

Shape, size and distribution of predatory drill-holes on molluscan shells from the Tsukiyoshi and Togari Members of the Miocene Mizunami Group

東條 文治 *Bunji Tojo*

(人間発達学部教養部会)

大野 照文 *Terufumi Ohno*

(京都大学総合博物館)

Abstract

Bivalve and gastropod shells from the Tsukiyoshi and the overlying Togari Members of the Miocene Mizunami Group, central Japan show frequently predatory drill-holes. Examinations of drill hole general shape, relationship between hole's and ellipticity against size, between hole size and shell size, hole position on shell, as well as principal component analysis discriminate majority of the drill-holes of two members from each other, with the best result in the principal component analysis. Comparison of the results with previous reports on drill-hole characteristics indicate that the drill-holes from the Tsukiyoshi Member are formed by muricid gastropod, whereas holes from the Togari Member by naticid gastropods. This result is in accordance with the fossil occurrence; the Tsukiyoshi Member yields only muricid *Rhizophorimurex tiganouranus* as predatory gastropod, where as the Togari Member yields only naticid *Euspira meisensis*.

Further presently examined bivalve material shows negative relationship between the development of pallial sinus and predation rate. Because the pallial sinus is a good proxy of bivalves' burrowing depth, the result, therefore, may indicate that burrowing is one of the effective habits for the bivalves in escaping from predation.

Key words: drill-hole, measurement, muricid, Mizunami Group, naticid, predation

1. Introduction

Predation is one of the most important factors of natural selection and information on predator-prey relationship in fossil records should provide us with a reliable basis in understanding the dynamics of evolution of biotic interaction. Although it is in general difficult to get insight into such a relationship in fossil records, ubiquitously occurring drill-holes made by predators are easily recognizable on molluscan fossil shells, providing reliable evidence on the predator-prey relationship. For this reason, there have been many studies on characters of drill-holes they form as well as identification of predators

basing on such characters (e.g. Ziegelmeier, 1954; Carricker, 1961, 1981; Reyment, 1966; Arua and Hoque, 1989) and prey selection by predator (e.g. Kitchell et al., 1981; Kelley, 1991; Kelley and Hansen, 1993, 1996).

Although previous studies have been mainly related with commonly occurring muricid and naticid gastropod predators, Kowalewski (1993) pointed out that there are several other predators including octopods producing distinct drill-holes. He also showed a good match between qualitative and quantitative discrimination of predator. However some of such characters are easily destroyed during diagenesis or lost in cleaning procedure to excavate drill-holes, making the criterial practically useless.

As Kowalewski mentioned, identification of predatory drill-holes are suffered from preservation condition. In the present study, in addition to qualitative evaluation, we carried out quantitative analysis on predatory drill-holes on Miocene molluscan prays in using the characteristics robust throughout post-mortem degradation of shells including the positions of drill-holes, which varies depending on prey or predator species (Thomas, 1976; Colbath, 1985).

In this study, we analyzed the predatory drill-holes on the molluscan fossils from the Tsukiyoshi and the overlying Togari Members of the Miocene Mizunami Group, central Japan. Mizunami Group is correlated to the mid-Neogene climatic Optimum1 or the conspicuous transgression just before it. Tsukiyoshi and Togari members are both about 30m thick and yield many fossil molluscan shells with predatory drill-holes on them. Further, Tsukiyoshi Member yields one and sole muricid predatory gastropod, *Rhizophorimurex tiganouranus*, while the Togari Member one and sole naticid predatory gastropod *Euspira meisensis* (Itoigawa et. al, 1981). So it is very interesting to examine if the fossil predatory drill-holes on bivalve shells correspond to the occurrence of predator occurrence in the two members. For this purpose we carried out qualitative as well as quantitative analysis of these drill-holes. The principal component analysis of measured data revealed as the most powerful method in discriminating observed drill-holes into two separate groups corresponding to the selective occurrence of different predator gastropod taxa from the two members.

In the presently examined material, bivalves with different degree of pallial sinus development are suffered from predatory drilling. Degree of development of the pallial sinus is a good proxy of the bivalve's relative burrowing depth (Kondo, 1987). Therefore, we also compared the predation rate and the relative burrowing depth expressed in pallial sinus development for the present material.

2. Material and method

Mizunami Fossil Museum kindly allowed us to examine their molluscan collection from Togari and Tsukiyoshi Members of the Miocene Mizunami Group, central Japan. In Table 1, commonly occurring species are listed together with information about their predatory drill-holes on them. In the present study, for bivalve fossils, one valve is treated as representing one individual. Only complete valves were incorporated into the present study, because incomplete valves might have carried drill-holes on the part which is now lost.

For the qualitative analyses of the drill holes, following characteristics are documented visually: general shape, either cylindrical or parabolic, position on the prey shell surface as well as number on each shell.

For the quantitative analyses, drill-holes are approximated by fitting ellipse and the lengths of maximum and minimum axes are measured. The image of drill-hole outline is traced on a computer and a fitting ellipse for the traced outline is automatically calculated by "Scion Image" (Table 2). To give the measure to compare the relative hole position on the different prey species and size, four values are measured as listed in Table 3 (see also Figure 3); angle values are measured on Nikon profile projector V12-B. The measured data were then analyzed including principal component analysis. Specimens which have bad preservation of the drill-hole shape are excluded from measurements (*Felaniella usta* 2 specimen, *Phacosoma nomurai* 1 specimen, *Hiatula minoensis* 1 specimen of Togari Member).

3. Results

General shape of drill-holes

The number of specimens and number of those with predatory drill-holes for each species are shown in Table 1. Drill-holes can be classified into three types with visual observation. Cylindrical type of drill-hole is with cylindrical inner surface (Figure 1 A-D). Parabolic one has parabolic surface with a hole at its center; its surface is concave toward shell interior (Figure 1 E-H). The third type is those which cannot be assigned to either of the above two categories (unassignable in Table 1). Predation rates vary among prey species (0~16.8%). As shown in Table 1, the drill-hole type frequency for bivalve and gastropod preys together from Tsukiyoshi Member is: cylindrical drill-hole 28 (50.9%); parabolic drill-hole 0 (0%); and unassignable drill-hole 27 (49.1%). In the Togari Member, only bivalves show predatory drill-holes. The drill-hole type frequency

Table 1. Visible characteristics of drill-holes.

	n	s1	s2	s3	nd	sd	pd	ud	pray ratio
Togari Member									
Bivalvia									
<i>Keenocardium andoi</i>	167	28	0	0	28	0	28	0	28/167=16.8%
<i>Felaniella usta</i>	136	12	0	0	12	0	9	3	12/136=8.8%
<i>Phacosoma kawagensis</i>	63	6	0	0	6	0	5	1	6/63=9.5%
<i>Phacosoma nomurai</i>	185	8	0	0	8	0	4	4	8/185=4.3%
<i>Cyclina japonica</i>	8	0	0	0	0	0	0	0	0/8=0%
<i>Hiatula minoensis</i>	36	1	0	0	1	0	0	1	1/36=2.8%
Tsukiyoshi Member									
Bivalvia									
<i>Phacosoma kawagensis</i>	146	13	9	1	34	16	0	18	23/146=15.8%
<i>Cyclina japonica</i>	224	12	1	0	5	1	0	4	5/47=10.6%
<i>Clementia papyracea</i>	45	0	0	0	0	0	0	0	0/45=0%
<i>Hiatsula minoensis</i>	38	0	0	0	0	0	0	0	0/38=0%
Gastropoda									
<i>Vicarya yokoyamai</i>	146	13	9	1	34	16	0	18	23/146=15.8%
<i>Vicaryella ishiiiana</i>	47	5	0	0	5	1	0	4	5/47=10.6%

Table 2. Mean size and flatness of the elliptic outline of the drill-holes

Provenance of samples	n	hole size ((Max+Min)/2)		flatness (Min/Max)	
		mean	st. dev.*	mean	st. dev.*
Tsukiyoshi	55	1.78 mm	0.33mm	1.15	0.10
Togari	55	2.41mm	0.91mm	1.06	0.04

*st. dev. = standard deviation.

Table 3. Parameters for determining the location of the drill-hole on prey shell surface.

L1: distance between the umbo and the intersecting point of the line which runs through the umbo and the center of the drill-hole and the shell margin.

L2: distance between umbo and the center of the drill-hole.

A1: angle between the following two lines;

line connecting the umbo and intersecting points of the shell anterior margin and a circle with a radius of L2

line connecting the umbo and intersecting points of the shell anterior margin and a circle with a radius of L2.

A2: angle between the following two lines:

Line connecting the umbo and drill-hole center

The other is connecting the umbo and the intersecting point between anterior margin and a circle with a radius of L2.

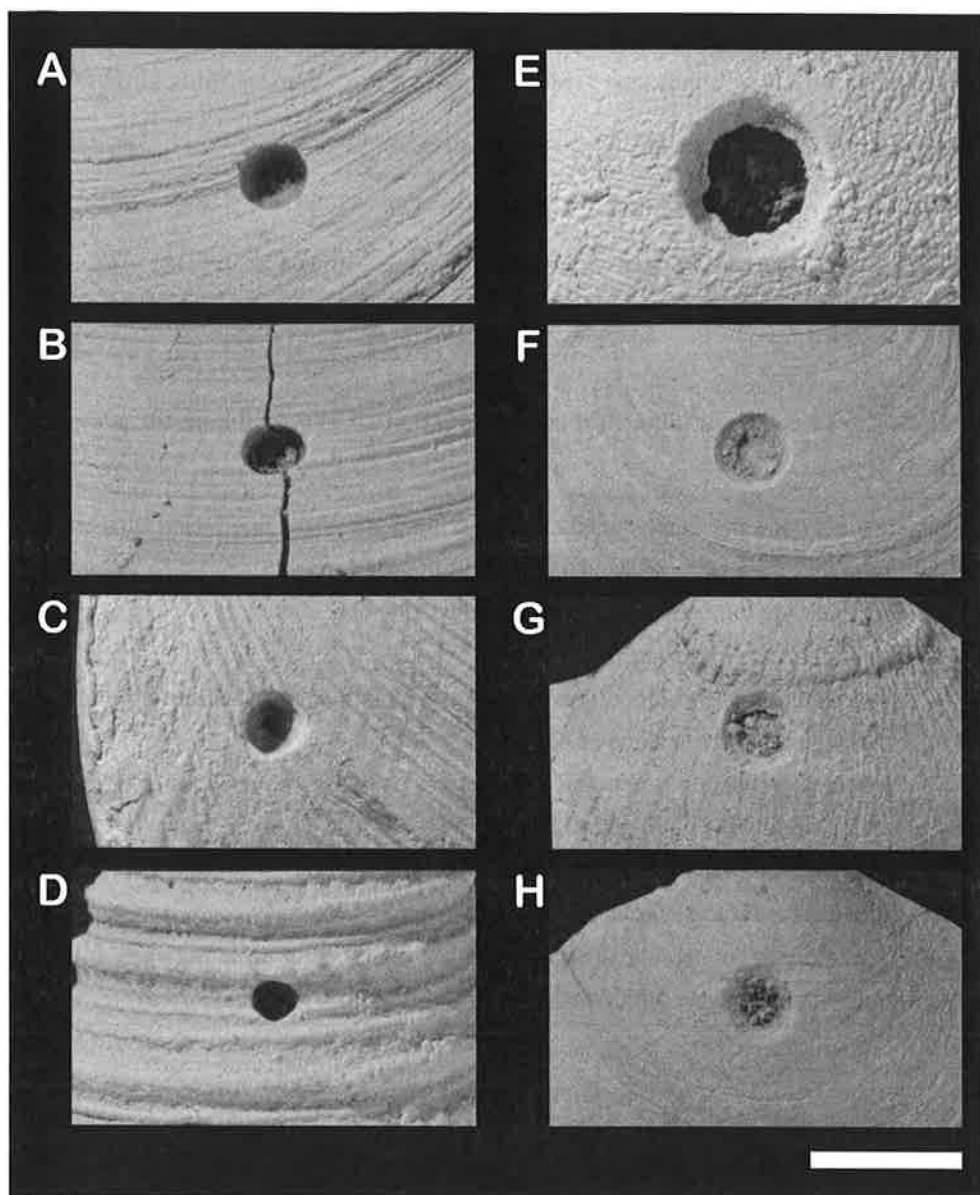


Figure 1

The drill-holes on fossils. A-D: cylindrical drill-holes from the Tsukiyoshi Member: A: on *Phacosoma kawagensis*, B, C: on *Cyclina japonica*, D: on *Vicarya yokoyamai*, E-H: parabolic drill-holes from the Togari Member: E: on *Phacosoma nomurai*, F: on *Phacosoma kawagensis*, G: on *Keenocardium ando*, H: on *Felaniella usta*. Scale bar is 5mm long for A to F, and is 1cm long for G and H.

of these bivalves is; cylindrical drill-hole 0 (0%), parabolic drill-holes 46 (83.6%), and unassignable drill-hole 9 (16.4%).

Generally, the drill-holes formed by the muricid are cylindrical to subcylindrical and those formed by naticid are parabolic (Table 1 of Kowalewski, 1993). Thus, we may conclude that the cylindrical drill holes representing little more than half of the those from the Tsukiyoshi Member are attributable to the muricid. So far as assignable drill holes are concerned, the Tsukiyoshi samples does not include any parabolic drill-holes, which is concordant with the absence of naticid predator fossils from the member. Parabolic ones amounting to more than 80% of the drill-holes from the Togari Member are attributable to the naticid. As for assignable drill holes, the Tsukiyoshi samples lack parabolic drill-holes, which suggests the absence of muricid predators from the member. Therefore, so far as the assignable drill-holes are concerned, result of our visual inspection here is concordant with the fact that the Tsukiyoshi Member yields only muricid *Rhizophorimurex tiganouranus* as predatory gastropod, whereas the Togari Member the naticid *Euspira meisensis* as predatory gastropods (Figure 2). Each gastropod is common in the corresponding member, but does not occur in the other member at all.

However, thirty-six of the total 110 drill-holes (32.7%) from the two members are left as unassignable either to cylindrical type or to parabolic one. Difficulty in assignment is caused by, for example, unsuccessful boring action, incomplete cleaning of specimens. Morphology vertical to the hole may not be recorded and also liable to diagenetic loss, if the prey shell is very thin.

Drill-hole outline shape and size

The outline of the drill-holes on the surface of the presently examined specimens varies from oval to circular. Therefore the outline of drill-hole surface can be approximated by an ellipse (Figure 3 right); its major axis (Max) and minor axis (Min) are measured. Further, Max/Min as well as (Max+Min)/2 are calculated for each drill-hole. Max/Min is the flatness of the ellipse; if the Max/Min value is near 1, then the outline of drill-hole is almost circular, whereas the outline is more elliptical when the value is larger than 1. (Max+Min)/2 is a proxy of drill-hole size. Results are summarized in Table 2 as well as in Figure 4A and 4B. The mean size of Tsukiyoshi drill-holes is about 1.8 mm, while that of the Togari ones is larger with wider range of variety. The mean shape of the Tsukiyoshi drill-holes is weakly oval with its flatness of 1.16, while that of the Togari drill-holes almost circular as its flatness of 1.06 indicatres.

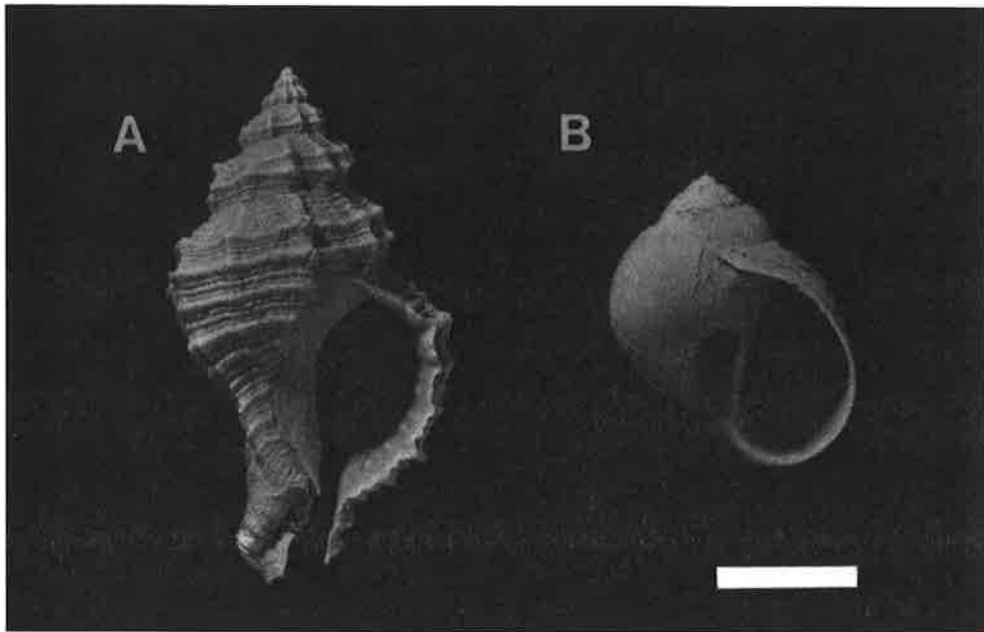


Figure 2
 Predatory gastropods. A: muricid *Rhizophorimurex tiganouranus* from the Tsukiyoshi Member. B: naticid *Euspira meisensis* from the Togari Member. Scale bar is 1cm long.

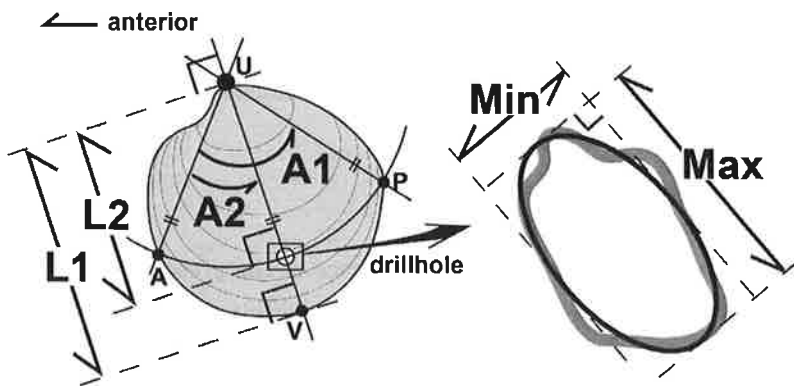


Figure 3
 Measured parameters:
 Right: Max: a major axis of the ellipse. Min: a minor axis of the ellipse. In the present study, the outline of drill-holes on the outer surface is approximated by an ellipse.
 Left: Parameters defining the drill-hole position on bivalve shell surface. U: umbo, V: intersection point between shell margin and the line that passes the umbo and the center of the drill-hole. L1: distance between the umbo (U) and the intersection point between shell margin and the line that runs through the umbo and the center of the drill-hole and the shell margin (V). L2: the distance from umbo (U) to the center of the drill-hole (C). A and P: anterior and posterior intersection points between the circle with its center on umbo (U) and a radius of L2, respectively. A1: the angle between the line UA and line UP. A2: the angle between the line UA and line UV.

Therefore, irrespective of the nature whether the prey is bivalve or gastropod, Tsukiyoshi specimens are dominated by elliptical drill-holes of more or less constant diameter of about 1.8 mm, whereas the Togari samples are dominated by circular ones with wide variety in diameter. According to Kowalewski (1993), the drill-holes caused by muricids are circular to subcircular, whereas those by naticids are circular. Elliptic drill-holes of Tsukiyoshi samples thus have more similar to those caused by the muricid, while those of Togari samples to those by naticid drill-holes. However, because Kowalevski (1993) did not give the value indicating the ellipticity of the holes for both naticids and muricids, this conclusion should be regarded with reservation. There is, also, a considerable overlap of data points from the two members in the area represented by smaller and circular ones in Figure 4A and 4B.

Drill-hole size and prey shell length.

The relationship between the drill-hole size ($(\text{Max}+\text{Min})/2$) and the prey shell maximum length (=maximum antero-posterior length for bivalves and length between apex to the latest whorl for gastropods) is plotted on Figure 4C. In the Tsukiyoshi samples, the drill-hole size is almost constant at about 2mm, despite of the prey shell size increase. In the Togari samples, drill-hole size increases as the prey shell size increases. Drill-hole size alone can not be used as diagnostic feature in distinguishing the predators, because both the muricids and the naticids have similar diameter range of their drill-holes (Kowalevski, 1993). However, the samples from the two members show different distribution patterns when their mean size is plotted against prey maximum shell length. This suggests the existence of two different predators, each of which is responsible for forming drill-holes within one formation.

Because the regression curves for two members on Figure 4C cross together at around the point where the maximum prey shell length is about 10 mm and the drill-hole size of about 2 mm, if fossils with smaller body size may occur in Tsukiyoshi Member, data plots from these two members may overlap each other.

Position of drill-holes on the prey bivalve shell

For bivalves, we carried out the study of position of drill-holes on the prey shell. Gastropod data are not included because of the difficulty of comparison with bivalves.

Visual observation

Position of the predatory drill-holes on prey bivalve shells is plotted on line-drawings

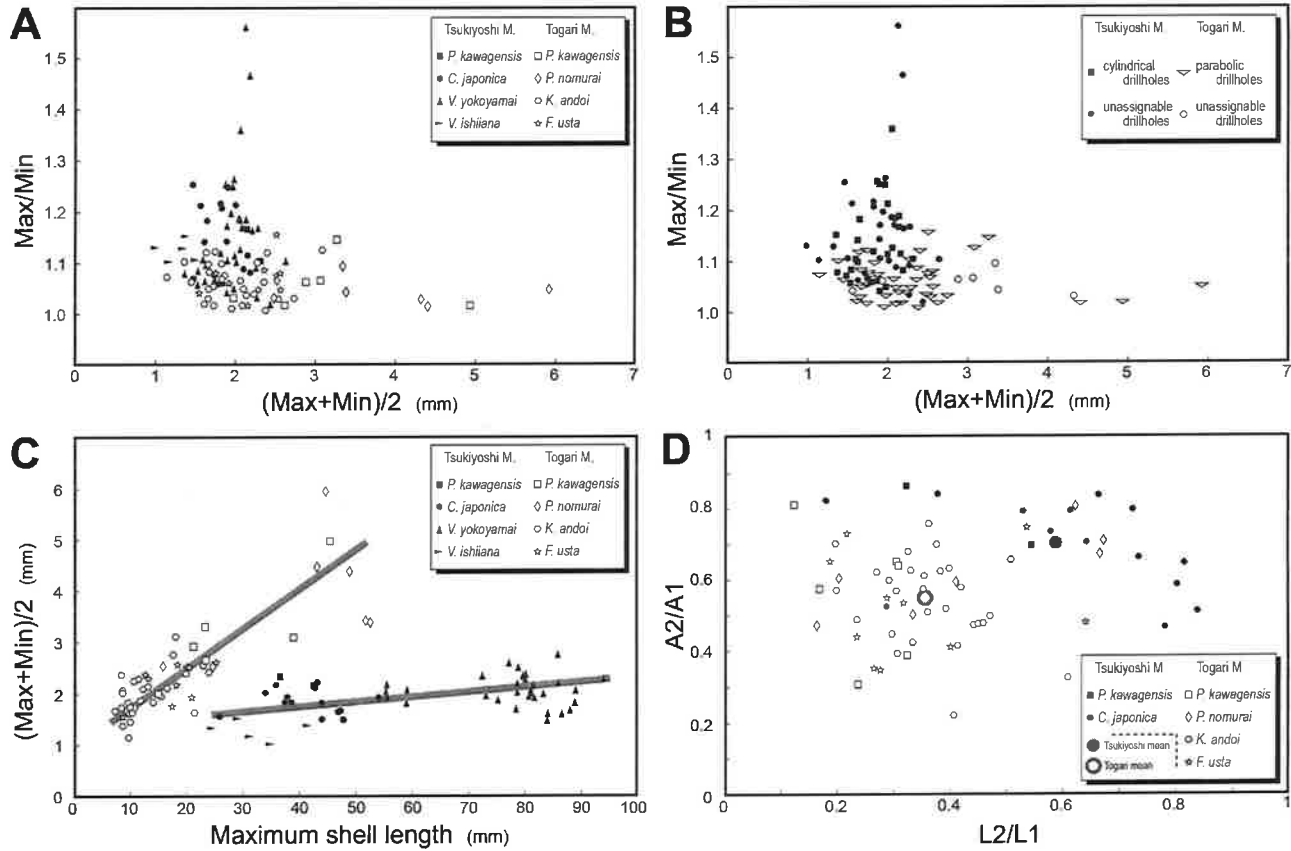


Figure 4

A: (Max+Min)/2 plotted against Max/Min. Symbols represent species from the two members. B: the same plot as A with symbols representing drill-hole general shape from the two members. C: maximum shell length plotted against (Max+Min)/2 with symbols representing species from the two members. D: L1/L2 plotted against A1/A2 with symbols denoting species from two members.

of shell general outline of the prey species in Figure 5. The drill-holes are generally concentrated to umbonal region of prey shells from the Togari Member. Drill-holes on the *Cyclina japonica* shells from the Tsukiyoshi Member tend to be located more near the shell margin and especially its posterior margin (Figure 5). Only two drill-holes of *Phacosoma kawaagensis* observed in the present study also are located near the shell posterior margin.

Numerical examination

For numerical evaluation of the drill-hole position on the prey bivalve shells, we measured four parameters listed in Table 3 (see also Figure 3).

As a proxy of the hole position in relation to umbonal (=dorsal)-ventral direction of the prey shell, we calculated $L2/L1$. As the $L1/L2$ value increases, the hole migrates from the umbo to the ventral margin. As a proxy of the hole position in relation to anterior-posterior direction, we calculated $A2/A1$. As the $A2/A1$ value increases, the hole migrates from anterior to posterior part of the shell.

In Figure 4D, $L1/L2$ is plotted against $A1/A2$. In Tsukiyoshi samples, the mean value of $L2/L1$ is 0.70; the mean value of $A2/A1$ is 0.59. In Togari samples, the mean value of $L2/L1$ is 0.55; the mean value of $A2/A1$ is 0.36. Though data from both members are scattered widely, Tsukiyoshi Member drill-holes are generally located more distant from umbo and nearer to posterior margin (upward in living position). The positions of Togari Member drill-holes are located more umbonal in comparison with the Tsukiyoshi ones.

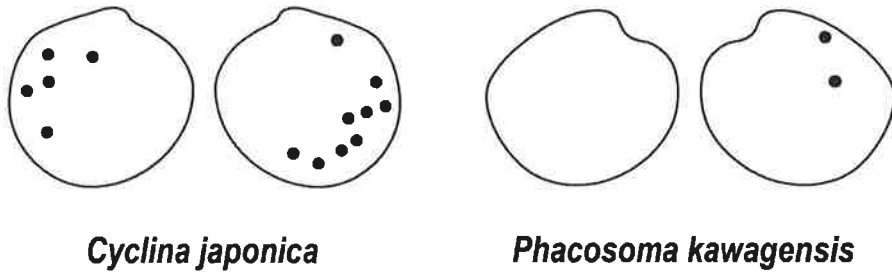
Both visual observation and numerical analysis of the drill-hole position on the prey bivalve shells reveal the drill-hole of Togari samples are located more umbonal and central, whereas those from the Tsukiyoshi samples are located more posterior and more marginal.

Referring to Thomas (1976), who shows that the drill-holes by naticid tend to be located around the part of the prey shell (*Glycimeris*) center to umbo, the present observation suggests Togari bivalve shells are suffered from the naticid predator, whereas the prey bivalve shells from the Tsukiyoshi member do not exhibit this tendency. This is again concordant with the fossil predator occurrence from the two members.

4. Principal components analysis on data from bivalve prey shells

The above described visual and numerical analyses all indicate that the muricids

Tsukiyoshi Member



Togari Member

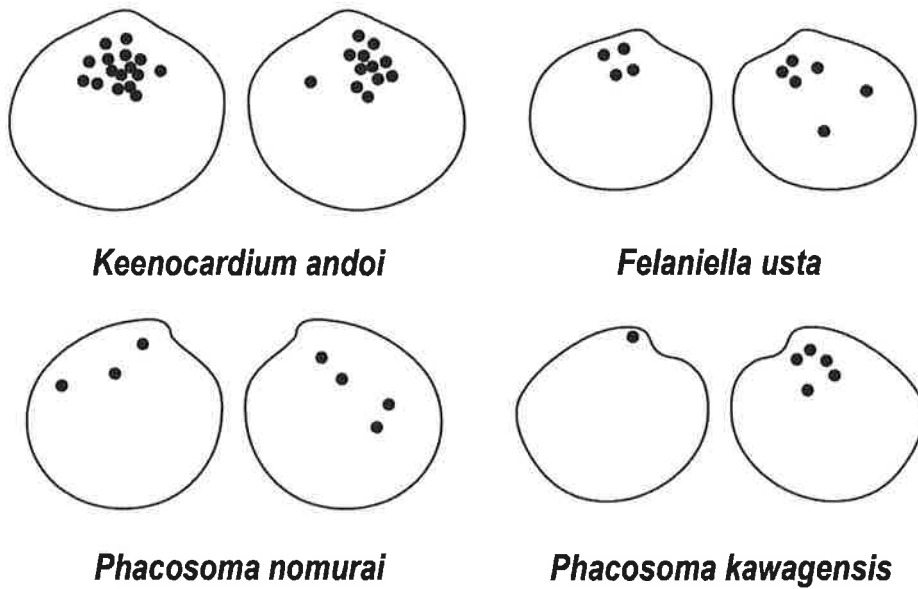


Figure 5
Schematic diagrams showing the positions of drill-holes on bivalve shell surface.

are responsible for the drill-holes on the prey shells of the Tsukiyoshi member, whereas the naticids for those of the Togari member. However, because of the existence of unassignable drill hole in their general morphology, overlap in the samples from two members in the numerical analyses (Figure 4A, 4B and 4D) as well as potential possibility of crossing of regression curves (Figure 4C), we can not be sure, that all the Tsukiyoshi samples are caused by muricids and all the Togari samples by naticids.

To test, if we can separate two sample groups more sharply, we employed principal component analysis with the data from bivalve samples. We used following variables: $(\text{Max}+\text{Min})/2$, Max/Min , $L2/L1$, and $A2/A1$. The principal component analysis carried out with correlation matrix of these four parameters (Figure 6) clearly discriminates samples of Tsukiyoshi Member from those of the Togari Member on the axis of principal component 1. For all the principal components of these analyses, eigen values and eigen vectors are shown in Figure 6.

The contributions of four variables $(\text{Max}+\text{Min})/2$, Max/Min , $L2/L1$, and $A2/A1$ to the principal component 1 in the present analysis are almost equal to each other. Larger $(\text{Max}+\text{Min})/2$ value is reflected in larger value on principal component 1. Larger Max/Min value corresponds to the smaller value on the principal component 1. Larger $L2/L1$ results in smaller value on principal component 1. Larger $A2/A1$ value is reflected in smaller value on principal component 1.

As a result, a line crossing the value of about -0.8 on the horizontal axis of principal component 1 and vertical to this axis divides samples from two members clearly. Togari Member data are scattered on the right hand of the line, whereas those from the Tsukiyoshi Member data on the opposite side. The result of the principal component analysis is consistent with the conclusion drawn from the preceding numerical analyses (Figure 4). Further, better discrimination in the present analysis suggests that principal component analysis using four parameters is more effective than the preceding two for the identification of the difference of drill-holes types.

5. Prey's burrowing depth and predation rate.

Now, we would like to focus on predation rate (Table 1). In the following discussion, the data of *Cyclina japonica* in Togari Member is neglected because of its very small individual number. The bivalves that have weak pallial sinus such as *Keenocardium andoi* and *Felaniella usta* suffer from higher predation rate (16.8~8.8%). Those with moderately developed pallial sinus, such as *Phacosoma kawagensis*, *Phacosoma nomurai*, and *Cyclina japonica* show moderate predation rate (9.5~4.3%). Finally, the those having

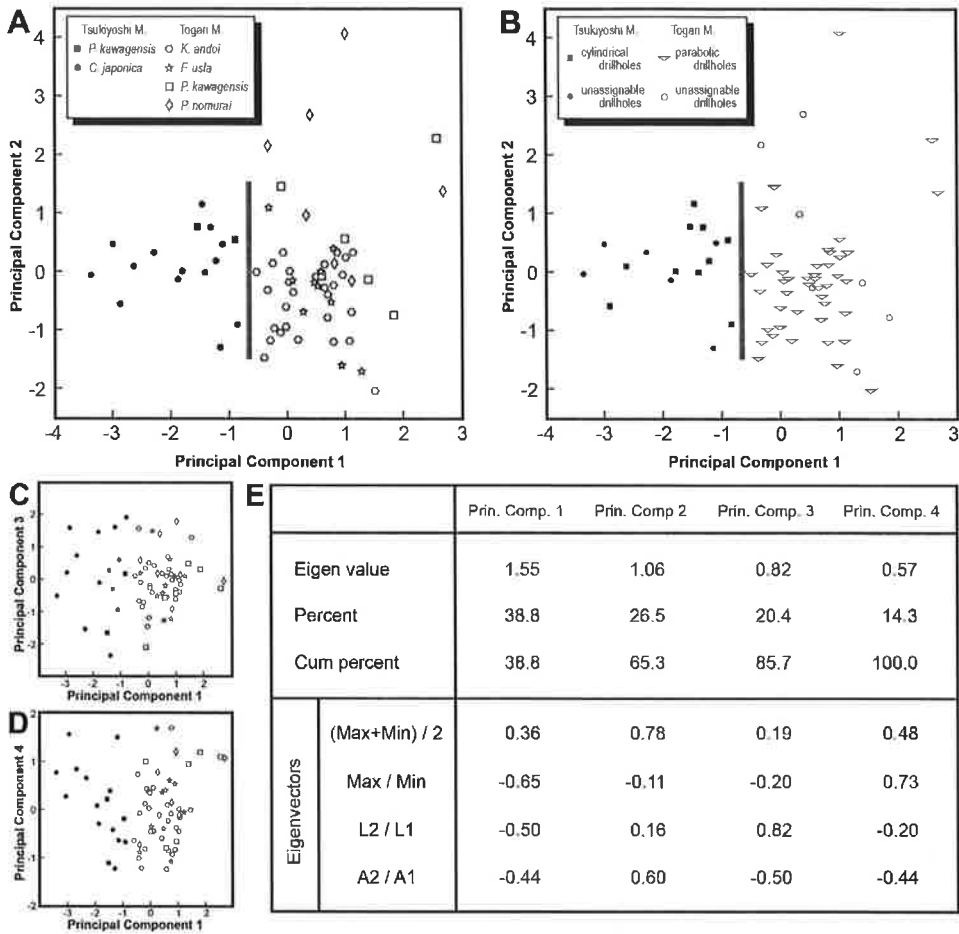


Figure 6

Principal component ordination of drill holes obtained with 4 variables ((Max+Min) / 2, Max/Min, L2/L1, A2/A1). A: The coordinate system of principal components 1 and 2. Symbols denote bivalve species from the two members. B: plots of drill-hole types on the same coordinate system as A. C and D: Bivalve species from the two members plotted on the coordinate system of principal components 1 and 3 (C) of principal components 1 and 4 (D). Symbols same as on A. and species plot on the axes principal component 1 and 3. E: the table for the eigen values and eigenvectors for each principal component.

well developed pallial sinus, such as *Clementia papyracea*, *Hiatula minoensis* have low predation rate (2.8~0%).

Development of the bivalve molluscan pallial sinus is positively related with their burrowing depth (Kondo, 1987). The negative relationship between predation rate and the development of pallial sinus stated above, therefore, means that the deeper burrowers can escape from the gastropod predation.

Vicarya yokoyamai and *Vicaryella ishiiana*, both extinct and occurring abundantly from the Tsukiyoshi Member, also show predatory drill-holes. *Vycarya yokoyamai* shows high predation rate like shallowly burrowing bivalves. Perhaps this extinct gastropod lived on the surface like their present day analogues, i.e., *Telescopium* or *Terebralia*. *Vicaryella ishiiana* might have been a shallow to moderately deeper burrower, as its predation rate falls between the shallow burrowing and moderately deep burrowing bivalves.

6. Discussion

Visual observation on drill-hole for cylindrical or parabolic drill-hole type, numerical analysis of hole ellipticity and size, and visual as well as numerical study on position of drill-holes on the prey shell all indicate that the majority of the drill-holes on Tsukiyoshi samples are caused by muricid gastropods whereas those on Togari samples by naticid gastropods. Although the analysis of relation between drill-hole size and prey shell size does not have power in identifying the predators, it showed data from the two members forming different trends and thus supports the inference of the predator. This is concordant with the fossil occurrence: sole occurrence of muricid *Rhizophorimurex tiganouranus* in Tsukiyoshi Member and sole occurrence of naticid *Euspira meisensis* in Togari Member. However, any of these analyses could not discriminate samples from two groups perfectly.

Finally we carried out principal component analysis for drill-hole data on bivalves. There are two variations for the analysis: one using correlation matrix and the other with co-dispersion matrix. The former is suitable when parameters of different units are involved. Because in our present analysis, we use parameters for distance expressed with the unit mm and three non-dimensional parameters, we employed the former method for our analysis. As a result, the principal component 1 separates the Tsukiyoshi and Togari data quite well. Further, the eigenvectors exhibit that all parameters ($(\text{Max}+\text{Min})/2$, Max/Min , $L2/L1$, $A2/A1$) contribute to the principal component 1 almost equally. This suggests that all parameters are indispensable to discriminate one

member's data from the other. This is reasonable, because our other numerical analyses using these parameters yielded a good, though not perfect, discrimination of the data from the two members.

On Figure 6B, the data for the samples, which could not be assigned to either cylindrical or parabolic type by visual inspection, are represented by solid circles for Tsukiyoshi samples and by open circles for Togari samples. If these unassignable drill-holes are caused by any cryptic predator(s), which have no fossil occurrence, these points should be clustered. This is not the case with the unassignable samples plotted on Figure 6B. This suggests it is not necessary to assume a third predator responsible for the formation of drill-holes of the prey shells examined in the present study. Further, either Tsukiyoshi data within themselves or Togari data within themselves do not show any clustering. This suggests that for each member samples, we do not assume the existence of plural predator within each member. In conclusion, the present study combining visual and numerical examination including principal component analysis demonstratively indicate that all the predatory drill-holes of the Tsukiyoshi samples are very probably formed by single muricid gastropod species *Rizophorimurex tiaganouranus*, whereas all the predatory drill-holes of the Togari samples very probably by single naticid gastropod species *Euspira meisensis*.

Kowalevski (1993) employed besides maximum and minimum diameters, perimeter, area of internal outline of drillholes as the variables which indicate drillhole shape for multivariate analysis. However, perimeter and internal outline are liable to damage during preparation of materials with less well preservation condition (see, for example, damage on the lower left corner of Figure 1E). Therefore, in this study we applied only maximum and minimum diameter of the drill-hole to avoid unnecessary noises. The quality of principal component analysis in this study, measured with percent of eigenvalue of the principal component 1, does not attain that of Kowalewski (1993). However our analysis could yield meaningful discrimination of material, which indicates that choice of maximum and minimum diameter for describing outline of the drill-hole is practical for the analysis of the fossils of which preservational condition is not ideal.

Comparison of burrowing depth suggested by the degree of development of pallial sinus and predation rate indicates that the deep burrower suffer less predation than the shallow burrower. It is well known that the frequencies of predatory drillhole are different in species. Burrowing habitat may be one of the factors influence to predation frequency. Predation pressure on mollusks is generally considered to have been increased since sometime in the Mesozoic. Present study shows the possibility to

elucidate the detailed history of predation pressure, if one examine the predation rates against burrowing depth suggested by pallial sinus development.

There have been no way for inferring the burrowing depth of fossil gastropods. However, in extrapolating this relationship, we could also infer the burrowing depth of two extinct gastropods. Gastropod shells may be reused by helmetclubs and might be suffered by predators attacking helmetclubs (Tanaka and Maeda, 1999), which may cause more drill-holes than those formed when gastropods were alive. And the predation efficiency are different in Gastropods. If we could distinguish between these postmortem drill-holes from the lethal drill-holes for the gastropods, which might be possible, i.e., by using principal components analysis, then there is a possibility of inferring their burrowing depth in referring to the burrowing depth-predation rate of the co-occurring bivalve fossils.

7. Conclusion

Bivalve and gastropod shells from the Tsukiyoshi and the overlying Togari Members of the Miocene Mizunami Group, central Japan show frequently predatory drill-holes. Examinations of drill hole general shape, relationship between hole's and ellipticity against size, between hole size and shell size, hole position on shell, as well as principal component analysis discriminate majority of the drill-holes of two members from each other, with the best result in the principal component analysis. Comparison of the results with previous reports on drill-hole characteristics indicate that the drill-holes from the Tsukiyoshi Member are formed by muricid gastropod, whereas holes from the Togari Member by naticid gastropods. This result is in accordance with the fossil occurrence; the Tsukiyoshi Member yields only muricid *Rhizophorimurex tiganouranus* as predatory gastropod, where as the Togari Member yields only naticid *Euspira meisensis*.

References

- Arua, I. And Hoque, M., 1989: Study of the shape of Naticid and Muricid borings in plan view in Eocene prey from southeastern Nigeria. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 72, p. 357-362.
- Carricker, M. R., 1961: Comparative functional morphology of boring mechanisms in gastropods. *Am. Zool.*, 1, p. 263-266.
- Carricker, M. R., 1981: Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia*, 20, p. 403-422.
- Colbath, S.L., 1985: Gastropod predation and depositional environments of two molluscan communities from the Miocene Astria Formation at Beverly beach state park, Oregon. *Journal of Paleontology*, v. 59, no. 4, p. 849-869.
- Itoigawa, J., Shibata, H., Nishimoto, H., and Okumura, Y., 1981: Miocene fossils of the Mizunami group, central Japan - 2. Molluscs - *Monograph of the Mizunami Fossil Museum*, No. 3 -A.
- Kelley, P. H., 1991: The effect of predation intensity on rate of evolution of five Miocene bivalves. *Historical Biology*, 5, p. 65-78.
- Kelley, P. H. and Hansen, T.A., 1993: Evolution of the naticid gastropod predator-prey system: an evolution of the hypothesis of escalation. *Palaios*, v. 8, p. 358-375.
- Kelley, P. H. and Hansen, T.A., 1996: Naticid gastropod prey selectivity through time and the hypothesis of escalation. *Palaios*, v. 11, p. 437-445.
- Kitchell, J. A., Bogges, C. H., Kitchell, J. F., and Rice, J. A., 1981: Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology*, vol. 7, p. 533-552.
- Kondo, Y., 1987: Burrowing depth of infaunal bivalves - observation of living species and its relation to shell morphology. *Trans. Proc. Palaeont. Soc. Japan*, no. 148, p. 306-323.
- Kowalewski, M., 1993: Morphometric analysis of predatory drillholes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 102, p. 69-88.
- Reyment, R. A., 1966: Preliminary observations on gastropod predation in the western Niger delta. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2, p. 81-102.
- Tanaka, H. and Maeda, H., 1999: Shell-preservation and distribution of a potamidid gastropod. *Terebralia palustris* in Recent mangrove swamp. *Geol. Soc. Japan special pap.*, Vo. 54, p. 151-160.
- Thomas, R.D.K., 1976: Gastropod predation on sympatric Neogene species of *Glycymeris* (Bivalvia) from the eastern United States. *Journal of Paleontology*, v. 50, no. 3, p. 488-499.
- Zigelmeier, E., 1954: Beobachtungen über den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda Prosobranchia). *Helgoländer Wiss. Meeresunters.*, 5, p. 1-33.