossil occurrences of *M. tuberculata* from Neogene and Quaternary deposits are rare in Asia. Nomura (1935) reported this species from the Pleistocene Toukoshan Formation (referred to as Byoritu Beds in his report) in Houlong Township, Miaoli County (= Wangwa, Shinchiku-shu), northern Taiwan. Although the figure in the original publication is difficult to interpret, the accompanying description serves as evidence of its occurrence in Taiwan. Furthermore, Nomura (1935) also indicated its presence in the Miocene-Pliocene deposits of Java. Additionally, *M. tuberculata* has been reported from the Neogene of Nepal (Gurung *et al.* 1997).

### Superorder HYGROPHILA Férussac, 1822
### Superfamily LYMNAEOIDEA Rafinesque, 1815
### Family PLANORBIDAE Rafinesque, 1815
### Subfamily PLANORBINAE Rafinesque, 1815
### Tribe Planorbini Rafinesque, 1815

### Genus *Gyraulus* Charpentier, 1837

TYPE SPECIES. — *Planorbis albus* Müller, 1774, by subsequent designation.

### *Gyraulus* sp.
(Fig. 6H)

MATERIAL EXAMINED. — **Taiwan** • 2 specimens; Shuiniukeng (= Water Buffalo Valley), New Taipei City; Tananwan Formation; Early Pleistocene, Calabrian; ASIZF0100920, ASIZF0100941.

### DESCRIPTION

Shell discoid, pseudodextral, small (WSh: 3.5 mm) with rounded whorl periphery, slightly angulated. Almost imperceptible keel in the middle of the whorl. DIWb slightly longer than LWWb. WA longer than HA. Examined specimen with at least 3.3 whorls. Shell surface smooth, glossy, closer to aperture with evident growth lines. Whorl wide, convex, umbilicus deep, and concave, protoconch is visible. Suture deep. Aperture rounded.

### REMARKS

The members of family Planorbidae are known for their heterogeneous shell morphology, making species discrimination difficult (Hubendick 1955). Based on the rounded periphery of the sole well-preserved specimen, slightly visible keel in the middle of the shell, and the DIWb being much larger than in other genus, the specimen has been here assigned to the genus *Gyraulus*. Considering the small size (3.5 mm) of two obtained specimens, it is potentially subadult individuals, as general size of Taiwanese planorbids is 5-6 mm. The genus *Gyraulus* is represented by one species in Taiwan—*Gyraulus spirillus* (Gould, 1859), occurring with at least two morphotypes (Chen 2011). Although the studied specimen appears to be less angulated, it is possible

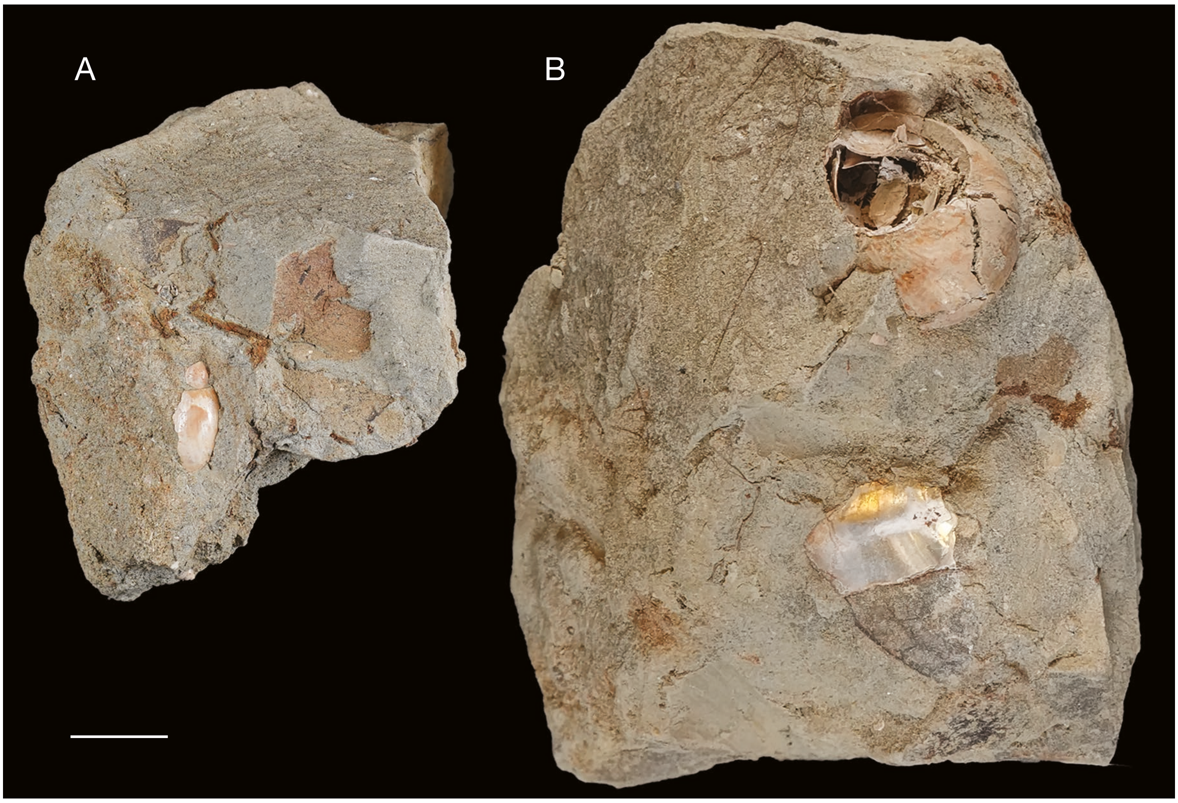

FIG. 7. — Lymnaeidae gen. et sp. indet. (**A**) and Unionidae gen. et sp. indet. (**B**) from the Lower Pleistocene Tananwan Formation, Shuiniukeng, northern Taiwan: **A**, ASIZF0100921; **B**, ASIZF0100922. Scale bar: 10 mm. Photos: Chia-Hsin Hsu.

that it belongs to one of the morphotypes of *G. spirillus. Gyraulus* has occurred in Asia since the Cretaceous (Isaji 2010), and has been reported from the Cenozoic deposits in China (Yen 1943).

### Family LYMNAEIDAE Rafinesque, 1815

### Lymnaeidae gen. et sp. indet.
(Fig. 7A)

MATERIAL EXAMINED. — **Taiwan** • 2 specimens; Shuiniukeng (= Water Buffalo Valley), New Taipei City; Tananwan Formation, Early Pleistocene, Calabrian; ASIZF0100921, ASIZF0100942.

#### DESCRIPTION

Shell small (up to 1.5 cm), oval and elongated, dextral. Exposed whorls slightly slopping, with long body whorl. Based on the exposed part of the spire, it appears to be short.

#### REMARKS

Identifying this specimen is challenging due to its partial embedding in sediments. However, the exposed whorls, including a dextral shell, a long body whorl and a shorter spire, suggest that it belongs to the family Lymnaeidae. In Taiwan, four extant species of this family have been reported, including *Galba truncatula* (Müller, 1774), *Orientogalba ollula* (Gould, 1859), *Radix auricularia* (Linnaeus, 1758), and *Radix plicatula* (Benson, 1842) (Chang 1991; Chen 2011; Chung & Shao 2022). The elongated body whorl of the studied specimens with a spire still higher than in *R. auricularia*, thus it makes them similar in general outline to *O. ollula* and *R. plicatula*, although better-preserved specimens are needed for more precise identification.

### Class BIVALVIA Linnaeus, 1758
### Order UNIONIDA Gray, 1854
### Family UNIONIDAE Rafinesque, 1820

### Unionidae gen. et sp. indet.
(Fig. 7B)

MATERIAL EXAMINED. — **Taiwan** • 1 specimen; Shuiniukeng (= Water Buffalo Valley), New Taipei City; Tananwan Formation, Early Pleistocene, Calabrian; ASIZF0100922.

#### DESCRIPTION

Flat fragment of the inner side of the valve with nacreous layer. The fragment represents ventral part of the shell. 2 cm in length and width. Shell surface appears smooth, no obvious sculpture.

### Remarks

Based on previous reports of freshwater bivalves in Taiwan (Chang 1991; Chung & Shao 2022), only one family, Unionidae Rafinesque, 1820, with nacreous shells are documented in this region. Representatives of Unionidae tend to have elongated shells of a bigger size with convex ventral margin. Although our specimen is fragmentary, the preserved mold on the bedrock reveals ventral part of the shell that highly resemble unionids. Better-preserved specimens from the study area are required for further identification.

## DISCUSSION

### Taxonomic composition and comparison with extant freshwater faunas

In the studied locality, we identified four predominantly well-preserved freshwater gastropod taxa, along with one bivalve species. The most abundant species is *Sinotaia quadrata* (n = 37), followed by the less common *Melanoides* aff. *tuberculata* (8), *Gyraulus* sp. (2), Lymnaeidae gen. et sp. indet. (2), and Unionidae gen. et sp. indet. (1). Among viviparid species, *S. quadrata* stands out as one of the most successful native species in East Asia and is the most common species in Taiwan (Pace 1973) and Japan (Hirano *et al.* 2015). In fact, this species has been reported in nearly all freshwater environments in Taiwan (Pace 1973), exhibiting considerable morphological variation across different localities (Chen, 2011). Extant populations of *S. quadrata* inhabit lakes, ponds, and irrigation canals, often in association with *Cipangopaludina chinensis* and *Corbicula fluminea* in East Asia (Hsu 1935).

The native range of *Melanoides tuberculata* spans the Indo-Pacific, Southern Asia, Arabia, northern Australia, the Near East, and much of Africa (Brown 1994). In Taiwan, this species represents one of the most commonly found species and has been reported from various localities (Pace 1973; Chao *et al.* 1987; Chang 1991; Chiu *et al.* 2002: Chen 2011).

The remaining taxa are not common in our collection. The genus *Gyraulus* is known for its diversity and nearly cosmopolitan distribution today (Hubendick 1955; Pace 1973). Recent representatives of this genus are reported from various localities in Eastern and Southeastern Asia, such as Taiwan (Pace 1973; Chen 2011), China (Hu *et al.* 2021), Singapore (Chan & Lau 2023), and Thailand (Brandt 1974).

For the family Lymnaeidae, different number of species have been reported (mostly four species; Chang 1991; Chen 2011; Chung & Shao 2022). Noteworthy, freshwater mytilids, the group that is widely distributed in East Asia, appeared in Taiwan only in the last century (Morton 2015). On the other hand, the family Unionidae was reported from Taiwan since Pleistocene (Hu 1992b; Tao & Hu 1992), and three species are currently known in Taiwan: *Sinanodonta woodiana* (Lea, 1834), *Pletholophus tenuis* (Gray, 1833), and *Nodularia douglasiae* (Gray, 1833) (Chung & Shao 2022).

In summary, the taxonomic composition of the fossil assemblage aligns closely with the current freshwater mollusk fauna of Taiwan. Both *S. quadrata* and *M. tuberculata* are common elements in extant Taiwanese freshwater ecosystems, while the other three taxa also include members widely distributed in the region (Chung & Shao 2022). However, our study represents a hand-picked composition of small species, as no sieving was carried out for millimeter-sized species, which are abundant in fossil aquatic fauna records, suggesting the potential presence of additional small-size species in this fauna that may have gone unnoticed.

### Preservation of juvenile shells

Many freshwater gastropods exhibit maternal care behaviors, where females carry juveniles through the vulnerable larval stage, thereby increasing the survival rate of the next generation (e.g., Jakubik 2012). The presence of juvenile shells within the female shells of extant viviparids has been well-documented (e.g., Jakubik 2006). However, fossil records of juvenile viviparid shells found inside female shells are extremely rare. One such case was reported on *Viviparus apameae galileae* (Schütt, 1993) and *Bellamya* sp. from the Early-Middle Pleistocene of Israel, which provided valuable information on the species' sex distinction, ecology, longevity, and fecundity (Ashkenazi *et al.* 2010).

In our study, among the 37 sampled *S. quadrata* specimens, two broken specimens were found to contain several juvenile shells inside the adult shell (Fig. 5A). This may offer important clues regarding viviparid ecology and reproduction. Although these specimens are insufficient for a detailed ecological analysis of longevity, fecundity, and survival strategy, they represent only the second known case in the fossil record – fossil juvenile shells found inside female shells. Future studies employing micro-computed tomography (μCT) could potentially uncover more juvenile shells.

### Biogeography and geographical isolation

Based on the widespread extant and fossil distributions and genetic evidence, *S. quadrata* has been inferred to originate in continental East Asia and migrated to surrounding islands (Hirano *et al.* 2015; Ye 2020). Fossil records in this study therefore represent the so far earliest evidence of the presence of *S. quadrata* in Taiwan. However, we cannot determine whether this species arrived in Taiwan much earlier than the recorded fossils, as we currently lack evidence from earlier periods.

In comparison, *S. quadrata* in Japan is believed to have a more recent history. The oldest *S. quadrata* fossils in Japan are from southern Kyushu, dating to 10 000-6000 years ago (Matsuoka unpublished data, reported in Ye *et al.* 2020), suggesting a relatively recent introduction compared to Taiwan. However, genetic studies (Ye *et al.* 2020) propose a naturally migration from continental East Asia to Japan around 70 000 years ago, much earlier than being introduced in association with agricultural expansion by human activities at about 8000 and 1200 years ago.

The different distribution pattern and dispersal histories of *S. quadrata* in Taiwan and Japan may reflect variations in geographical isolation during the Quaternary (Fig. 8;

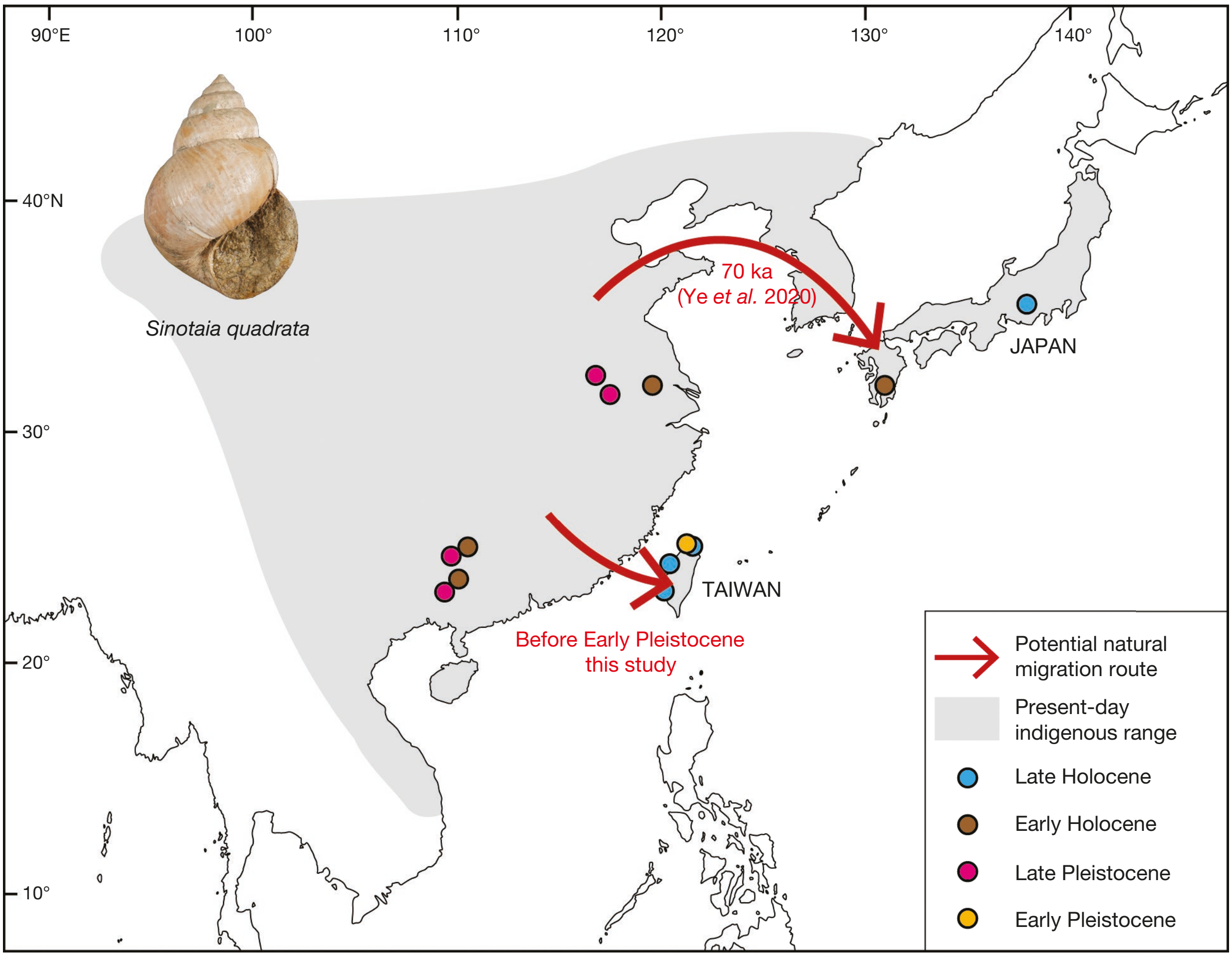

Fig. 8. — Biogeography of extant and fossil *Sinotaia quadrata* (Benson, 1842). Early Pleistocene: this study; Late Pleistocene: Yangtze Valley (Yen 1943), Kiangsu Province (Yen 1943), Guangxi Province (Odhner 1930); Early Holocene: Kweilin (Hsu 1935), Yixing (Huang *et al.* 2007), Guangxi (Wang 1983), southern Kyushu (Matsuoka unpublished, reported in Ye *et al.* 2020); Late Holocene: Honshu (Kurozumi 2013), Qingshui Zhongshe Site Shuijuetou Site, and Kiwulan Site (Taiwan Malacofauna Database 2013). The data of present-day indigenous range of *S. quadrata* is from Ye (2020). Base map was modified from Google Earth 7.3.6.

S2). Land bridges between Taiwan and the continental East Asia may have formed more frequently due to lower sea levels at depths around 80 m during glacial cycles (Ho *et al.* 2022), whereas land bridges between Japan and the continent likely formed less often and ephemeral due to deeper (around 150 m) surrounding seas (Lea *et al.* 2002). Additionally, the sampling layer was likely deposited during a sea-level lowstand period (possibly glacial period), as indicated by the cyclic sequence stratigraphy throughout the Tananwan Formation (Chuang *et al.* 2012), potentially supporting the hypothesis.

However, these interpretations remain speculative without additional evidence, and other scenarios cannot be ruled out. For example, populations of the freshwater mollusk *Semisulcospira libertina* Gould, 1859 (Semisulcospiridae) in northern Taiwan are thought to have originated from Japan, while those in southern Taiwan might have originated from South China or South Asia, based on Cytochrome c oxidase subunit I gene sequences (Chiu *et al.* 2017). On the other hand, passive dispersal via birds cannot be ruled out, as it regularly occurs in hermaphroditic species (such as pulmonates) as well as other snail groups (Harzhauser *et al.* 2016; Yu *et al.* 2021). More biogeographic studies of various taxa, alongside detailed analyses of multiple factors, are needed to fully understand the dynamics of paleogeography and its influence on present-day biodiversity.

## CONCLUDING REMARKS

The freshwater mollusk assemblage of the Tananwan Formation is represented by *Sinotaia quadrata*, *Melanoides* aff. *tuberculata*, *Gyraulus* sp., Lymnaeidae gen. et sp. indet., and Unionidae gen. et sp. indet. Key diagnostic characteristics, especially those of juvenile shells, were crucial for their identification. Interestingly, these juvenile shells discovered inside female *S. quadrata* fossils represent only the second fossil records of child-carrying in viviparids. These fossil records, with relatively precise dating, provide a valuable timescale for understanding species distribution and expansion.

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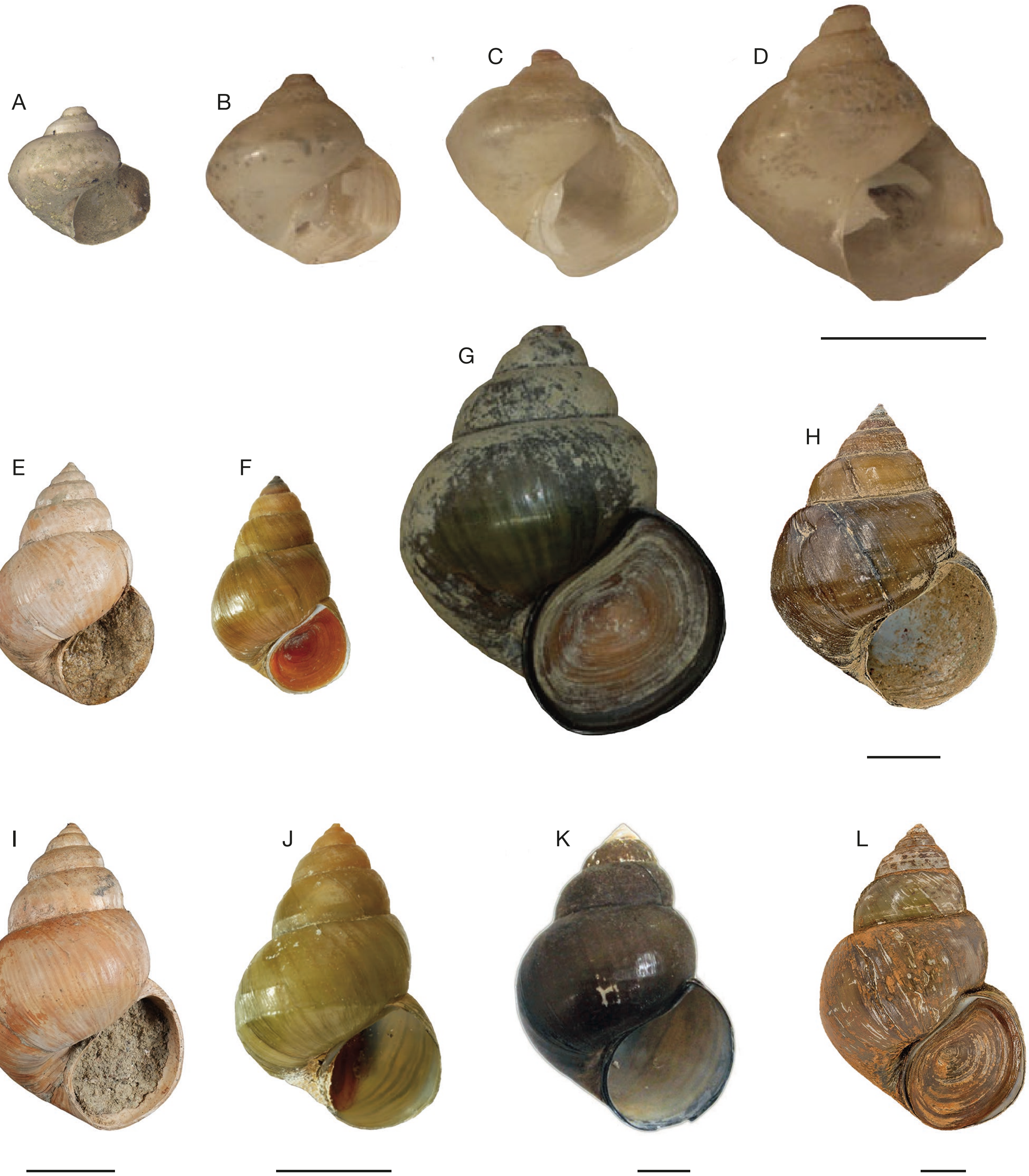
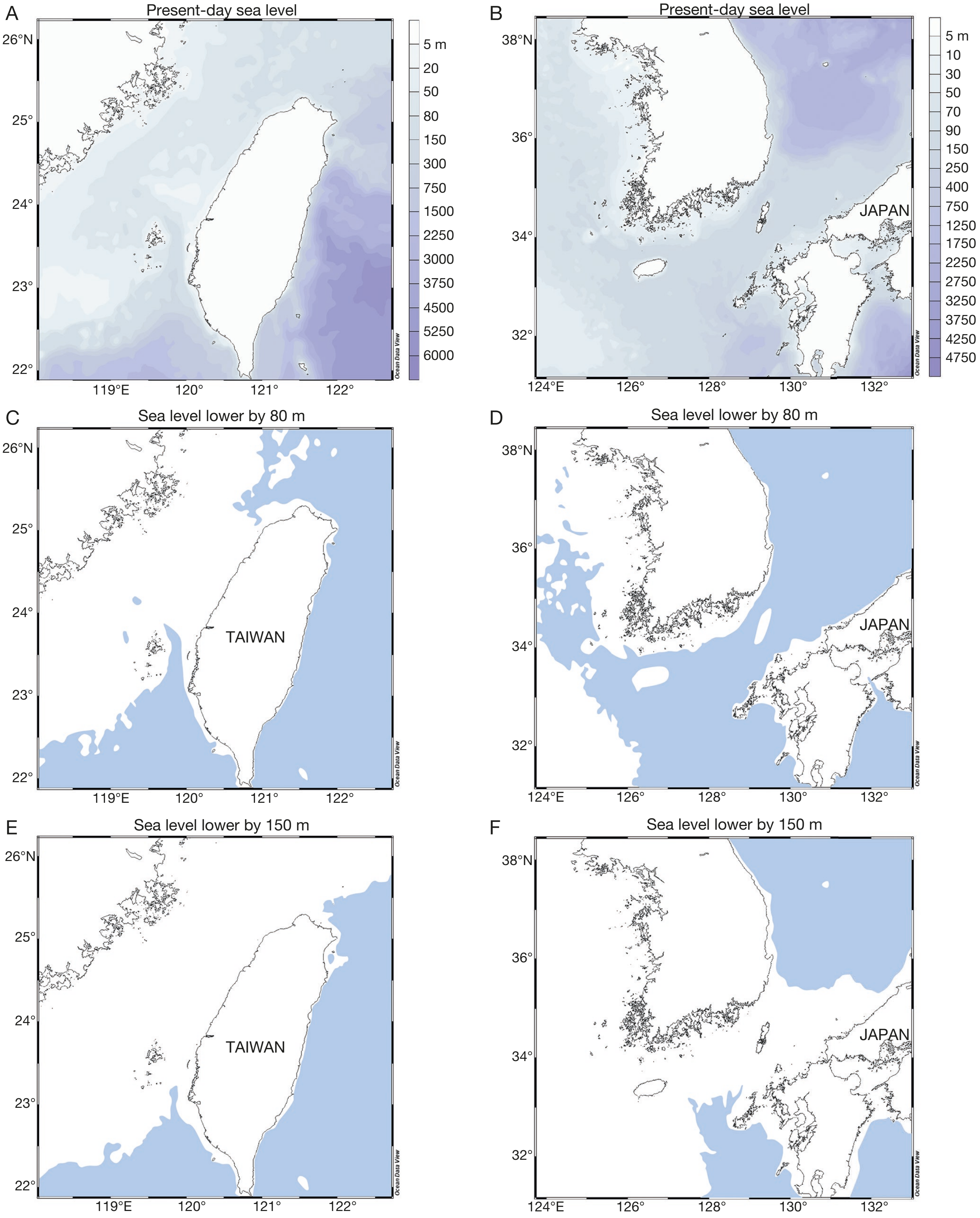


Appendix 1. — Figure S1, comparison to resemble species in juvenile shell (**A**-**D**), typical adult shell (**E**-**H**), and shell with similar morphotypes (**I**-**L**): **A**, *Sinotaia quadrata* (Benson, 1842) from Tananwan Formation (ASIZF0100907); **B**, *Sinotaia quadrata* from Japan (Hirano *et al.* 2015); **C**, *Cipangopaludina chinensis* (Gray, 1833) from Japan (Hirano *et al.* 2015); **D**, *Heterogen japonica* (von Martens, 1861) from Japan (Hirano *et al.* 2015); **E**, *Sinotaia quadrata* from Tananwan Formation (ASIZF0100893); **F**, *Sinotaia quadrata* from Ombrone river, Italy (invasive species in Italy; Cianfanelli *et al.* 2017); **G**, *Cipangopaludina chinensis* from Japan (Hirano *et al.* 2015); **H**, *Heterogen japonica* from Japan (Van Bocxlaer & Strong 2016). **I**, *Sinotaia quadrata* from Tananwan Formation (ASIZF0100894); **J**, *Sinotaia quadrata* from Ombrone river, Italy (invasive species; Cianfanelli *et al.* 2017); **K**, *Cipangopaludina chinensis* (Gray, 1833) from China (Lu *et al.* 2016); **L**, *Heterogen japonica* from Japan (Van Bocxlaer & Strong 2016). Scale bars: A-D, 5 mm; E-L, 10 mm. Photos: Chia-Hsin Hsu.



Appendix 2. — Figure S2, simulation of land bridge formations at different sea level in Taiwan Strait (**A**, **C**, **E**) and Tsusshima Strait (**B**, **D**, **F**): **A**, present-day sea level in Taiwan Strait; **B**, present-day sea level in Tsushima Strait; **C**, sea level lowered by 80 m in Taiwan Strait, showing the formation of a land bridge; **D**, sea level lower by 80 m in Tsushima Strait; **E**, sea level lower by 150 m in Taiwan Strait, showing the formation of a land bridge; **F**, sea level lower by 150 m in Tsushima Strait, showing the formation of a land bridge. Figures are generated by Ocean Data View (https://odv.awi.de/). Maps: Chia-Hsin Hsu.

Appendix 3. — Table S1, shell measurements of fossil *Sinotaia quadrata* (Benson, 1842).

| Species | Specimen number | WSh | HSp | HSh | HBW | HA | WA |
|---|---|---|---|---|---|---|---|
| *Sinotaia quadrata* | ASIZF0100893 | 20.76 | 11.07 | 31.27 | 22.37 | 17.41 | 11.87 |
| | ASIZF0100894 | 21.3 | 12.28 | 33.66 | 25.4 | 17.63 | 12.79 |
| | ASIZF0100895 | 22.79 | 12.73 | 33.67 | 25.71 | 18.06 | 13.38 |
| | ASIZF0100896 | 22.73 | 12.48 | 36.13 | 25.9 | 18.12 | 13.8 |
| | ASIZF0100897 | 25.78 | 15.05 | 39.35 | 28.22 | 19.41 | 15.15 |
| | ASIZF0100898 | 23.93 | 12.97 | 39.45 | 28.36 | 20.48 | 13.11 |
| | ASIZF0100899 | 19.54 | 10.19 | 30.7 | 21.82 | 15.84 | 12.4 |
| | ASIZF0100900 | 20.62 | 11.44 | 33.05 | 24.06 | 16.25 | 13.29 |
| | ASIZF0100901 | 17.97 | 10.38 | 29.08 | 21.53 | 15.62 | 10.67 |
| | ASIZF0100902 | 15.15 | 6.82 | 21.14 | 6.85 | 13.1 | 9 |
| | ASIZF0100903 | 12.85 | 6.57 | 18.72 | 14.61 | 11 | 8.32 |
| | ASIZF0100904 | 11.41 | 5.74 | 16.25 | 12.75 | 9.46 | 6.57 |
| | ASIZF0100905 | 9.78 | 3.32 | 10.29 | 8.98 | 7.64 | 5.93 |
| | ASIZF0100906 | – | – | – | – | – | – |
| | ASIZF0100907 | 4.33 | 0.67 | 4.2 | 3.4 | 2.85 | 1.9 |
| | ASIZF0100908 | 4.09 | 0.69 | 3.82 | 3.14 | 2.63 | 1.91 |
| | ASIZF0100909 | 3.1 | 0.37 | 2.89 | 2.43 | 1.81 | 1.57 |
| | ASIZF0100910 | – | – | – | – | – | – |
| | ASIZF0100911 | 3.15 | 0.41 | 3.5 | 3.05 | 2.23 | – |
| | ASIZF0100912 | – | – | – | – | – | – |
| | ASIZF0100923 | – | – | – | – | – | – |
| | ASIZF0100924 | 15.92 | 7.49 | 25.06 | 18.27 | 13.55 | 9.36 |
| | ASIZF0100925 | 16.96 | 8.29 | 25 | 18.22 | 12.76 | 12.17 |
| | ASIZF0100926 | 17.67 | 9.66 | 24.64 | 17.81 | 15.43 | 11.64 |
| | ASIZF0100927 | 15.24 | 8.31 | 24.14 | 16.53 | 12.65 | 9.65 |
| | ASIZF0100928 | 12.3 | 5.79 | 17.89 | 13.83 | 11.32 | 7.66 |
| | ASIZF0100929 | 8.61 | 3.3 | 13.01 | 10.46 | 8.18 | 6.03 |
| | ASIZF0100930 | 10.89 | 4.02 | 10.85 | 10.12 | – | – |
| | ASIZF0100931 | 9.61 | 4.01 | 13.61 | 10.61 | 8.18 | 5.77 |
| | ASIZF0100932 | 10.56 | 4.16 | 11.91 | 9.83 | – | – |
| | ASIZF0100933 | 9.93 | 3.24 | 11.21 | 9.71 | 8.53 | – |
| | ASIZF0100934 | 12.38 | 6.04 | 18.06 | 13.53 | 9.91 | 7.15 |
| | ASIZF0100935 | 12.87 | 6.33 | 18.41 | 13.74 | 10.5 | 7.63 |
| | ASIZF0100936 | – | – | – | – | – | – |
| | ASIZF0100937 | – | – | – | – | – | – |
| | ASIZF0100938 | – | – | – | – | – | – |
| | ASIZF0100939 | 2.74 | 0.65 | 3.1 | 2.51 | 1.94 | 1.08 |
| **Average adult** | | **15.9** | **8.07** | **23.46** | **17.17** | **13.52** | **10.15** |
| **Average juvenile** | | **3.48** | **0.56** | **3.5** | **2.91** | **2.29** | **1.62** |

Appendix 4. — Table S2, shell measurements of fossil *Melanoides* aff. *tuberculata*

| Species | Specimen number | WSh | HSp | HSh | HBW | HA | WA |
|---|---|---|---|---|---|---|---|
| *Melanoides* aff. *tuberculata* | ASIZF0100913 | 12.17 | 13.39 | 30.94 | 17.88 | 12.73 | 5.04 |
| | ASIZF0100914 | 5.76 | 6.49 | 13.6 | 7.85 | – | – |
| | ASIZF0100915 | 5.38 | 7.95 | 1.9 | 6.07 | – | – |
| | ASIZF0100916 | 5.58 | 8.18 | – | – | – | – |
| | ASIZF0100917 | 5.76 | 5.4 | 12.78 | 7.71 | 4.82 | – |
| | ASIZF0100918 | 5.34 | 7.23 | 12.19 | – | – | – |
| | ASIZF0100919 | 3.11 | 2.48 | 5.99 | 3.5 | – | – |
| | ASIZF0100940 | 6.04 | 5.23 | 13.34 | 8.14 | 4.81 | 2.9 |
| **Average** | | **6.14** | **7.04** | **12.96** | **8.53** | **7.45** | **3.97** |

Appendix 5. — Table S3, shell measurements of other fossil mollusks.

| Species | Specimen number | WSh | DIWb | HSh | LWWb | HA | WA |
|---|---|---|---|---|---|---|---|
| *Gyraulus* sp. | ASIZF0100920 | 3.51 | 1.37 | 1.1 | 1.2 | 0.84 | 1.05 |
| *Gyraulus* sp. | ASIZF0100941 | – | – | – | – | – | – |
| Lymnaeidae gen. et sp. indet. | ASIZF0100921 | – | – | – | – | – | – |
| Lymnaeidae gen. et sp. indet. | ASIZF0100942 | – | – | – | – | – | – |
| Unionidae gen. et sp. indet. | ASIZF0100922 | – | – | – | – | – | – |