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## GASTROPOD PREDATION ON CORBULID BIVALVES PALAEOECOLOGY OR TAPHONOMY?

by

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### SUMMARY

A case study on corbulid bivalves is presented, illustrating the complexity of bias and related problems, when attempting an objective analysis of gastropod drill-hole data. Phenomena, previously mentioned in literature, are re-examined and additional data are given on unsuccessful attacks. Acceptable palaeoecological explanations are suggested for the results obtained : the occurrence of corbulids in large monospecific clusters may cause some of the phenomena. Further research on this is needed.

On the other hand, taphonomical bias seems to be another important parameter, making it impossible to reach firm conclusions. Therefore, the impact of taphonomy needs further investigation, before palaeoecological value can be given to data on gastropod drill-holes.

Keywords : gastropod drill-holes, palaeoecology, taphonomy.

### RÉSUMÉ

Dans une étude de corbulidés (mollusques, bivalves) les problèmes qui rendent difficile une analyse objective des perforations de gastéropodes perceurs sont illustrés. Les phénomènes mentionnés antérieurement par plusieurs auteurs sont reexaminés; des données nouvelles pour des perforations inachevées sont discutées. Quelques explications plausibles d'ordre paléocologique sont présentées : c'est ainsi que les corbulidés forment souvent des associations monospécifiques et ceci pourrait expliquer certains des phénomènes observés. D'autre part, la taphonomie est un facteur très important; il semble prudent pour le moment de s'abstenir de conclusions hâtives qui pourraient s'avérer prématurées. De nouvelles recherches plus approfondies sont nécessaires pour démontrer définitivement que l'analyse numérique des perforations a vraiment une valeur paléocologique.

### INTRODUCTION

Gastropod drill-holes are usually assigned to three families : the Naticidae, Cassidae (o. Mesogastropoda) and Muricidae (o. Neogastropoda) of which only the Naticidae and Muricidae attack bivalve prey (CARRIKER, 1981 ; HUGHES and HUGHES, 1981). Other possible predatory drillers are not considered here, since their importance is assumed to be negligible (TAYLOR *et al.*, 1983).

A revision of the life-habits of Muricidae and Naticidae was given by CARRIKER (1981). Important is, that both families use a similar drilling method : shell-material,

which has previously been weakened by a chemical agent, is rasped away by the radula.

Drill-holes, made by the different families, tend to have a specific shape (see Fig. 1 A-C). A detailed account of the differences is given by CARRIKER and YOCHELSON (1968). These differences also give information on the life-habits of the prey-species : Recent Naticidae are reported to take infaunal prey, whereas Muricidae attack epifaunal animals. The frequencies of drilled shells are often used to give a measure of predation-intensity.

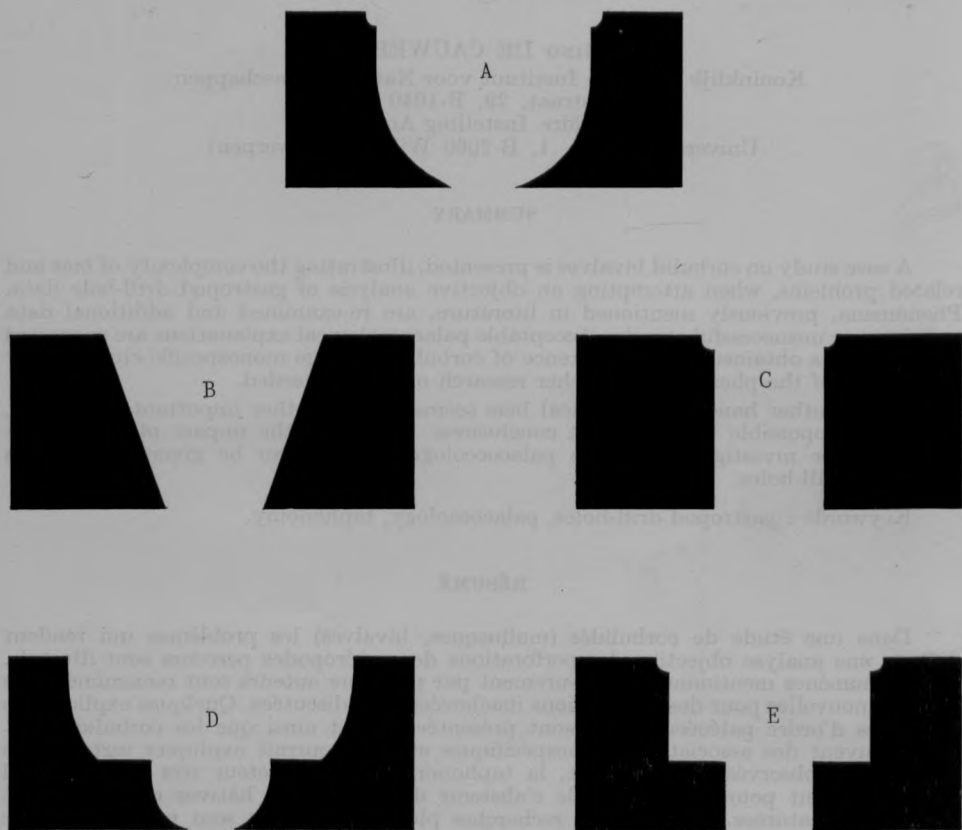


Fig. 1. — Lateral section of several types of gastropod drill-holes. A : naticid; B, C : muricid; D, E : « concentric » (see text for more information on the « concentric » holes). Drill-hole dimensions depend largely on the size of the predator and prey species (KITCHELL *et al.*, 1981), but diameters vary from less than 1 mm up to 8 mm, while valves of up to 3 mm thickness can be penetrated (personal observations).

The present study is concerned with the usefulness and the practical problems of drill-hole data, such as the frequencies mentioned above. Therefore, a case study is presented of the predation on a particular bivalve family : the Corbulidae.

Corbulids (o. Myoida, superfam. Myacea) are small, inequivalved bivalves with short siphons and a single byssus thread. They inhabit sands to muddy sands, but their globose shell-form greatly limits their burrowing abilities (YONGE, 1946 ;

STANLEY, 1970 ; LEWY and SAMTLEBEN, 1979) (see Fig. 2). First appearing in Jurassic times, they radiated mostly during the Cretaceous and Eocene, and are still successful today. Recent as well as fossil species are often found in large monospecific groups and beds (LEWY and SAMTLEBEN, 1979).

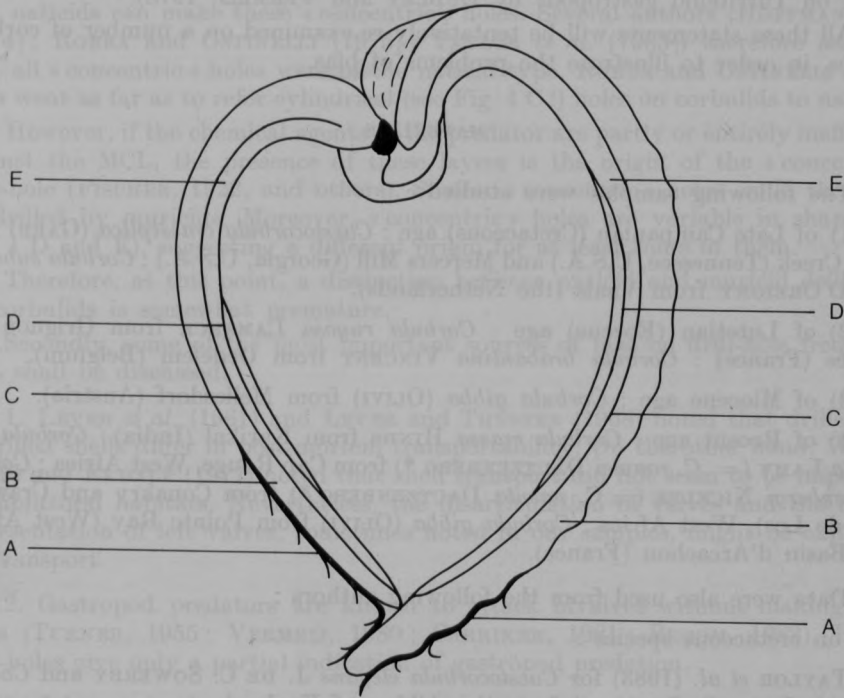


Fig. 2. — Cross section of a specimen of a corbulid bivalve (based on LEWY and SAMTLEBEN, 1979). A : periostracum layer; B : outer shell layer; C : first medium conchioline layer; D : second medium conchioline layer; E : inner shell layer (see text for information on the medium conchioline layers (= MCL)).

The family is of special interest, because corbulids have a typical morphological feature : internal, periostracum-like layers are found between the outer and inner shell-layers (TAYLOR *et al.*, 1973). These were named « middle conchioline layers » (MCL) by LEWY and SAMTLEBEN (1979). They seem to represent a barrier against the chemical agents of the gastropod predator, because numerous incompleated drill-holes have been found on corbulid species. In the same way, the MCL probably cause irregularities in drill-hole morphology (see Fig. 1 D, E) so that the « concentric » drill-hole which then arises, can not be assigned to either of the classical naticid or muricid types (see Fig. 1 A-C) (JEFFREYS, 1865 ; FISCHER, 1922, 1963 ; YONGE, 1946 ; ZIEGELMEIER, 1954 ; HOFFMAN *et al.*, 1974 ; KOJUMDJIEVA, 1974 ; ROBBA and OSTINELLI, 1975 ; LEWY and SAMTLEBEN, 1979 ; TAYLOR *et al.*, 1983). A short discussion of the « concentric » drill-hole is presented later in this paper.

Another interesting feature of predation on corbulids is the preference of the gastropod predator for the right, larger valve (SOHL, 1969 ; HOFFMAN *et al.*, 1974 ; KOJUMDJIEVA, 1974 ; ROBBA and OSTINELLI, 1975 ; TAYLOR *et al.*, 1983).

It has been suggested that gastropod predation increased during geologic time. Yet, FISCHER (1963) noted, that a Recent corbulid species seemed to have been attacked less frequently, showing also relatively more incompleated drill-holes.

TAYLOR *et al.* (1983) on the other hand, stated that corbulids suffered a major increase in drilling predation from the latest Mesozoic to the Eocene (a trend also noted on Turritellid gastropods by DUDLEY and VERMEIJ, 1978).

All these statements will be tentatively re-examined on a number of corbulid species, in order to illustrate the problems of bias.

#### MATERIALS

The following samples were studied :

1) of Late Campanian (Cretaceous) age : *Caestocorbula crassiplica* (GABB) from Coon Creek (Tennessee, U.S.A.) and Mercers Mill (Georgia, U.S.A.) ; *Corbula substriatula* D'ORBIGNY from Vaals (the Netherlands).

2) of Lutetian (Eocene) age : *Corbula rugosa* LAMARCK from Grignon and Parnes (France) ; *Corbula brabantina* VINCENT from Oedelem (Belgium).

3) of Miocene age : *Corbula gibba* (OLIVI) from Mellesdorf (Austria).

4) of Recent age : *Corbula crassa* HINDS from Karikal (India) ; *Corbula latocostata* LAMY (= *C. roumei* DAUTZENBERG \*) from Cap Rouge, West Africa ; *Corbula dautzenbergi* NICKLES (= *C. nasuta* DAUTZENBERG \*) from Conakry and Crawford (Iles de Los), West Africa ; *Corbula gibba* (OLIVI) from Pointe Ray (West Africa) and Basin d'Arcachon (France).

Data were also used from the following authors :

1) on cretaceous species :

TAYLOR *et al.* (1983) for *Caestocorbula elegans* J. DE C. SOWERBY and *Corbula truncata* J. DE C. SOWERBY from the Albian of England.

SPEDEN (1970) for *Corbulamella gregaria* MEEK and HAYDEN from the Fox Hills Formation, Maastrichtian of South Dakota, U.S.A.

2) on Lutetian (Eocene) species :

TAYLOR (1970) for *Corbula rugosa* LAMARCK and *Corbula gallica* LAMARCK from Damery, France.

FISCHER (1963) for the same species from Grignon, France.

ADEGOKE and TEVESZ (1974) for *Corbula amekiensis* (EAMES) from Nigeria.

3) on Miocene species :

HOFFMAN *et al.* (1974) for *Corbula gibba* (OLIVI) from Poland.

KOJUMDJIEVA (1974) for the same species from Dobroucha (old and new sample), Lassen and Lipen (Bulgaria).

4) on Pliocene species :

ROBBA and OSTINELLI (1975) for *Corbula gibba* (OLIVI) from Italy.

(\*) Systematic corrections of these KBIN labels are based on NICKLES (1955).

## METHODS

The first point of discussion is the division of the drill-hole data in two sets, each set being specific for a predator family. The basis of such a division is the typical morphology of each drill-hole-type. As mentioned above, corbulids carry holes with a special morphology (see Fig. 1 D and E). ZIEGELMEIER (1954) proved that naticids can make these « concentric » holes. Several authors (HOFFMAN *et al.* [1974]; ROBBA and OSTINELLI [1975]; TAYLOR *et al.* [1983]) therefore assumed that all « concentric » holes were of the naticid type. ROBBA and OSTINELLI (1975) even went as far as to refer cylindrical (see Fig. 1 C!) holes on corbulids to naticids.

However, if the chemical agents of the predator are partly or entirely ineffective against the MCL, the presence of these layers is the origin of the « concentric » drill-hole (FISCHER, 1922, and others). Similar « concentric » holes could then also be drilled by muricids. Moreover, « concentric » holes are variable in shape (see Fig. 1 D and E), suggesting a different origin for at least some of them.

Therefore, at this point, a distinction between naticid and muricid drill-holes on corbulids is somewhat premature.

Secondly, some of the most important sources of bias on drill-hole frequency data shall be discussed.

1. LEVER *et al.* (1961) and LEVER and THYSSEN (1968) noted that drilled and undrilled shells differ in post-mortem transportability. On the other hand, WARME (1969) and EKDALE (1977) noted that shell transport did not seem to be important in sublittoral habitats. Nevertheless, the disarticulation of valves and the underrepresentation of left valves, sometimes noted in our samples, might be explained by transport.

2. Gastropod predators are known to attack bivalves without making drill-holes (TURNER, 1955; VERMEIJ, 1980; CARRIKER, 1981; BROOM, 1982). Hence, drill-holes give only a partial indication of gastropod predation.

3. Other animal groups, such as trematods, clionid sponges, brachiopods, cephalopods (*Octopus*), etc... (CARRIKER and YOCHELSON, 1968; BROMLEY, 1970, 1981; BROMLEY and SURLYK, 1973) also drill. Recent representatives of these groups make holes of a size and shape which are very different from the naticid or muricid hole. The only exception is perhaps *Okadaia elegans*, a nudibranch which has been reported to drill holes resembling naticid ones (YOUNG, 1968; KAY, 1979; BROMLEY, 1981).

4. Predation by valve-destruction, mainly by fishes, removes part of the shell-population. Frequencies of drilled shells might hereby be influenced (GREEN, 1968).

5. A number of factors, such as the abundance of predators, the presence or absence of favoured prey-species, etc... can influence the predation intensity on a given species to such an extent, that differences have been noted between localities (VERMEIJ, 1980; KITCHELL *et al.*, 1981).

To these generally cited problems we add the following :

6. Some valves can be so badly damaged, that it is difficult to point out whether they have been drilled or not. Additionally, the decay of the MCL can result in the « separation » of outer and inner shell-layers (LEWY and SAMTLEBEN, 1979). I noted this especially on right valves. The presence of drill-holes may facilitate



the MCL-decay, and once « separated », drilled shellparts might be more easily destroyed. All this would influence the noted predation intensity.

7. The present study also compares the data of several authors. The amount of predation in these studies is often measured by calculating « predation frequencies » (PF). This is the frequency of attacked individuals. Another measure, however, is here called the drilling frequency (DF). This is the frequency of attacked valves.

PF can be best measured on a sample with bivalved specimens. When the sample includes a majority of disarticulated valves, the PF is calculated by taking the double value of the DF (e.g. TAYLOR *et al.*, 1983). This is correct when : a) right valves and left valves occur in equal amounts or b) when there is no valve-preference.

In our experience, as was stated above, this is not always the case. A more objective calculation method would therefore have been the sum of the DF of right and left valves separately.

8. The data I took from work by previous authors may have been obtained by different counting methods. TAYLOR *et al.* (1983) for example, stated, that they rejected all doubtful holes. ADEGOKE and TEVESZ (1974) apparently did not.

I checked my own methods with those of FISCHER (1963) and compared our results on *Corbula rugosa* from Grignon. A  $X^2$ -test (with continuity correction) shows no significant difference ( $0.1 > p > 0.05$   $N_1 = 512$   $N_2 = 107$ ) although my DF-value is higher.

The impact of all these (and other) problems is unknown and further study is certainly needed. At present, some measures can be taken, trying to minimize the bias : DF-values of both valves, and sometimes PF-values (calculated as the sum of right and left valve DF) are taken as predation intensity measures. The number of « damaged » valves (valves, on which the presence or absence of drill-holes cannot be ascertained) and « separated » shell-parts is mentioned separately as the number of « rejected » valves. This number is excluded from all frequency-calculations. We also use the total number of attacks in order to calculate the frequency of incomplete drill-holes.

## RESULTS

All valve-frequencies obtained on corbulids are represented in table 1. Frequencies of attacks are noted in table 2.

When analysing these results, it becomes obvious that the counting methods of different authors make comparisons difficult. Apparently, there is no consensus on the use or the exact meaning of DF- or PF-values. Some authors (HOFFMAN *et al.*, 1974 ; ROBBA and OSTINELLI, 1975 ; SPEDEN, 1970) did not clearly explain how they obtained their PF-value. PF's based on disarticulated valves are probably biased :

on Recent *Corbula gibba* samples, which contained bivalved specimens, I found that attacks on the left and right valve of the same individual are possible.

DF- and PF-values differ within the same geological period (previously noted on Turritellid gastropods by DUDLEY and VERMELJ, 1978) and even within the same species (KOJUMDJIEVA, 1974), illustrated herein by the two Recent samples of *Corbula gibba*. As a result, it becomes difficult to say whether « differences » stated to occur between geological periods were really significant. TAYLOR *et al.* (1983)

TABLE 1

Period	Species	Location	Drilling Rates										Frequencies		
			Valve-numbers												
			Right valves			Left valves			valve total						
			T	B	BI	T	B	BI	T	B	BI	RV	LV	T	
Recent	<i>Co. crassa</i>	India*	335	72	50							.215			
			130R	16R	—										
	<i>Co. laticosta</i>	W. Africa*	947	69	23	1108	63	29	2055	132	52	.073	.057	.064	
			8R			7R			15R						
	<i>Co. dauzenbergi</i>	Conakry*	100	34	3	110	33	8	210	67	11	.340	.300	.319	
		Iles de Los*	115	16	4	110	26	8	225	42	12	.139	.236	.187	
	<i>Co. gibba</i>	W. Africa*	126°	1°	1°	126°	2°	2°	126°	2°	2°	.008°	.016°	.016°	
		France*	183°	26°	22°	183°	11°	11°	183°	33°	29°	.142°	.060°	.180°	
Pliocene Miocene	<i>Co. gibba</i>	Italy							804°	126°				.160°	
	<i>Co. gibba</i>	Poland							928°					.270°	
		Lassen	140	22	13							.157			
		Lipen	116	11	3							.095			
		Dobroucha, old	222	49	12							.221			
		Dobroucha, new	516	75	19							.145			
		Austria*	387	74	63	56	9	8	443	83	7	.191	.161	.187	
			108R						108R						

Period	Species	Location	Drilling Rates												
			Valve-numbers									Frequencies			
			Right valves			Left valves			valve total			RV	LV	T	
			T	B	BI	T	B	BI	T	B	BI				
Eocene	<i>Co. brabantina*</i> <i>Co. rugosa</i>	Belgium*	276	130	8	39	1	—	315	131	8	.471	.026	.416	
		Damery							179	25	1			.139	
		Grignon							107	16	5			.149	
		Grignon*	315	96	16	209	25	9	524	121	25	.305	.120	.231	
	<i>Co. gallica</i>	Parnes*		60R	12R	2R	4R			64R	12R	2R			
				313	75	21	265	29	3	578	104	24	.240	.109	.180
		Damery		130R	28R	1R	3R			132R	28R	1R			
										27	5	5			.185
			Grignon							106	26	14			.245
			Nigeria							89°	25°	3°			.281°
Maastr. Campanian	<i>Cl. gregaria</i>	USA							332°					.346°	
		<i>Ca. crassiplica</i>	Coon Creek*	267	45	7	48	3	2	294	48	9	.169	.064	.153
	<i>Co. substriatula</i>	Mercers Mill*		67R		8R			75R						
				221	55	11	118	19	11	331	74	22	.249	.161	.218
		Vaals*		19R			3R			22R					
				207	37	11	277	33	10	484	70	21	.179	.119	.145
Albian	<i>Ca. elegans</i> <i>Co. truncata</i>	England							712	42				.059	
		England							145	7				.048	



had stated the existence of a major increase in frequencies after the Campanian. Our results do not permit to confirm this.

The slight Miocene frequency-decrease appearing in table 1 can be explained by collecting failures : only one species was sampled and many samples only contained right valves.

The reduced « vulnerability » of Recent corbulids, which FISCHER (1963) had suggested, is not confirmed by my results : at least two Recent samples have frequencies comparable to previous geological periods.

Incomplete drill-holes have been considered previously as important. This fact is confirmed here. Frequencies of incomplete holes on corbulids can sometimes be extremely high (91 % of all noted attacks on the Recent *Corbula gibba* of France were unsuccessful ! See table 2). There are nevertheless exceptions (*Corbula brabantina* with only 10 %) and a variability of frequencies of these holes within one geologic period and within one species is noted (e.g., *C. gibba* from the Miocene of Dobroucha (Bulgaria) and of Austria ; see table 1). These results do not enable us to recognize a general pattern of change in frequency of unsuccessful drilling.

Attacks on left valves seem more often unsuccessful than on right valves. Statistical analysis was able to prove this for *Caestocorbula crassiplica* (Mercers Mill, X<sup>2</sup>-test  $0.02 > p > 0.01$  N<sub>1</sub> = 60 N<sub>2</sub> = 19; Coon Creek, Fisher Exact Probability  $p < 0.01$  N<sub>1</sub> = 43 N<sub>2</sub> = 7). There is one exception however : *Corbula rugosa* from Parnes (Eocene).

The data of table 1 show higher DF-values on the right valve (except for *Corbula dautzenbergi* from Iles de Los [Recent]). Statistical proof could be reached for *Corbula rugosa* (Grignon, X<sup>2</sup>-test  $p < 0.001$  N<sub>1</sub> = 315 N<sub>2</sub> = 209 ; Parnes, X<sup>2</sup>-test  $p < 0.001$  N<sub>1</sub> = 313 N<sub>2</sub> = 265), for *Corbula brabantina* (Fisher Exact Probability  $p < 0.01$  N<sub>1</sub> = 276 N<sub>2</sub> = 29) and for one Recent sample of *Corbula gibba* (France, X<sup>2</sup>-test  $0.01 > p > 0.001$  N<sub>1</sub> = N<sub>2</sub> = 183).

#### DISCUSSION

Our results allow us to endorse the following statements (previously mentioned in the introduction) on gastropod predation on corbulids : at least some species were preferably attacked on the right valve, whilst incomplete drill-holes do occur in relatively large numbers.

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*Table 1* : Rates of attacked valves, in numbers and frequencies. Complete information on species-names and locations is given in « Materials ». When localities are marked with \*, data are from personal investigations. Data in numbers are given for each valve separately and for the valve totals. Three categories were used : T : the total number of investigated valves. B : the total number of attacked valves. BI : the number of valves carrying only unsuccessful attacks. Values, marked with « R » give the number of « rejected » valves (see « Methods » for explanation). When marked with °, the values in « valve-totals » are calculated on *individuals*, not valves.

The frequencies of attacked valves (DF-values) are given in the last three columns for RV : right valves LV : left valves T : both valves. When marked with °, the frequency of drilled individuals (PF-value) is given instead of the DF-value of T.

TABLE 2

Period	Species	Location	Attacks									
			Numbers						Frequencies			
			Right		Left		Total		RV	LV	T	
			T	BI	T	BI	T	BI				
Recent	<i>Co. crassa</i>	India	76	57						.750		
	<i>Co. laticosta</i>	W. Africa	71	25	65	31	136	56	.352	.477	.301	
	<i>Co. dautzenbergi</i>	Conakry	40	7	43	16	83	23	.175	.372	.277	
		Iles de Los	19	6	32	14	51	20	.316	.438	.392	
Miocene	<i>Co. gibba</i>	France	31	27	14	14	45	41	.871	1	.911	
	<i>Co. gibba</i>	Austria	80	68	10	9	90	77	.850	.900	.855	
	Eocene	<i>Co. brabantina</i>	Belgium	137	14	1	0	138	14	.093	0	.092
<i>Co. rugosa</i>		Grignon	85	32	27	14	112	46	.376	.519	.411	
		Parnes	64	26	33	6	97	32	.406	.182	.330	
Campanian	<i>Ca. crassiplica</i>	Coon Creek	43	5	7	6	50	11	.116	.857	.220	
		Mercers Mill	60	16	19	11	79	27	.267	.579	.342	

Table 2 : This table gives all noted attacks on the species which were investigated personally. Complete information on species names and localities is given in « Materials ». Attack-number data are given for separate valves and for valve totals. Two categories were used : T : total number of noted attacks. BI : number of unsuccessful attacks. The proportion of unsuccessful attacks is given in the three last columns for RV : right valves LV : left valves T : both valves.

Yet, exceptions to these facts exist (see Results).

Changes in predation intensity during geological history are not confirmed by our results altogether. Discrepancies between previous interpretations and our own can be explained by our somewhat larger number of samples. FISCHER (1963) had a reasonable sample of Eocene material, but did not give precise data for other periods. TAYLOR *et al.* (1983, p. 543) admitted that they only had limited material available for some geological periods. My results show a possible major increase in predation before the end of the Mesozoic, rather than in the Palaeogene (it should be noted that TAYLOR *et al.* [1983] did not have the opportunity to study predation on corbulid samples of Late Cretaceous age). However, the existence of a broad frequency-variability within a given geologic period makes statements on « major increases » through geologic time difficult to prove objectively. Gastropod predation on corbulids started in Early Cretaceous times and probably did increase later on. It remains doubtful, however, whether through the study of a very large number of samples of varied ages and proveniences, this increase, though plausible, could be proved beyond contention. The distribution of predation within different clusters of corbulids in one locality and the parameters regulating it, should be studied, before further objective research on the evolution of predation can be undertaken.

The presence of incomplete drill-holes was explained in the introduction. The possibly greater proportion of these holes in the left valve can have been caused by manipulation-difficulties for the predator. This might be the explanation for the apparant right valve preference also, but predators might just simply have problems with the thick periostracum layer on the left valve. Even right/left valve surface proportions may have something to do with it.

How do we explain the fact, that animals, who seem so resistant against the gastropod attack, continue to be sought by these predators throughout geologic time (see table 1). This seems contradictory to the prey-selection model of KITCHELL *et al.* (1981) : small prey, with an effective valve armour (valve thickness, as well as the MCL) surely must represent high drilling investment and low benefits. Corbulids, however, are sluggish burrowers, not very mobile, and occur in very large clusters (see Introduction). Valves with multiple drill-holes therefore not only illustrate their resistance to the attack, but also the relative ease with which they can be caught (ROBBA and OSTINELLI, 1976 ; LEWY and SAMTLEBEN, 1979 ; TAYLOR *et al.*, 1983).

In regions with large corbulid clusters, predators might be « forced » to live on these animals, since the high search-cost on other (and better) prey would probably not be recouped by higher benefits. The more corbulids dominate a fauna, the more the predator might be inclined to pick them as prey. Further research on the effect of large clusters on the predation behaviour is needed, since it also partially explains local frequency-variability within the same species.

All these explanations are plausible and are probably part of the truth. However, the results also show that some species do not line up with the others (see Results). Suitable explanations are possible here also, but bias is one of them.

Bias might also have influenced our major results : right valves, for instance, are usually more readily classified as « rejected » (see Methods and table 1). This indicates, that right valves are even more often attacked than stated. On the other hand, absence of « rejected » left valves might mean, that these are more easily destroyed. In fact, we know nothing of possible differences in the taphonomy of both valves before and after disarticulation. The distorted right valve/left valve ratio (already mentioned in Methods) might be a reflection of this.

More generally, we can ask : do the differences and phenomena noted reflect real palaeoecological or only taphonomical circumstances? Several problems in connection herewith were mentioned (see Methods) and the list can be enlarged : did predators, for instance, really attack only live prey, or did they also take dead ones, confused by the over-all presence of chemical attractants in the exhalant water in the corbulid cluster (see CARRIKER, 1981)?

It has to be admitted, that the problems might have been somewhat overstated. Nevertheless, they make an objective use of drill-hole data extremely difficult. To my opinion, we shall only be certain of the usefulness of fossil data, when much more research is done on Recent faunas and on the impact of taphonomic processes. Blind use of fossil data is pointless.

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#### LIST OF USED ABBREVIATIONS

- MCL : middle conchioline layers (LEWY and SAMTLEBEN, 1979).  
 PF : predation frequency ; the frequency of attacked individuals.  
 DF : drilling frequency ; the frequency of attacked valves.

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