# Predator–prey interactions based on drillholes: A case study of turritelline gastropods from the Pleistocene Szekou Formation of Taiwan

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ABSTRACT: Drillholes on shells provide a useful way to investigate prey and predator relationships. The current study documents predator–prey interactions exemplified by a faunal assemblage of the fossil gastropod *Turritella cingulifera* from the Pleistocene Szekou Formation in Hengchun Peninsula, Taiwan. All recognisable skeletal and shell fragments that are larger than 3 mm in size were collected and recorded. Processed bulk sediments (5.24 kg) contained 1462 molluscan shells, including 824 specimens of *T. cingulifera*, and 27 non-molluscan invertebrates. In the current study, approximately 41.6% (609/1462) of molluscs are drilled with at least one hole. Drilling intensities (DIs) regardless of shell completeness in all gastropods, bivalves and the turritelline gastropod *T. cingulifera* are 0.546, 0.060 and 0.413, respectively. DI on turritellids is significantly lower than that on other gastropods ($\chi^2$= 21.039, $P < 0.001$). Furthermore, the percentage of drillholes that occur in multiply drilled specimens is 34.7% (95/275) for turritelline gastropods based on complete to nearly complete specimens ($n = 588$). Our study shows no significant preference of drillhole position either on the suture or on the whorl ($\chi^2 = 0.055$, $P = 0.814$). Most drillholes are located in whorls two to four proximal to the aperture. Drillhole diameters of the shells with one drillhole and ones with multiple drillholes are 1.0 and 0.5 mm on average, and the results of Mann–Whitney tests indicate that they are significantly different ($P < 0.001$). The first turritelline gastropod shell with an incomplete drillhole from Taiwan is documented here. The dominant drilling predators were naticids based on the drillhole morphology and the presence of naticids in the same assemblage. No apparent prey size selectivity is observed, so a 'size refugium' does not exist for the turritellids in the current study.

KEY WORDS: drilling frequency, Naticidae, palaeoecology, Quaternary geology, site stereotypy, Turritellidae.

Drilling predation represents the most abundant evidence of predation in the marine fossil record (Klompmaker *et al.* 2019) because drillholes preserved well in prey shells and drillholes are common for at least the late part of the Phanerozoic. Hence, the evolutionary history of drilling predation is well documented based on the long and rich marine fossil record (Hoffman *et al.* 1974; Dudley & Vermeij 1978; Dudley & Dudley 1980; Vermeij *et al.* 1980; Kitchell *et al.* 1981; Allmon *et al.* 1990; Kowalewski 1990; Tull & Böhning-Gaese 1993; Hagadorn & Boyajian 1997; Oji *et al.* 2003; Kelley & Hansen 2003; Klompmaker 2009; White 2009; Gordillo & Archuby 2012; Mallick *et al.* 2013; Martinelli *et al.* 2013; Paul *et al.* 2013; Johnson *et al.* 2017; Mondal *et al.* 2017; Archuby & Gordillo 2018; Klompmaker *et al.* 2019; Chattopadhyay *et al.* 2020;

Klompmaker & Kittle 2021) to the point that large, global analyses of different aspects of predation have become possible. For example, Huntley & Kowalewski (2007) found a positive correlation between predation intensity and marine diversity and Klompmaker *et al.* (2017) found that predators, as inferred from drillhole size, became larger relative to their prey throughout the Phanerozoic.

However, palaeontological data are heavily biased toward data from Europe and North America (Raja *et al.* 2021), which may distort the true global signal. Thus, more studies from other continents are more than welcome (Kojumdjieva 1974). Taiwan is underrepresented, even in Asia, for predation studies (Klompmaker *et al.* 2019, Fig. 3). Hayasaka & Hayaska (1960, p. 31, Fig. 15) illustrated a fossil gastropod shell *Cerithium kochi*,

which is now revised as *Rhinoclavis kochi* (Philippi, 1848) (https://www.molluscabase.org/aphia.php?p=taxdetails&id=139068 on 18 December 2022), with evidence of one drillhole from Taiwan. Subsequently, a few studies (Wang 1984; Chen *et al.* 1991; Hu & Tao 1991) mentioned drilling predation, but there is only one thesis on predator–prey interactions in Taiwan, using molluscan fossils from the Holocene Tainan Formation (Ji 1998). The molluscan faunas from the Pleistocene Szekou Formation are well documented (Wang 1984; Chen *et al.* 1991; Hu & Tao 1991), but drillholes in molluscan shells did not receive attention until now. The current work represents a quantitative study focusing on the predator–prey interactions exemplified by drillholes based on Taiwanese material.

## 1. Regional geology

The study area (22°00′49″N; 120°42′54″E) is located in the Hengchun Peninsula, the southernmost tip of Taiwan (Fig. 1a–c). Because of arc–continent collision, Hengchun is part of the accretionary prism bounded by a series of thrust faults. Fossiliferous marine successions are exposed in the western Hengchun tableland, Hengchun Peninsula bounded by the Hengchun Fault (Chen 2016). Local stratigraphic units are summarised in Chen & Lee (1990).

The studied fossils are recovered from the Szekou Formation, a Late Pleistocene unit composed of brownish sandy mudstone, underlying the Hengchun Limestone and overlain by the Taiping Red Bed (Chen 2016) (see Taiping Fm. in Fig. 2). The depositional environment of the Szekou Formation was a lagoonal setting enclosed by barrier islands represented by the Wanlitong Limestone (Chen *et al.* 2005). Chen *et al.* (1991) identified the following faunal assemblages from the Szekou Formation:

*Eucrassatella–Venus* assemblage; *Conus–Fissidentalium* assemblage; *Modiolus* assemblage; *Cultellus–Solecurtus* assemblage; *Pinna–Turritella* (PT) assemblage; *Crassostrea* assemblage; and *Batillaria–Cyclina* assemblage. According to the current study, three faunal assemblages are present in the studied area. The studied fauna belongs to the PT assemblage, which occurs near the upper part of the succession (Fig. 2).

## 2. Material and methods

### 2.1 Material

The current study is based on a single bulk sample, implying randomness of shells collected. Bulk sediments (5.24 kg) were taken from the fossil site (Fig. 2). Shells were sieved out of the sediments with a mesh size of $3 \times 3$ mm and recorded ($n = 1489$) (Table 1). Among all mollusc shells ($n = 1462$), there are 1280 gastropods, 168 bivalves and 14 scaphopods in the studied bulk sample. We studied drilling intensities (DIs in Table 1) in skeletal elements such as gastropods, bivalves and scaphopods separately, and subsequently focused our more detailed analyses on the most abundant species, the gastropod *Turritella cingulifera* Sowerby 1825 (=*Turritella filiola* Yokoyama 1928); see Section 2.4. The general morphology and the number of whorls of this species are illustrated (Fig. 3a). Examples of one drillhole and multiple drillholes are included (Fig. 3b–e). Variations of drillhole shapes are documented (Fig. 4a1–c2). Measurements were made using digital images in the freeware program ImageJ. Results are visually summarised (Figs 5a–c; 6a–d). Potential predators responsible for the parabolic drillholes are illustrated (Fig. 7). Studied and figured specimens are deposited at the Department of Geosciences, National Taiwan University (NTUG). Original measurements are included as supplementary
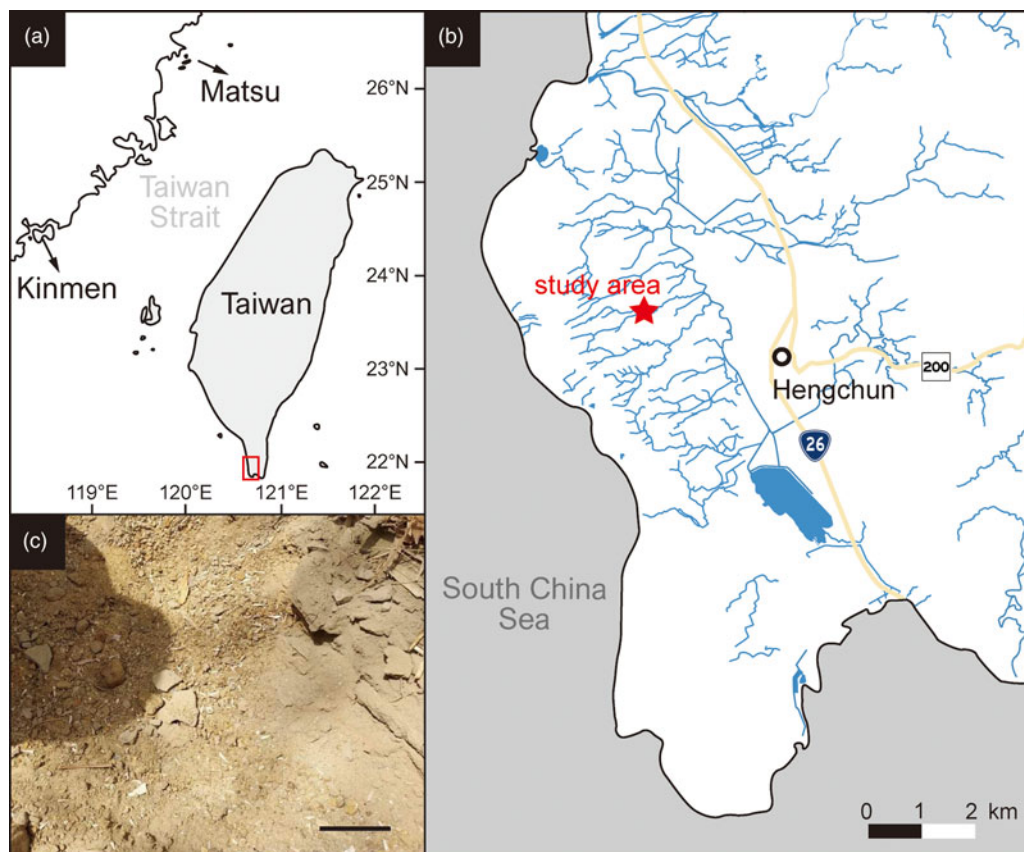


**Figure 1** Maps of Taiwan (a, b) and an outcrop photograph (c) showing the locality of the study site. (a) Map of Taiwan with the studied region indicated by the red rectangle. (b) Close-up of Hengchun with the study site indicated by the red star (22°00′49″N, 120°42′54″E). (c) Outcrop photograph. Scale bar = 5.0 cm.
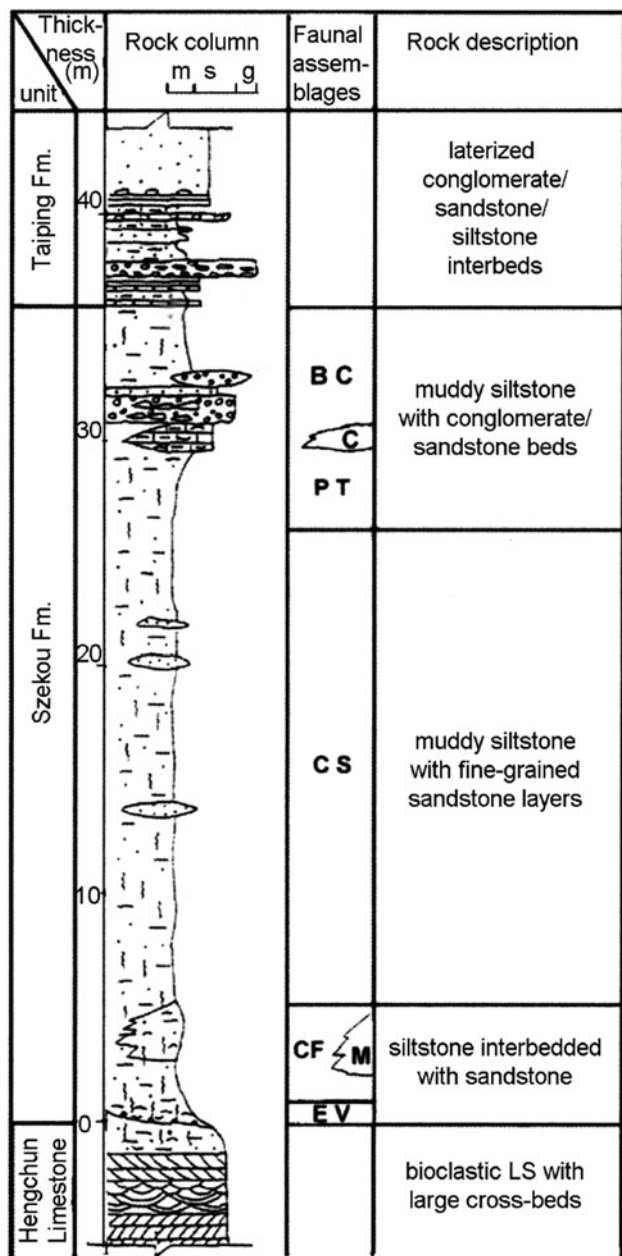
**Figure 2** Stratigraphic column of Szekou Formation (modified from Chen *et al.* 1991, Fig. 3). Samples are taken from the *Pinna–Turritella* biofacies.

**Table 1** Summary of the results of drilling predation on molluscan shells of Szekou, Taiwan.

| Group | *n* | Drilled | RF | DI[1] |
|---|---|---|---|---|
| Gastropoda, *Turritella cingulifera* | 824 | 340 | 0.564 | 0.413 |
| Gastropoda, others | 456 | 249 | 0.312 | 0.546 |
| Bivalvia | 168 | 20 | 0.115 | 0.060 |
| Scaphopoda | 14 | 0 | 0.010 | – |

| | CD | Inc. | Tot. | Mult. | PE | MULT |
|---|---|---|---|---|---|---|
| Turritelline gastropods (*n* = 588) | 273 | 1 | 274 | 95 | 0.004 | 0.347 |

RF, relative frequency (equation 1 in Section 2.2); DI, drilling intensity (equation 2 in Section 2.2); CD, number of complete drillholes. Inc., number of incomplete drillholes; Tot., total number of drillholes; Mult., number of drillholes in multiply bored specimens; PE, prey effectiveness (=Inc./Tot.); MULT, Mult./Tot.
[1]The equation used for Bivalvia is different (equation 3 in Section 2.2).

material (Appendix 1) available at https://doi.org/10.1017/S1755691023000130.

## 2.2 Equations

To calculate the relative frequency (RF) of taxa in the current study, the following equation is used here:

$$RF = n/N \tag{1}$$

where:

$n$ = the number of specific fossil remains present in the sample; and

$N$ = the total number of skeletal fossils present in the sample.

To calculate drilling intensity (DI) for gastropods, the following equation is used here:

$$DI = N_d/N \tag{2}$$

where:

$N_d$ = the number of drilled specimens; and

$N$ = the total number of specimens.

To calculate DI for bivalves, the following equation (see Kowalewski 2002) is adopted here:

$$DI_b = N_{dv}/(N_v * 0.5) \tag{3}$$

where:

$N_{dv}$ = number of valves with a complete drillhole; and

$N_v$ = the total number of valves.

## 2.3 Charts and statistics

Kolmogorov–Smirnov tests for normality yielded values consistent with the distributions of values of shell length and drillhole diameter being a poor fit to a normal distribution at the $P < 0.01$ level. Therefore, we used non-parametric statistical tests, including Spearman's rank correlation coefficient, Kruskal–Wallis (K-W) tests and Mann–Whitney (M-W) tests. PAST version 4.10 was used, also for data visualisations (Fig. 5a–c).

## 2.4 Taxonomic issue

Taxonomic identifications are based on the work by Hu & Tao (1991). However, many molluscan species' assignments have been revised since. For instance, the taxonomic status of the turritelline gastropod *Turritella filiola* Yokoyama 1928, has been reviewed and revised several times. Robba *et al.* (2007, pp. 25–26) synonymised the Pliocene occurrence of *T. filiola* in Taiwan with *Haustator* (*Kurosioia*) *cingulifera* (Sowerby 1825). According to the World Register of Marine Species, however, this species is not recognised as a valid species of *Haustator* (https://www.marinespecies.org/aphia.php?p=taxdetails&id=754400). Thus, the taxonomic status of *T. filiola* is revised as *Turritella cingulifera* Sowerby 1825, based on the MolluscaBase (https://molluscabase.org). Furthermore, valid species of Taiwanese fossil molluscs recognised by MolluscaBase are reported here.

## 2.5 Shell completeness

True shell completeness with the presence of the protoconch is rare in adult gastropods. Johnson *et al.* (2017) reported that only one out of 100 specimens of *Turritella bacillum* Kiener 1843, collected from Hong Kong is preserved with a protoconch. 'Complete or nearly complete' specimens here are shells with either or both partially broken aperture and/or apical part as defined in Mallick *et al.* (2013). Roy *et al.* (1994) showed that drilled bivalve shells are significantly weaker than undrilled shells under point-load compression experimental conditions, but Dyer *et al.* (2018) found no difference in DI during compression experiments using gastropods. The current study focuses on the effect of drilling predation based on complete or nearly
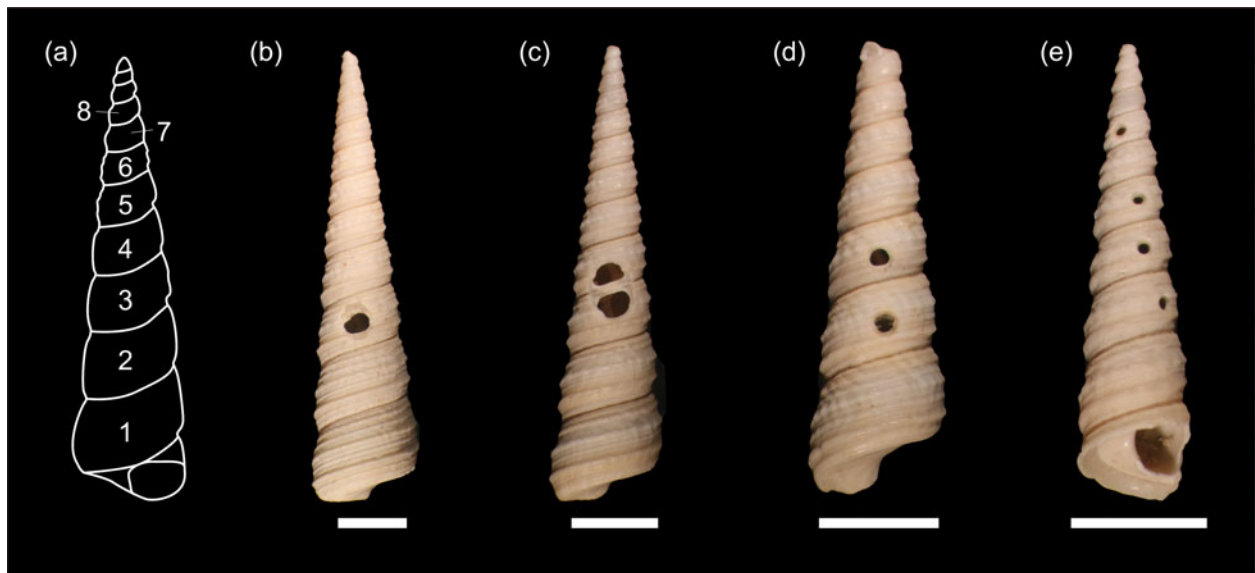
**Figure 3** General morphology of *Turritella* (a) and examples of specimens of *Turritella cingulifera* with drillholes (b−e). (a) *Turritella* with the whorl numbers used herein. (b) Specimen with one drillhole on the whorl (NTUG300-FI00002). (c) Specimen with one drillhole on the suture (NTUG300-FI00003). (d) Specimen with two drillholes (NTUG300-FI00004). (e) Specimen with more than two drillholes (NTUG300-FI00005). Scale bars = 3.0 mm.

complete samples, and fragmentary remains within the bulk sample will be utilised in a future study.

## 2.6 Terminology

Standard terminology used for studying prey–predator interactions as defined in Kelley *et al*. (2001) are adopted here. In



**Figure 4** Three types of drillholes observed from the Szekou molluscs. (a1, a2) Cylindrical drillhole in *Fissidentalium vernedei* (Sowerby 1860) (NTUG300-FI00001) from different angles. This specimen is from the *Conus–Fissidentalium* faunal assemblage (CF in Fig. 2) and is not included in the current study. (b1, b2) Parabolic drillhole in *Turritella cingulifera* (NTUG300-FI00002) from different angles. (c1, c2) Incomplete drillhole in *T. cingulifera* (NTUG300-FI00006) from different angles. Scale bars = 1.0 mm.

particular, prey effectiveness is defined as 'the ratio of incomplete drillholes in a sample to total number of attempted holes,' and multiply drilled specimens of all drillholes (MULT) is defined as 'the number of drillholes that occurred in multiply bored specimens divided by the total number of attempted drillholes' (Kelley *et al*. 2001, pp. 167–68).

## 3. Results

### 3.1 Drilling intensity

The overall bulk sample yielded 1489 skeletal fragments and shells, including 1280 gastropods, 168 bivalves, 14 scaphopods, 23 scleractinian coral fragments, three bryozoan fragments and one echinoid test. Among all molluscan shells, 87.6% (1280/1462) are gastropods, 11.5% represent bivalves and 1% are scaphopods (Table 1). DIs are 0.46, 0.06, and 0.00 for gastropods, bivalves and scaphopods, respectively (DI in Table 1).

Among all gastropods, *T. cingulifera* is the most abundant gastropod taxon in the studied sample (64.4%, 824/1280). Overall DI for *T. cingulifera* is 0.413. Among *T. cingulifera* specimens, complete to nearly complete shells (see Section 2.5) ($n = 588$) were analysed further (Fig. 5a, b), and its DI is 0.371 (218/588).

### 3.2 Drillhole types

Two basic types of drillhole shapes were observed in the current study: cylindrical drillholes ( = ichnospecies *Oichnus simplex* Bromley 1981) (Fig. 4a1, a2); and parabolic drillholes ( = *Oichnus paraboloides* Bromley 1981) (Fig. 4b1, b2). Oval holes ( = *O. ovalis* Bromley 1993; see Archuby & Gordillo 2018; Klompmaker & Kittle 2021) are not observed. One incomplete drillhole is documented herein (Fig. 4c1, c2). Only parabolic drillholes of *O. paraboloides* are recognised on specimens of *T. cingulifera*.

### 3.3 Multiply drilled specimens

For complete to nearly complete specimens ($n = 588$) of *T. cingulifera*, the number of complete drillholes is 273. The number of holes on multiply drilled specimens is 95. Prey effectiveness (PE in Table 1) is 0.004. Among all drillholes counted, MULT is 0.347 (95/274) (Table 1). Distributions of *T. cingulifera* without drillholes, one drillhole and multiple drillholes are illustrated (Fig. 5b). Drillholes occur in all shell length bins. The results
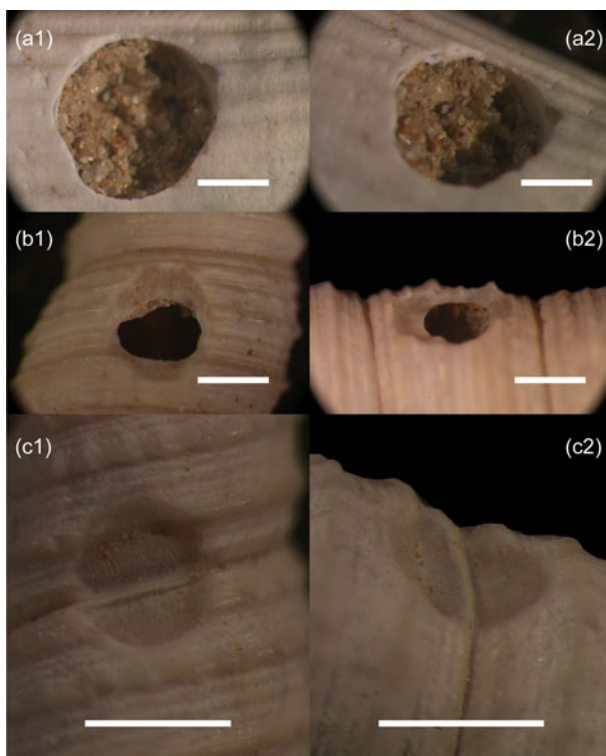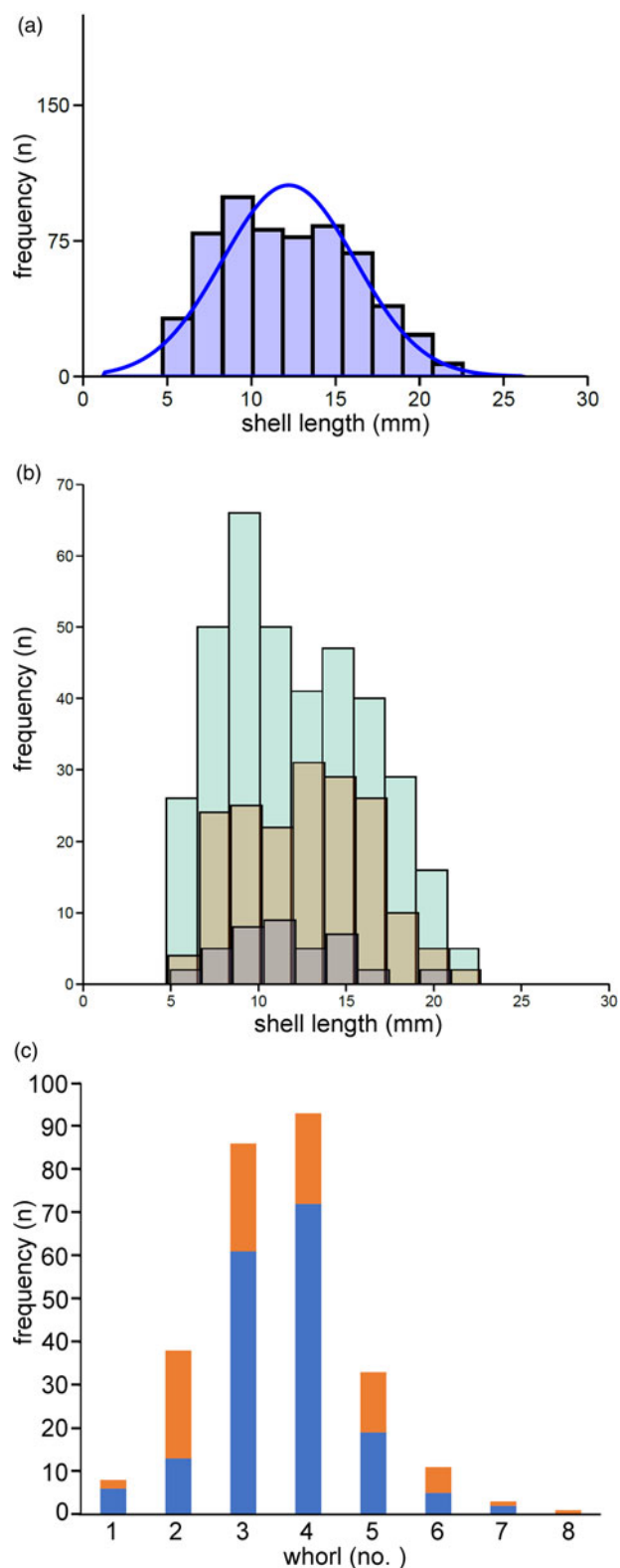
**Figure 5** Summary charts of complete to nearly complete specimens of *Turritella cingulifera* recovered from the Pleistocene Szekou Formation of Taiwan. (a) Histogram of shell length frequency ($n = 588$) divided into 10 bins with a normal distribution curve. (b) Histogram (non-stacked) of shell-size frequency containing three categories: shells without drillhole ($n = 370$) in green; shells with one drillhole ($n = 178$) in yellow brown; and shells with multiple drillholes ($n = 40$) in grey. (c) Drillhole position frequency based on 273 drillholes in 218 shells. Blue colour = one drillhole ($n = 178$); Orange colour = multiple drillholes (95 drillholes on 40 shells). Number on the x-axis indicates the whorl number with 1 being the closest to the aperture (see Fig. 3a).

of K-W tests indicate that there is no significant difference ($P = 0.17$) for shell length among specimens with different numbers of drillholes.

## 3.4 Site stereotypy

Among shells with a single drillhole, holes are found in a range of places on the shell from whorl 1 to whorl 7. Whorl 4 is drilled with the highest frequency (72), with the adjacent whorl 3 location also having a high incidence of drillholes (61). In the sample of shells with multiple drillholes, whorls 2 and 3 were tied at 25 drillholes each (Fig. 5c). Furthermore, specimens with one drillhole on the suture are fairly uncommon (11.2%, 20/178). They appear as two small openings above and below the suture (Fig. 3b). The only incomplete drillhole is found on the suture of a shell (Fig. 4c1, c2).

## 3.5 Size selectivity

Considering only the complete or near-complete specimens ($n = 588$), *T. cingulifera* shells range from 4.7 to 22.6 mm in length. More than 80% of drillholes (181 out of 218) occur in the range from 6.5 mm to 17.2 mm (Fig. 5b) in shell length. Shell length and drillhole size are plotted and analysed further (Fig. 6a–d). For the specimens with a single drillhole, the size ranges from 5.4 to 21.3 mm and the size ranges from 4.7 to 20.0 mm for holes on shells with multiple drillholes (Fig. 6b). The results of Kruskal-Wallis tests indicated that there is no significant difference ($P = 0.17$) for shell length among specimens with different numbers of drillholes.

## 3.6 Hole size versus shell length

For specimens with one drillhole ($n = 178$), hole size ranges from 0.2 to 2.6 mm with a mean of 1.0 mm and a standard deviation (SD) of 0.5 mm. For specimens with multiple drillholes ($n = 95$), the hole size ranges from 0.1 to 1.1 mm with a mean of 0.5 mm and a SD of 0.2 mm (Fig. 6c). The results indicate that the drillhole size in the single drillhole group is significantly larger than the multiple drillhole group ($P < 0.001$, M-W test).

For shells with one drillhole ($n = 178$), the hole size/shell length ratio ranges from 0.019 to 0.261 with a mean of 0.078 and a SD of 0.039. For holes on shells with multiple drillholes ($n = 95$), the hole size/shell length ratio ranges from 0.012 to 0.101 with a mean of 0.043 and a SD of 0.020 (Fig. 6d). The results indicate that the drillhole to shell length ratio is significantly larger for the single drillhole group compared to the multiple drillhole group ($P < 0.001$, M-W test).

# 4. Discussion

## 4.1 Prey preference

Our study covers material from the late phase (Late Cretaceous–Holocene) of predation history as defined in Kowalewski *et al.* (1998). DIs in *T. cingulifera* and other gastropods are 0.413 (0.371 for nearly complete specimens) and 0.546, respectively (Table 1). A contingency test shows that DI in *T. cingulifera* is significantly lower than that in other gastropods ($\chi^2 = 21.039$, $P < 0.001$). The overall DI (0.460) for all gastropods is relatively high compared to previous studies in other countries (Vermeij *et al.* 1980; Kowalewski *et al.* 1998; Mallick *et al.* 2013). According to Allmon *et al.* (1990) and Kelley & Hansen (2003), however, high DIs (>0.40) occurred locally among Cenozoic and recent turritelline assemblages.

## 4.2 Multiply drilled specimens

Making one drillhole is both time and energy consuming (Guerrero & Reyment 1988), and many efficient predators often attack the prey with one strike or multiple predators may attack one individual at the same time. It is theoretically possible that multiple small muricids preyed on one larger prey simultaneously, but this scenario is unlikely due to the small size range of *T. cingulifera* (4.7 mm to 21.3 mm). Moreover, the parabolic drillholes
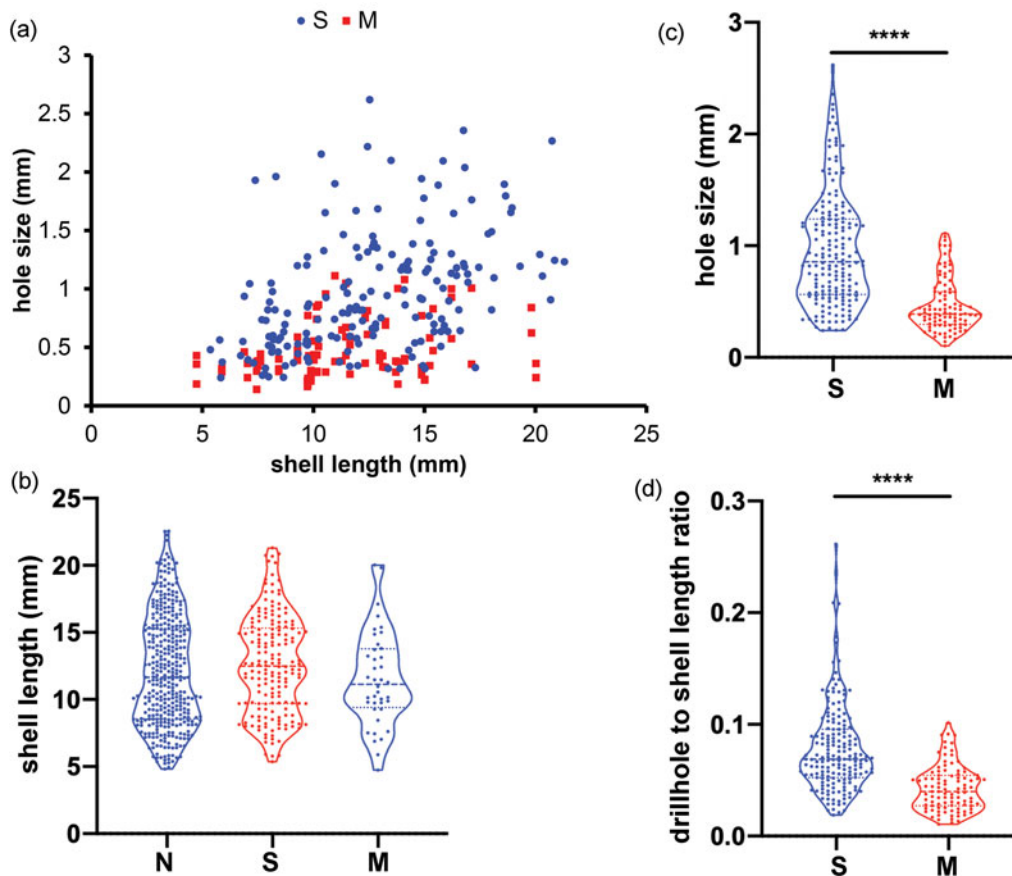
**Figure 6** Bivariate plot (a) and violin plots (b–d) of complete to nearly complete specimens of *Turritella cingulifera*. (a) Scatter plot of the shell length and drillhole size. Results of Spearman's rank correlation coefficient found a significant positive correlation between shell length and drillhole size for single holes ($r = 0.48$, $P < 0.001$), and for holes in specimens with more than one hole ($r = 0.29$, $P < 0.001$). (b) The number of shells without drillhole, with one drillhole, and shells with multiple drillholes are 370, 178 and 40, respectively. The results of Kruskal–Wallis tests indicate that there is no significant difference ($P = 0.17$) for shell length among specimens with different numbers of drillholes. (c) The number of shells with a single drillhole and multiple drillholes are 178 and 40 (95 holes on 40 specimens), respectively. The results indicate that the drillhole size in the single drillhole group is significantly larger than the multiple drillhole group ($P < 0.001$, Mann–Whitney (M-W) test). (d) The results indicate that the drillhole to shell length ratio is significantly larger for the single drillhole group compared to the multiple drillhole group ($P < 0.001$, M-W test). N = shell specimen without drillhole; S = specimens with one drillhole; and M = multiply drilled specimens.

on this turritellid are attributed to naticids (see below) that wrap their foot around the prey prior to drilling. Mallick *et al.* (2013) studied Late Cretaceous turritelline gastropods below the Cretaceous–Palaeogene boundary in southern India and calculated 0.0155 for unsuccessful drillholes and 0.0377 for MULT for *Turritella dispassa* ($n = 451$). Hagadorn & Boyajian (1997) reported that the incidences of multiply drilled turritelline shells are 0.129 and 0.097 for Miocene and Pliocene faunas from the United

States Gulf and Atlantic Coastal Plains. In general, MULT is associated with a high incidence of incomplete drillholes (see Klompmaker & Kittle 2021). In our study, there is only one specimen with one incomplete drillhole (Fig. 4c1, c2), suggesting that predators rarely abandoned a drillhole while actively drilling due to a disturbance and/or that turritellids did not suffocate prior to completion of the drillhole (see Ansell & Morton 1987).

### 4.3 Site stereotypy

The distribution of drillholes on the prey's shell is a proxy for site selectivity and predator drilling preference (see Hagadorn & Boyajian 1997). Shell thickness is not uniform across the shell because the shell is thicker in the suture than on the whorl wall. Two site selectivity analyses are presented: (a) drilling on the whorl versus on the suture; and (b) distance from the aperture. Among specimens with one hole, 11.2% (20/178) occur on the relatively thick suture. In addition, the specimen with an incomplete drillhole also occurs on the suture. For specimens with multiple holes, 10.3% (10/97) of the drillholes occur on the suture.

The second measure of site stereotypy is the relative distance of holes by labelling the whorl number in which holes occurred (Fig. 3a). Allmon *et al.* (1990) suggested predator preference for the thinner parts (whorl in our study) of the shell and sites located two or three whorls behind the aperture of turritelline
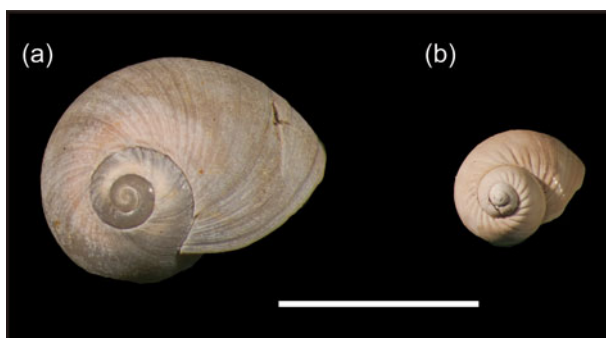


**Figure 7** Two species of naticid gastropods recovered in the current study. (a) *Polinices peselephanti* (Link 1807–1808) (NTUG300-FI00007). (b) *Neverita didyma* (Röding 1798) (NTUG300-FI00008). Scale bar = 5.0 mm.

shells since the Late Cretaceous. Hagadorn & Boyajian (1997) noted a shift in the drill-site selection from the Miocene predators to Pliocene predators by selecting drill sites further away from the aperture (with preference for sites located near the shell centre). In comparison, our Pleistocene predators preferred drilling whorls three to four proximal to the aperture for specimens with one hole and whorls two and three for shells with multiple drillholes (Fig. 5c). Our results parallel findings by Allmon et al. (1990). Most soft tissues are located in these whorls based on the anatomy of living turritellines (Allmon 2011).

### 4.4 Size selectivity

By comparing non-drilled and drilled shell-size distributions, we can determine if there are prey sizes that predators less frequently drilled or did not drill (i.e., size refugia) (Hagadorn & Boyajian 1997). In our study, specimens are divided into three groups: specimens with one drillhole (group S in Fig. 6a–d), shells with multiple drillholes (group M in Fig. 6a–d), and non-drilled shells (group N in Fig. 6b). Our results show that specimens with drillholes are covering the full range of available shell size (Fig. 5b, 6b). The K-W test $P$-value of 0.17 indicates there is no size refugium.

### 4.5 Drillhole size and predator/prey size correlation

Drillhole size is a proxy for the size of predators (Klompmaker et al. 2017, and references therein), and our study shows that holes in shells with one drillhole were made by predators that are significantly ($P < 0.001$) larger than those in specimens with multiple drillholes. Hagadorn & Boyajian (1997, p. 377) stated that 'by selecting prey that are most suited (with respect to size) to their drilling capabilities, predators can maximise their chances for successful predation'. Correlation of predator size (indicated by the size of drillholes) and prey size (indicated by the shell length) is adopted as a proxy for evaluating predator/prey size relations. For specimens with one drillhole (group S in Fig. 6d), hole size/shell length ratio has a mean of 0.078 with a range from 0.019 to 0.261. For shells with multiple drillholes (group M in Fig. 6d) hole size/shell length ratio has a mean of 0.043 with a range from 0.012 to 0.101. Our study shows that the relative hole size/shell length ratio in specimens with one drillhole is significantly larger ($P < 0.001$ based on the M-W test) than that in shells with multiple drillholes. Possible explanations are that soft tissues may not always have been consumed successfully and completely by the drillers due to a small hole size or that smaller predators were disrupted more frequently while consuming soft tissue. Another drillhole was created.

### 4.6 Predator identification

Although cylindrical drillholes are present in the current study (Fig. 4a1, a2), drillholes found in T. cingulifera are all parabolic in cross-section (Fig. 4b1, b2). Such holes are usually attributed to naticid gastropods (e.g., Kojumdjieva 1974; Bromley 1981; Kelley & Hansen 2003). There are nine naticid specimens representing two species, Polinices peselephanti and Neverita didyma (MolluscaBase 2022) (Fig. 7a, b), recovered in the current study. They are suggested here as potential drillers/tracemakers. The possible presence of a central boss in the centre of the single incomplete drillhole (Fig. 5e, f) cannot be confirmed as supporting evidence for a naticid origin of this drillhole (e.g., Kabat 1990) because this area is obscured by the presence of a suture. As indicated by the presence of a cylindrical hole (Fig. 4a1, a2), there may be muricid gastropods present in the Szekou fauna (Chen et al. 1991; Hu & Tao 1991), but they are absent in the PT biofacies in this bulk sample study.

There is one turritelline specimen with one incomplete drillhole (Fig. 4c1, c2) in the current study. Although there are many ways to produce an incomplete drillhole, one hypothesis

is the presence of secondary predator preying on the driller, causing the driller to abandon its drilling action and resulting in an incomplete drillhole on its prey (Chattopadhyay & Baumiller 2007). Based on the overall high richness of the Szekou fauna with 257 mollusc species (Chen et al. 1991), this hypothesis may be viable.

### 4.7 Living habitats and survival strategy for *Turritella*

Some previous, incorrect reconstructions of the orientation of living turritellids inferred that they crawled on the substrate surface (see Allmon 2011; Figs 62, 63). Living turritellids are mainly sessile, semi-infaunal suspension feeders in shallow marine settings with sea temperatures below 20 °C (White 2009; Allmon 2011). Being (semi-)infaunal implies more encounters with the predominantly infaunal naticids (Kelley & Hansen 2003). The drilling pressure for turritellids has been relatively high since the Eocene (Dudley & Vermeij 1978; White 2009).

Size refugia were thought to be one of the survival strategies against drilling predation. A small size refugium for prey sizes <5 mm (Chattopadhyay et al. 2020) and large size refugium for prey size >20 mm (Klompmaker et al. 2019) have been reported. No size refugium has been found in the current study (Fig. 5b, 6b). This agrees with the conclusions based on a Miocene turritellid assemblage in Maryland, USA (Dudley & Dudley 1980). The lack of size refugium begs the question how they were able to survive high predation pressure by drillers.

In the current study, we show that DI on turritellids is significantly lower than that on other gastropods ($\chi^2 = 21.039$, $P < 0.001$). Turritelline gastropods in general have very high reproduction rates (Allmon 2011) and they are the most abundant gastropods (824 out of 1280; Table 1) in our study. Given that a size refugium from drillers is not available, the high reproduction rates may be a survival strategy against the high drilling predation pressure for T. cingulifera during the deposition of the Szekou Formation.

## 5. Conclusions

Highlights of our findings are summarised below:

- This is the first bulk sample study on DI on Szekou molluscs.
- DIs are 0.46 and 0.06 for gastropods and bivalves. No drillholes are observed on scaphopods in the PT biofacies.
- The primary predators of T. cingulifera from the Pleistocene Szekou Formation are naticids based on the abundance of parabolic drillholes and the presence of naticid specimens.
- Drillhole sizes are significantly different between shells with one drillhole and specimens with multiple drillholes. Drillhole diameters of the shells with one drillhole and with multiple drillholes are 1.0 mm and 0.5 mm on average, respectively.
- Turritellines with incomplete drillhole(s) are rare, and the current study reports the first example from Taiwan.
- With no size refugium and a high drilling intensity for T. cingulifera, their infaunal habitat with a relatively high reproduction rate may be a possible survival strategy for T. cingulifera in the Szekou fauna.

## 6. Supplementary material

Supplementary material is available online at https://doi.org/10.1017/S1755691023000130.

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## 9. Conflict of interest

None.

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