Geologie en Mijnbouw 66: 293–296 (1987)

Predation intensity in an Eocene molluscan assemblage from southeastern Nigeria

Ingela Arua[1] & Mominul Hoque[2]
[1] *Department of Geology, University of Nigeria, Nsukka, Nigeria;* [2] *Geo Mechanics, Inc. Elizabeth, PA 15037, USA*

Received 28 April 1987; accepted 27 July 1987

Abstract

A quantitative assessment of naticid and muricid borings in mainly small (<10 mm) gastropod and bivalve shells from the Ameki Formation (Eocene) shows that the degree of shell ornamentation appears to have played a significant role in predation intensity. It was observed in gastropods that a smooth shell is preferred by predators to an ornamented one. In bivalves a growth-lined shell is preferred to either a ribbed or a mixed one (growth lines and ribs present) and a ribbed shell is preferred to a mixed shell. It is suggested that the predation intensity was controlled by the predator-defensive adaptation.

The favoured predator food source during the Eocene in Nigeria was bivalves, as far as shown by fossil shells.

Introduction

On examining about 12,312 mainly small (<10 mm) gastropod and bivalve shells from the type area of the Eocene Ameki Formation around Ameke-Bende (Fig. 1) it turned out that many of them showed borings derived from naticids and muricids as determined by criteria given by Ziegelmeier (1954), Carriker (1955), Hancock (1959), Reyment (1966, 1967), Carricker & Yochelson (1968), Taylor (1970), Adegoke & Tevesz (1974), Bromley (1981), Taylor (1982), Yochelson et al. (1983) and Taylor et al. (1983).

With its excellently preserved molluscan assemblage the Ameki Formation affords an opportunity for a quantitative assessment of the borings. Therefore, in the present study the intensity of predation is determined quantitatively by a count of the drilled shells in relation to the number of shells. The data are statistically analysed.

Ameki bored gastropods and bivalves

Of the 7270 gastropod shells belonging to 32 species, about 11.5 percent are bored. The shells are either ornamented or smooth. It is found that among the 6044 ornamented shells 638 are bored while 5406 show no evidence of borings. Among the 1226 smooth shells, 197 are bored, the rest are free of any boring (Table 1).

A total of 5042 bivalve shells belonging to 23 species have been studied. It is found that 633 shells (12.5%) are bored while 4409 shells show no sign of predation. On the basis of types of shell sculpture, the bivalves can be divided into three groups: shells with growth lines (g), shells that are ribbed (r) and shells with mixed ornaments, growth-lines + ribs (m). Table 1 shows that predation in growth-lined, ribbed and mixed bivalve shells are 17.5, 11.4 and 5.8 percent respectively.

In order to interpret the information obtained from Table 1 it is felt necessary to find out whether

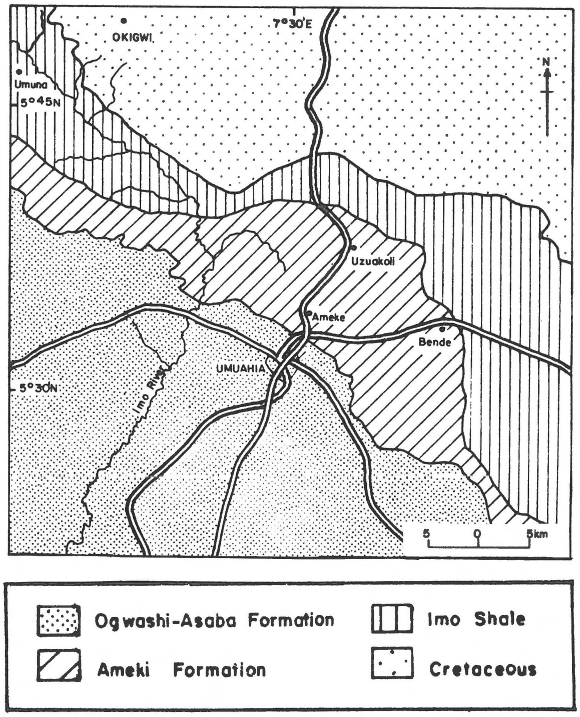

Fig. 1. Map showing the type area of the Ameki Formation between Ameke and Bende.

the observed frequencies (f_o) of bored ornamented and smooth gastropod shells are significantly different from their expected frequencies (f_e). Similarly it would be interesting to know if the discrepancy between the observed frequencies (f_e) of growth-lined, ribbed and mixed bivalve shells and their expected frequencies (f_e) is real. In other words, have the observed frequency distributions of various types of bored gastropod and bivalve shells arisen from a chance sampling? Table 2 shows the calculated chi-square test. The calculated chi-square value in each case is larger than the table chi-square value at 99% confidence level for one or two degrees of freedom. The null hypothesis, H_0 is therefore rejected in each case ($P<0.001$), i.e. the difference between the observed frequency and the expected frequency is real or significant.

Preference estimation (Smooth shells vs. ornamented shells)

The magnitude of discrepancy between the observed frequency and the expected frequency, shown as positive values (f_o–f_e) under the Difference Matrix Column (Table 2), also reveals a 'more-than-expected' incidence of boring in a certain type of shell. A positive value, therefore, is indicative of preferential boring of the shell type of predators. From the Difference Matrix Column of Table 2, the following observations can be made:

1. a smooth gastropod shell is preferred to an ornamented gastropod shell;

Table 1. Distribution of borings in gastropod and bivalve shells.

	Type of shell sculpture	Number of shells	Number of species	Number of bored shells/ species	Percentage bored	Boring ratio	Number of non bored shells/ species
Gastropods	Ornamented	6044	25	638/17	10.6	1:9.5	5406/8
	Smooth	1226	7	197/4	16.1	1:6.2	1029/3
	Sub-total	7270	32	835/21	11.5	1:8.7	6435/11
Bivalves	Growth-lined (g)	1401	13	245/6	17.5	1:5.7	1156/7
	Ribbed (r)	3137	4	359/4	11.4	1:8.7	2778/0
	Mixed (m)	504	6	29/4	5.8	1:16.7	475/2
	Sub-total	5042	23	633/14	12.5	1:7.9	4409/9
Grand total		12312	55	1468/35	11.9	1:84	10844/20

2. a growth-lined bivalve shell is preferred to either a ribbed one or a mixed one; and
3. a ribbed bivalve shell is preferred to a mixed bivalve shell.

Preference estimation (gastropods vs bivalves)

The chi-square value is also used to test the null hypothesis H_0, i.e. whether there is no significant difference between the observed frequency and the expected frequency of bored gastropods and bivalves (Table 2). The calculated chi-square value (2.86) falls between the values of 90 percent and 95 percent confidence level at one degree of freedom. It means that the difference between the observed frequency f_o and the expected frequency f_e is significant at 90 percent confidence level but not significant at 95 percent level. The positive value of difference matrix, however, indicates a slight preference for bivalve shells to gastropods by predators.

Discussion

The results of the preference estimation smooth shells vs. ornamented shells appear to be in sharp contrast to the contention held by Adegoke & Tevesz (1974) who studied the gastropod predation pattern in the Eocene of Nigeria and noted that the coarsenesss of sculpture and shell thickness did not

Table 2. Chi-square tests for bored gastropod and bivalve shells.

Shell type		Observed frequency matrix		Total shells	Expected frequency matrix		Difference matrix (fo-fe)	Bored shells $(fo-fe)^2/fe$	Calculated χ^2 value & tabled χ^2 value with degrees of freedom	Comments H_0 – Null hypothesis i.e. difference between f_o & f_e is not significant
		bored (fo)	non-bored		bored (fe)	non-bored				
Gastro-pods	ornamented	638	5406	6044	694.2	5349.8	−56.20	4.55	$\chi^2 = 26.98$	H_0 rejected (P = 0.001), i.e.
	smooth	197	1029	1226	140.8	1085.2	+56.20	22.43	$\chi^2_{0.99} = 6.64$ for one	smooth shells preferred to
	total	835	6435	7270	835	6435	0	26.98	degree of freedom	ornamented shells
Bi-valves	growthlined	245	1156	1401	175.9	1225.1	+69.1	27.15	$\chi^2 = 48.82$	H_0 rejected (P = 0.001),
	ribbed	359	2778	3137	393.8	2743.2	−34.8	3.08	$\chi^2_{0.99} = 9.21$	i.e. growth lined shells preferred
	mixed	29	475	504	63.3	440.7	−34.3	18.59	two degrees of freedom	to either ribbed or mixed shells
	total	633	4409	5042	63.3	4409	0	48.82		
	growthlined	245	1156	1401	186.5	1214.5	+58.5	18.35	$\chi^2 = 26.55$	H_0 rejected (P = 0.001), i.e.
	ribbed	359	2778	3137	417.5	2719.5	−58.5	8.20	$\chi^2_{0.99} = 6.64$ for one	growth lined shells preferred
	total	604	3934	4538	604	3934	0	26.55	degree of freedom	to ribbed shells
	growthlined	245	1156	1401	201.5	1199.5	+43.5	9.39	$\chi^2 = 35.49$	H_0 rejected (P = 0.001), i.e.
	mixed	29	475	504	72.5	431.5	−43.5	26.10	$\chi^2_{0.99} = 6.64$ for one	growth-lined shells preferred
	total	274	1631	1905	274	1631	0	35.49	degree of freedom	to mixed shells
	ribbed	359	2778	3137	334.3	2802.7	+24.7	1.82	$\chi^2 = 13.18$	H_0 rejected (P = 0.001), i.e.
	mixed	29	475	504	53.7	450.3	−24.7	11.36	$\chi^2_{0.99} = 6.64$ for one	ribbed shells preferred to
	total	388	3253	3641	388	3253	0	13.18	degree of freedom	mixed shells
Class	gastropoda	835	6435	7270	866.83	6403.17	−31.83	1.17	$\chi^2 = 2.86$	H_0 can not be rejected
	bivalves	633	4409	5042	601.17	4440.83	+31.83	1.69	$\chi^2_{0.95} = 3.84$ for one	(P = 0.05); can be rejected
	total	1468	10844	12312	1468	10844	0	2.86	degree of freedom	at 90% confidence level ($\chi^2_{0.90} = 2.71$) i.e. bivalves preferred to gastropod shells only at 90% level

constitute major deterrents to borings. According to them, the smooth shells do not appear to be preferentially drilled. The conclusion was based on 351 bored gastropod and 83 bored bivalve shells. Yochelsonet al. (1983) while studying bored scaphopods observed that coarsely ribbed scaphopod species show a high rate of predation. In contrast, smooth or finely ribbed forms are almost never bored. Reyment (1966) who worked on the predator-prey relationship for ostracods in the Western Niger Delta found that smooth or slightly ornamented shells are most readily attacked by predators. In the case of bivalves, he noted that the strongly sculptured species *Cardium papillosum* is a preferred prey for the predators while many smooth-shelled bivalves are not bored at all. Dudley & Vermeij (1978), however, observed that smooth-shelled gastropods in their collection were more often preyed upon than ornamented ones.

On the basis of statistical tests in this study, it appears that the less ornamented shells of bivalves and gastropods in the Ameki Formation are preferred to strongly ornamented shells. Therefore, ornamentation as a predator-defensive adaptation appears to have controlled the predation intensity.

Adegoke & Tevesz (1974) in their study on gastropod predation in Nigeria during the Eocene noted that the favoured predator food source was gastropods and that since the Eocene, a most significant change in food preference from gastropods to bivalves took place. The observation from the chi-square test fails to confirm the statement of Adegoke & Tevesz (1974). It appears therefore that bivalves as far as shown by fossil shells, were the favoured predator food source already during the Eocene in Nigeria. Ameki bivalves are mainly infaunal, as naticids are, while many of the ornamented gastropods are epifaunal, and will therefore be rather preyed upon by muricids.

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