

# FEEDING HABITS OF PREDATORY GASTROPODS IN A TERTIARY (EOCENE) MOLLUSCAN ASSEMBLAGE FROM THE PARIS BASIN

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**ABSTRACT.** The distinctive boreholes produced by two predatory gastropod superfamilies, the Muricacea and the Naticacea, can be recognized in their molluscan prey in a fossil assemblage from the Calcaire Grossier (Eocene, Lutetian) from Dameray in the Paris Basin. Possible predators are six species of Naticacea and two of Muricacea. About 7000 mollusca representing 40 species were examined for boreholes of either type. The most common prey species of the Muricacea were the epifaunal bivalve *Ostrea plicata*, the shallow burrowing bivalve *Venericardia serrulata* and the epifaunal gastropod *Omalaxis serrata*. The Naticidae fed upon deeper burrowing bivalves as well as *Venericardia serrulata* but very rarely upon epifaunal bivalves. Their principal prey species was the burrowing gastropod *Mesalia regularis* as well as a varied selection of other burrowing gastropods with a marked tendency towards cannibalism within the superfamily. The position of the borehole upon the prey species can give information on the behaviour and mode of attack of the predator.

It is widely known that members of several families of Recent gastropods obtain their food by boring holes through the calcareous exoskeletons of prey (Carriker and Yochelson 1968). The families with this ability are the Naticidae, Muricidae, and the Cassidae; of these, the two former feed regularly upon other molluscs and the latter usually feeds upon echinoderms. Gastropod boreholes have been recognized in molluscs and brachiopods of many ages (Fischer 1922, 1960, 1962, 1963, 1964, 1966, Bucher 1938, Hayasaka 1933, Siler 1965, Brunton 1966, Carter 1967, Carriker and Yochelson 1968). However, the holes, particularly in the Palaeozoic, need not have been produced by members of the families of Recent gastropods listed above.

To the palaeontologist the recognition of these boreholes gives one of the few pieces of positive, rather than circumstantial, evidence of feeding. Previous work on boreholes in fossils has been limited to records of their occurrence and a discussion of possible predators. The present study of predation on a molluscan assemblage, from the Calcaire Grossier (Eocene, Lutetian) of the Paris Basin shows that boreholes of the Naticacea and Muricacea can be distinguished and with certain reservations inferences about the dietary preferences and the biology of the predators can be made.

## BORING IN RECENT GASTROPODS

A detailed summary of boring mechanisms and borehole morphology has recently been made by Carriker and Yochelson (1968). It appears that all Recent Naticacea bore holes, and the work of Ankel (1937), Ziegelmeier (1954, 1961), and Carriker (1961) has established that they bore by means of rotatory action of the radula assisted by a secretion from an accessory boring organ situated at the ventral tip of the proboscis. The hole produced by this process is neat and circular with a broad bevelled outside rim producing a wide conical shape (see figure in Carriker and Yochelson 1968).

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Incomplete borings show a characteristic central boss. Naticids are usually infaunal gastropods, highly active but usually only bore when they and the prey are buried in the sand. The foot is exceptionally broad and used as a plough when moving through the sand. The prey is grasped and virtually enveloped in the foot while being manipulated into the correct position for boring to commence. Boring takes place by alternations of rotatory rasping of the radula and the application of the accessory boring organ to the site. When the hole is complete, the proboscis is closely applied and the contents of the prey dragged out and pieces cut off by the jaws. Recent naticids usually feed upon infaunal bivalves and occasionally upon gastropods when the need and opportunity arises (Paine 1963).

Independently the Muricacea have evolved a similar method of boring using the radula with the aid of a secretion from an accessory boring organ situated in the foot. The boring process is essentially similar to that of the naticids but the resulting hole is rather different. The hole is straight-sided, or tapers slightly inwards, the outer parts may be ragged and irregular; a bevelled rim is sometimes produced but it is never as wide or neat as that of the naticids. Members of the Muricacea are almost exclusively epifaunal and movements appear rather clumsy when compared with those of the highly motile naticids. In many species the foot is poorly developed and they are unable to move rapidly in pursuit of prey and have limited, if any, powers of excavating prey from sediment (Paine 1963). However, on rocky shores muricids are very successful predators feeding upon byssate bivalves, limpets, and barnacles. Muricids such as *Urosalpinx* and *Ocenebra* are common predators of oyster beds (Carriker 1955, Hancock 1960).

The ability to drill holes enables naticids and muricids to attack and eat bivalves larger than themselves. However, when attacking gastropods the size and mobility of the prey are important limiting factors (Paine 1963). Ansell (1960) considers that naticids may not be able to hold and manipulate much larger bivalves successfully and consequently do not recognize them as suitable food.

Carter (1967) has pointed out that there have been many attempts to show a preferred boring site for naticids but that most of this has been inconclusive and conflicting. Ansell (1960) reasonably considers that the site of boring by naticids depends upon the shape of the prey and predator and in any one species of prey there would be a preferred site but that the position of the borings would be expected to differ for each prey/predator combination. Muricids generally do not show preferred sites for boring when feeding upon epifaunal prey. However, when bivalves are attached in tight byssate groups only certain portions of the prey may be available for boring.

#### PREDATION IN THE CALCAIRE GROSSIER ASSEMBLAGE

Part of a large block of Calcaire Grossier limestone originating from Bed iii (Abrard 1925) at Dameray, near Epernay in the Paris Basin, has been examined. It is a loosely cemented shell sand composed mainly of broken and whole mollusc shells; echinoids, *Ditrupa*, polyzoa, and foraminifera are also very common.

Preservation of the fossils is excellent; many bivalves are preserved with the valves together and all growth stages of many species are present, including even the planktonic veliger stages of the molluscs. It appears that very little post-mortem sorting has

taken place. The numbers of individuals of each species extracted from the rock gives some indication of their relative abundance in the assemblage. About 7000 molluscs were examined representing 40 species of which 29 showed evidence of predation by boring gastropods (Table 1).

#### *Potential predators*

Molluscan genera in the Calcaire Grossier assemblage are sufficiently similar to, or the same as Recent genera to assume that they probably had similar habits. Thus it is possible to pick out the potential hole-boring predators in the assemblage and make the assumption that no other gastropod genus represented in the assemblage was a borer into other molluscs. The possibility that some holes may have been drilled by octopus must not be discounted (Pilson and Taylor 1961), but these are much more irregular than those of the Muricacea.

Possible hole-borers are represented by six species of Naticacea and two Muricacea. Only two species of naticids are at all common, these being *Natica epiglottina* and *Euspira labellata*. Wrigley (1949) considers that *Lunatia*, a Recent genus, is synonymous with *Euspira*; feeding in the former has been described in detail by Zeigelmeier (1954). Three species of *Ampullina* occur, *A. patula*, *A. sigaretina*, and *A. parisiensis* but only the first occurs in any numbers. This genus became extinct during the Miocene but it is so similar in morphology to Recent naticids that it is reasonable to assume that it was a borer. The only other naticid present is *Sinum clathratum* of which only five specimens were found; feeding in a Recent species of this genus has been described by Paine (1963). Only two species of muricids were found, *Pteropurpura tricarinatus* and *Poiriera frondosus*; whilst it cannot be assumed that all muricids are borers, these two species are the only available potential borers of straight-sided holes in the assemblage. These muricids are surprisingly uncommon, only 20 specimens of *P. tricarinatus* and 16 of *P. frondosus* were found. *P. tricarinatus* shows great morphological resemblance to the Recent 'Oyster drill' *Ocenebra*.

#### *Predation*

Each mollusc was examined for presence, type (muricid or naticid), and success or failure of the boring. The results of this examination and the numbers examined are shown in Table 1. Amongst bivalves the most common and most commonly attacked species are *Venericardia serrulata* and *Ostrea plicata*. *O. plicata* is a cemented epifaunal species frequently occurring in attached groups. It is attacked exclusively by muricids; of the 103 borings seen there was a slight preference for right, upper valves (58 borings) as opposed to the lower left valve (42 borings). There is no apparent preferred site for the attacks. This behaviour is slightly puzzling, for it would be expected that attacks on the attached, more inaccessible and thicker, lower valve would be fewer than on the thin, right, upper valve, seemingly the more obvious site for attack. A similar sort of behaviour has been observed on living species by Carriker (1955) who records that in *Urosalpinx* the site of drilling is not limited to any specific region or to any position which is easier to penetrate. Another Recent muricid predator, *Nucella lapillus* (Linnaeus), will frequently attempt to bore the thick ligamental area of *Mytilus edulis* Linnaeus whilst other individuals at the same locality may be boring at the shell margins

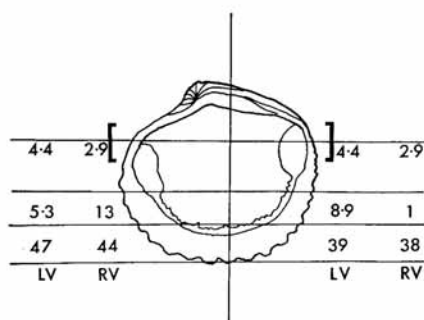
TABLE 1

<i>Prey species</i>	<i>Number examined</i>	<i>Naticid bored</i>	<i>Muricid bored</i>	<i>Failed borings</i>
BIVALVES				
<i>Nucula mixta</i> Deshayes	19	2	5	
<i>Nuculana galliotina</i> Nyst.	29	0	0	
<i>Barbatia irregularis</i> Deshayes	45	4	0	
<i>Glycimeris pulvinata</i> (Lamarck)	215	9	2	
<i>Ostrea plicata</i> Solander	981	0	103	
<i>Venericardia imbricata</i> Deshayes	280	0	0	
<i>Venericardia serrulata</i> Deshayes	2,699	101	366	
<i>Crassatella dilatata</i> Deshayes	21	2	1	
<i>Crassatella grignonensis</i> Deshayes	51	10	0	
<i>Crassatella trigonata</i> (Lamarck)	177	2	2	
<i>Crassatella tumidum</i> (Lamarck)	20	0	3	
<i>Loxocardium bouei</i> (Deshayes)	200	2	6	1 muricid
<i>Calpitaria distincta</i> (Deshayes)	180	11	0	
<i>Aphrodina nitidula</i> (Lamarck)	77	13	0	2 naticid
<i>Castacallista laevigata</i> (Lamarck)	62	3	0	
<i>Bicorbula gallica</i> (Lamarck)	27	0	5	
<i>Corbula rugosa</i> Lamarck	179	2	22	1 muricid
GASTROPODS				
<i>Bittium</i> sp.				
<i>Calyptreaa aperta</i> Solander	65	6	0	
<i>Solarium olicatum</i> (Lamarck)	100	0	4	
<i>Omalaxis serrata</i> (Deshayes)	73	2	2	1 muricid
<i>Mesalia regularis</i> (Deshayes)	519	0	109	
<i>Rimella fissurella</i> (Linnaeus)	886	272	0	
<i>Marginella eburnea</i> (Lamarck)	227	12	1	
<i>Marginella ovulata</i> (Lamarck)	200	3	0	
<i>Natica epiglottina</i> (Lamarck)	31	5	0	
<i>Euspira labellata</i> (Lamarck)	115	9	0	10 naticid
<i>Ampullina patula</i> (Lamarck)	138	17	3	11 naticid
<i>Ampullina parisiensis</i> (d'Orbigny)	8	2	0	
<i>Ampullina sigaretina</i> (Deshayes)	2	0	0	
<i>Sinum clathratus</i> (Gmelin)	6	1	0	
<i>Ancilla buccinoides</i> (Lamarck)	5	0	0	
<i>Pteropurpura tricarinatus</i> (Lamarck)	119	9	2	
<i>Poiriera frondosus</i> (Lamarck)	20	0	0	
<i>Sycostoma pirus</i> (Solander)	16	0	0	
<i>Clavilithes noae</i> (Lamarck)	12	0	0	
<i>Ficus</i> sp.	5	0	0	
<i>Turris</i> sp.	145	5	0	
<i>Athleta (Volutospina) athleta</i> (Linn.)				
<i>Conus parisiensis</i> (Deshayes)	9	2	0	
<i>Ringicula ringens</i> (Lamarck)	66	0	0	

(personal observation). *Venericardia serrulata* is by far the most common bivalve, usually reaching a size of 15 mm. It was a shallow burrower and shows evidence of predation by both naticids and muricids; the latter making the most attacks. In attacks on this species most of the muricid bores are situated at the margin of the valves. These marginal bores at the commissure of the valves are semicircular and are frequently

situated in the interspace between the ribs. The bores are very similar to the illustrations by Carriker (1961) of boring by *Murex fulvescens* on *Mercenaria mercenaria*.

In an attempt to see if there was a preferred drilling site the shell was divided up into sectors and the frequency of attacks in each sector recorded (text-fig. 1). No preference



TEXT-FIG. 1. Diagram of inside of the right valve of *Venericardia serrulata* showing the percentage frequency of attacks in each sector for each valve. 215 attacked valves examined.

for right or left valves was shown, but in both valves there was a very marked preference for sites in the two sectors at the ventral margin towards the midline (Pl. 46, figs. 1, 2). Naticid bores into this species are usually completely enclosed as opposed to the marginal borings of muricids and situated towards the centre of the shell. Different sizes of *Venericardia* show different predation rates, most attacks taking place in the 3–6 mm. size range and least in the 11–15 mm. range. Small *Venericardia* are drilled by small holes indicating small predators. The regular preferred position of muricid bores in this species, as opposed to the indiscriminate attacks on *O. plicata*, is probably accounted for by the fact that

*Venericardia* is a burrower and always has the same orientation in the sediment so that the muricid must excavate and manipulate the prey in its foot prior to drilling. These processes probably follow fixed behaviour patterns, resulting in the apparently preferred drilling site. Epifaunal bivalves are usually byssally fixed or cemented allowing the muricids to crawl all over their prey and attack without prior manipulation with the foot.

The larger, thicker-shelled species *Venericardia imbricata* which reaches 40 mm. in length shows no evidence of predation or even attempted borings suggesting that adults of this species are not recognized as prey. Ansell (1960) found that large, thick-shelled individuals of *Venus striatula* had neither borings nor attempted borings and suggested that *Natica alderi* may be incapable of manipulating large heavy specimens in the foot.

By comparison with Recent members of the family *Bicorbula gallica* and *Corbula rugosa* can be assumed to have been very shallow burrowers, probably with their posterior end protruding from the sediment. They are eaten almost exclusively by muricids. In *B. gallica* most of the borings took place at the protruding posterior end, but in the smaller *C. rugosa* most borings took place towards the midline of the shell.

#### EXPLANATION OF PLATE 46

- Fig. 1. *Venericardia serrulata* Deshayes showing muricid boring,  $\times 12$ .  
 Fig. 2. *Venericardia serrulata* Deshayes showing muricid boring at valve margin, a common occurrence in the species,  $\times 18$ .  
 Fig. 3. Naticid boring in *Crassatella grignonensis* Deshayes,  $\times 12$ .  
 Fig. 4. Muricid boring on flat spire of *Omalaxis serrata* Deshayes,  $\times 20$ .  
 Fig. 5. Naticid boring in *Ampullina patula* (Lamarck) indicating cannibalism within the Naticacea,  $\times 11$ .  
 Fig. 6. *Mesalia regularis* (Deshayes) showing a naticid boring in the mid-portion of the spire,  $\times 14$ .

Deeper burrowing bivalves (indicated by deep pallial sinuses), such as *Aphrodina nitidula*, *Calpitaria distincta*, are attacked by naticids alone. No particular preference for left or right valves was shown, but in *A. nitidula* all the bores fall within the area bounded by the pallial lines. All naticid attacks on the burrowing *Crassatella grignonensis* took place approximately on a line from the umbo to the midpoint of the ventral margin (Pl. 46, fig. 3). Predation on the very thin-shelled, shallow burrower *Loxocardium bouei* is less than expected. A possible reason for this is that in common with several Recent species of Cardacea it may have had the ability to make leaping motions by rapid flexing of the foot; an effective escape mechanism. In *Nucula mixta* the muricid bores are distributed around the ventral margin, but the two naticid bores are situated at the anterior end. Four individuals of *Barbatia irregularis* were attacked by naticids. This is rather surprising as it is a byssate epifaunal bivalve and must have been attacked very close to the sediment surface.

Predation on gastropods was more exclusively by naticids, with a wide choice of prey; whereas predation by muricids is limited to a few species only. By far the most common gastropod in the fauna is a turrillid *Mesalia regularis*, a burrowing suspension feeder. This species shows a very high predation rate (Table 1) and must have been a principal item in the diet of naticids. Most of the attacks take place on individuals up to about 20 mm. in height. The hole is usually made about half-way up the spire (Pl. 46, fig. 6) with no preference for aboral or adoral sides; larger, thicker-shelled specimens of *Mesalia* show no evidence of attacks.

In all naticid attacks on gastropods there is a more definite preferred site than for attacks on bivalves. Species such as *Marginella eburnea*, *M. ovulata*, *Ancilla buccinoides*, and *Euspira labellata* show most of the attacks at the adoral surface very near to the aperture. These apparently preferred sites for boring arise possibly because gastropods are generally more active than bivalves and the ensuing struggles with predators induce stereotyped behaviour patterns on the part of both attacker and attacked. Cannibalism by naticids is common (Pl. 46, fig. 5) but it is impossible to tell if this is intra- or inter-specific, or both. An interesting feature of the cannibalism is the high incidence of failed borings, a reflection of the high mobility of this genus. Carriker (1961) records that laboratory-starved *Polynices* (naticids) exhibit a high degree of cannibalism but in the presence of bivalves will eat these first.

The only gastropod attacked by muricids to any extent is *Omalaxis serrata*. Little is known about the habits of this extinct genus, but by comparison with the related genus *Architectonica*, it is assumed to have been epifaunal. Of the muricid attacks on this species, 70 per cent took place on the flat top of the planispiral shell (Pl. 46, fig. 4), other attacks took place on the side of the whorl. The only other epifaunal gastropods, *Architectonica plicata*, *Capulus ungaricus*, and *Ringicula ringens*, show little or no predation by muricids.

It is noticeable that attacks on other gastropod predators such as *Sycum*, *Athleta*, *Clavilithes*, and *Turris* are uncommon, and where they do occur, as in *Turris*, they are confined to juveniles.

#### CONCLUSIONS

From an examination of the occurrence and distribution of the two different types of gastropod boreholes in the Calcaire Grossier fossil assemblage it is possible to

reconstruct, at least in part, the diets of the two gastropod superfamilies. It is possible to ascertain points of feeding overlap and possible sources of competition between the two superfamilies. Muricacea generally feed upon sedentary epifaunal prey, and Naticacea upon infaunal prey, both sedentary and motile; but shallow burrowing species are liable to be eaten by members of either superfamily. The site of the attack on the prey species can give information concerning the behaviour of the predator and prey. Study of fossil boreholes provides one of the few positive pieces of evidence in the reconstruction of food chains and trophic levels in fossil communities.

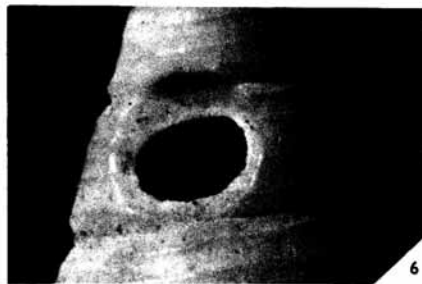
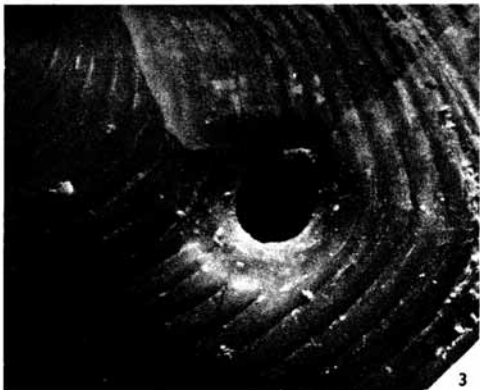
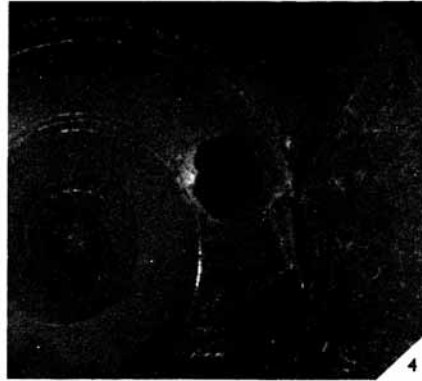
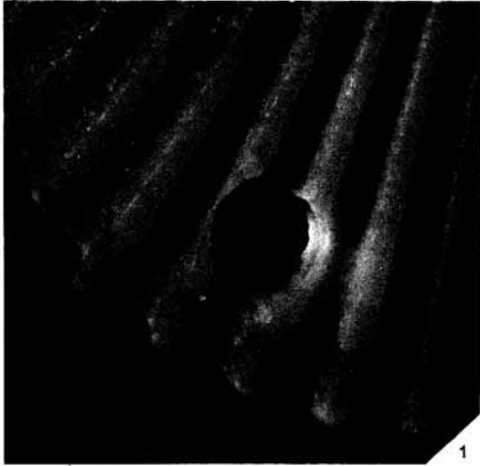
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