

ARE CONCHIOLIN SHEETS IN CORBULID BIVALVES PRIMARILY DEFENSIVE?

by ELIZABETH M. HARPER

ABSTRACT. Conchiolin sheets in corbulid bivalves have long been considered to offer some defence against predation by boring gastropods. Vermeij argued that most defences are exaptations rather than adaptations, but it has never been demonstrated whether conchiolin sheets in corbulids evolved in response to predation pressure or as a fortuitous benefit of an otherwise selected character (e.g. to retard shell dissolution, to prevent crack propagation, or to assist with hermetic sealing). A three pronged investigation was undertaken to resolve this question: a survey of failure rate of gastropod boreholes in corbulids over geological time, a survey of the distribution of conchiolin sheets in Recent corbulids in relation to various selection pressures, and an investigation into the temporal appearance of the sheets by direct (microstructural) and indirect (inferred from morphology and taphonomy) means. It is concluded that well developed conchiolin sheets first appeared at a time coincidental with the first reported gastropod boreholes and that they evolved primarily in response to that threat. Possession of conchiolin sheets may then have further influenced corbulid evolution in allowing the assumption of gross valve discordance in post-Jurassic taxa.

GOULD and Vrba (1982) considered aptations (beneficial traits) and distinguished between *adaptations* (traits whose perceived benefit for a specified function or effect has been enhanced by natural selection) and *exaptations* (traits whose benefits to the owner are secondary or incidental to the primary function to which they are adapted). Given that many traits may be multifunctional (i.e. beneficial in a number of unrelated ways) these functions should be divisible into adaptations and exaptations. Vermeij (1982) believed most anti-predatory aptations to be exaptations.

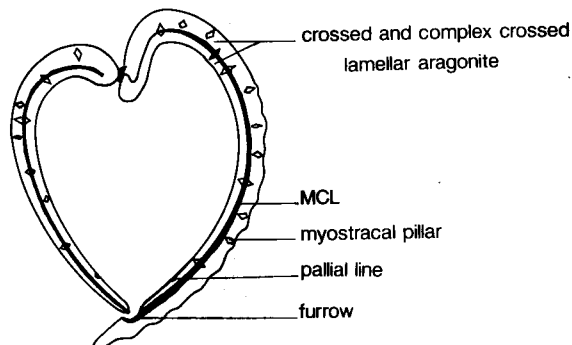
Vermeij (1983) noted that the bivalved form of both bivalves and brachiopods is susceptible to damage, and that even non-lethal attacks will often be ultimately fatal because of their poor ability to repair marginal damage. It therefore follows that both must have been affected by the 'sudden' increase in predation pressure following the Mesozoic Marine Revolution (MMR) of Vermeij (1977, 1987) and are likely to display a number of defensive adaptations. For the bivalved molluscs a large number of defences have been described (Carter 1968; Ansell 1969; Vermeij 1987). Harper and Skelton (1993a) noted the desirability of testing to ascertain whether changes in morphology and life habit are truly defensive. Even so, although it may be possible to demonstrate experimentally that a specific trait confers a selective advantage against a given predator, it may be more problematic to show that it evolved directly in response to that threat and was thus an adaptation. For example, Logan (1974) considered the functional morphology of the spines of the bivalve *Spondylus americanus*. He discusses six functions for these spines, all of which are demonstrable. Only two of these may be described as directly defensive (protection of the gape and promoting the growth of camouflaging algae), the remainder being concerned with anchorage, discouraging epibionts and providing support for sensory outposts.

In order to distinguish whether a defensive aptation is a true adaptation rather than an exaptation two basic requirements need to be demonstrated. Firstly, that the trait truly is beneficial in the respect postulated, which requires experimental testing; and secondly, that there is a plausible temporal coincidence between the evolution of the trait and that of the supposed selective agent?

Such requirements are not easily fulfilled. Vermeij (1987) outlined five predatory methods, for each of which he listed many different exponents. Different predatory methods may require similar defensive strategies; for example, spines may thwart crushers, borers, prisers and whole animal

ingesters (Harper and Skelton 1993a). The 'sudden' evolution of predators at the beginning of the Mesozoic included large numbers of prising forms (e.g. extra-oral feeding asteroids), and crushing groups (e.g. various crustaceans, nautiloids, fish and reptiles). It may be difficult, therefore, to tie the evolution of a perceived defence to a particular predatory group. There is, however, one type of predation which may be easier to study in this light. The boreholes produced by gastropods (muricids, naticids and marginellids) in their bivalve prey are quite distinct (Carriker and Yochelson 1968; Ponder and Taylor 1992), are easily recognizable in the fossil record, and are distinguishable from other predatory borers (e.g. octopods, see Bromley 1993). This form of predation is quite different from the others enumerated by Vermeij (1987), in that it relies largely upon chemical solution of the shell (see Carriker 1981) rather than physical breaking or forcing apart of the valves. Consequently the defensive requirements against this means of predation are very different (Harper and Skelton 1993a). For example, Harper (1991) showed experimentally that the cemented habit provided defence against prising and crushing predators, but in experiments reported by Harper and Skelton (1993a) it was found to have no value against boring gastropods. Defences against boring gastropods are also interesting since the evolution of this type of predation occurred late in the MMR. Despite records of gastropod-like boreholes in Triassic bivalves (Fürsich and Jablonski 1984), boring did not become a major cause of death until the Cretaceous, when the first unequivocal naticid and muricid boreholes in bivalves and gastropods are recorded from the Albian Blackdown Greensand of England, where a significant proportion of the fauna is bored (Taylor *et al.* 1983).

This paper concentrates on the evolution of conchiolin sheets within the shells of members of the Corbulidae, a trait which frequently has been referred to as a defensive adaptation against boring gastropods (see below), and seeks to determine whether this is an adaptation or an exaptation.



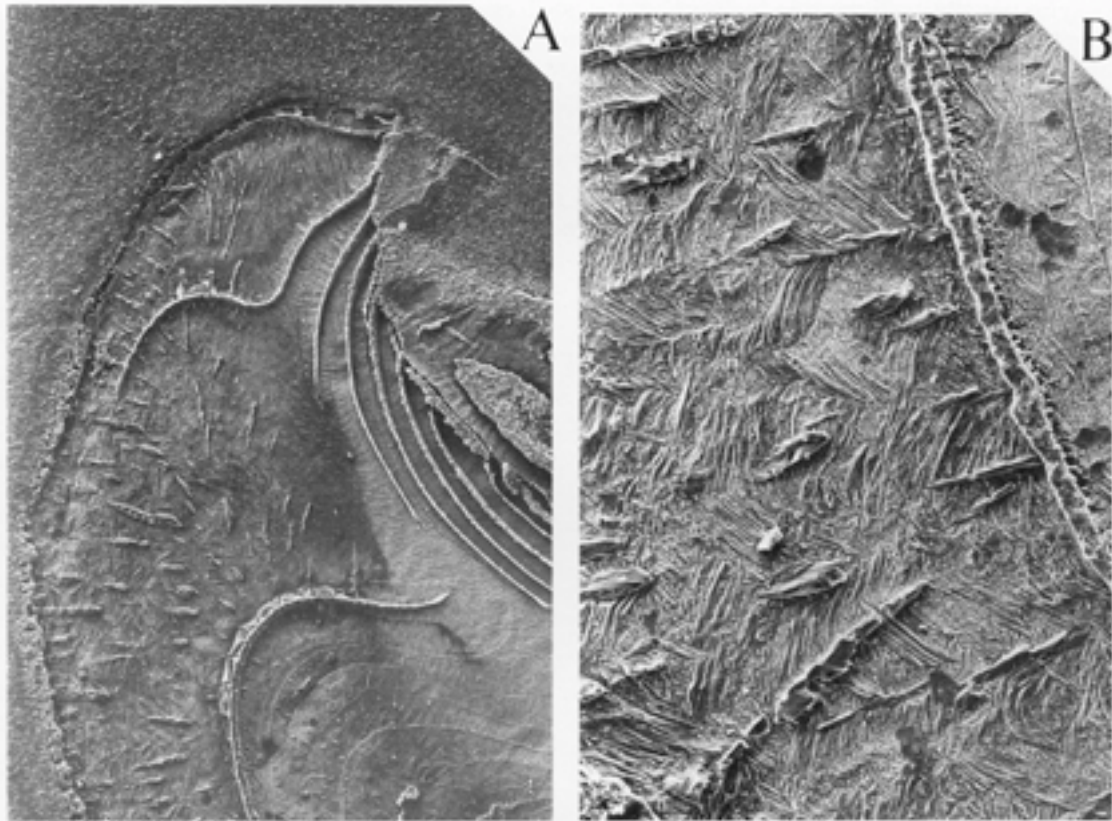
TEXT-FIG. 1. Cross section through a generalized corbulid valve showing microstructure (based on Lewy and Samtleben 1979).

CORBULID BIVALVES

The Corbulidae are small infaunal bivalves with an evolutionary history dating back to the Tithonian (Hallam 1976). The supraspecific taxonomy of the family has been dealt with by Vokes (1945). Traditionally the Corbulidae have been placed within the superfamily Myoidea along with the Myidae and a number of small extinct families (see Newell *in* Moore 1969). However, Morton (1990) pointed out a number of important differences between the corbulids and the Myidae, such as shell structure and anatomical complexity, and suggested that an affinity with the Veneroidea is equally likely.

The biology of the corbulids has been described in detail for *Corbula gibba* (Yonge 1946), *C. caribaea* (Stanley 1970) and *C. crassa* (Morton 1990). These living species are sluggish shallow burrowers in a variety of substrates from mud to sandy gravel. They are markedly inequivalve and inequilateral, often with pronounced co-marginal ridges. Morton (1990) regarded them as 'superficially uninspiring' but conceded that one of their redeeming features is their unusual valve microstructure. As described by Taylor *et al.* (1973), both valves are comprised solely of aragonite,

with two major units: an outer crossed lamellar layer, and an inner complex-crossed lamellar layer. These layers are separated by the prismatic pallial myostracum and traversed by myostracal pillars. Conchiolin sheets up to 30 μm thick occur within both of these microstructural units and in both valves (Text-figs 1–2). The presence of conchiolin sheets is an unusual arrangement but, contrary



TEXT-FIG. 2. Electron micrographs of Recent *Corbula crassa* Reeve, etched to reveal conchiolin sheets; SM X.24528; Hong Kong. A, umbo region; $\times 44$. B, detail of cross lamellar microstructure, MCL and myostracal pillars; $\times 93$.

to the suggestion of Lewy and Samtleben (1979) and Anderson *et al.* (1991), is not unique to the corbulids; homologous sheets are also found in many oysters (e.g. *Saccostrea cucullata*), corbiculoids, and unionioids (Taylor *et al.* 1969).

Conchiolin sheets are of two types: the main conchiolin layer(s) (MCL) which cover(s) the entire surface of the valve, and more numerous lesser sheets which are less continuous with a more patchy distribution. In *Corbula crassa* Morton (1990) recognized around twenty of the secondary sheets, particularly in the postero-ventral region. Rather than being formed by entrapment of the periostracum within the shell, as suggested by Yonge (1946) and Taylor *et al.* (1973), Morton found conchiolin to be secreted periodically by the outer surface of the mantle lobe, alternately with aragonite. The presence of the MCL within the shell represents a line of weakness. Decay of this organic layer frequently leads to splitting of the valves (Lewy and Samtleben 1979; de Cauwer 1985). Lewy and Samtleben noted that such taphonomic splitting has caused considerable taxonomic problems where the separated portions of the valves have been described as different species or even different genera.

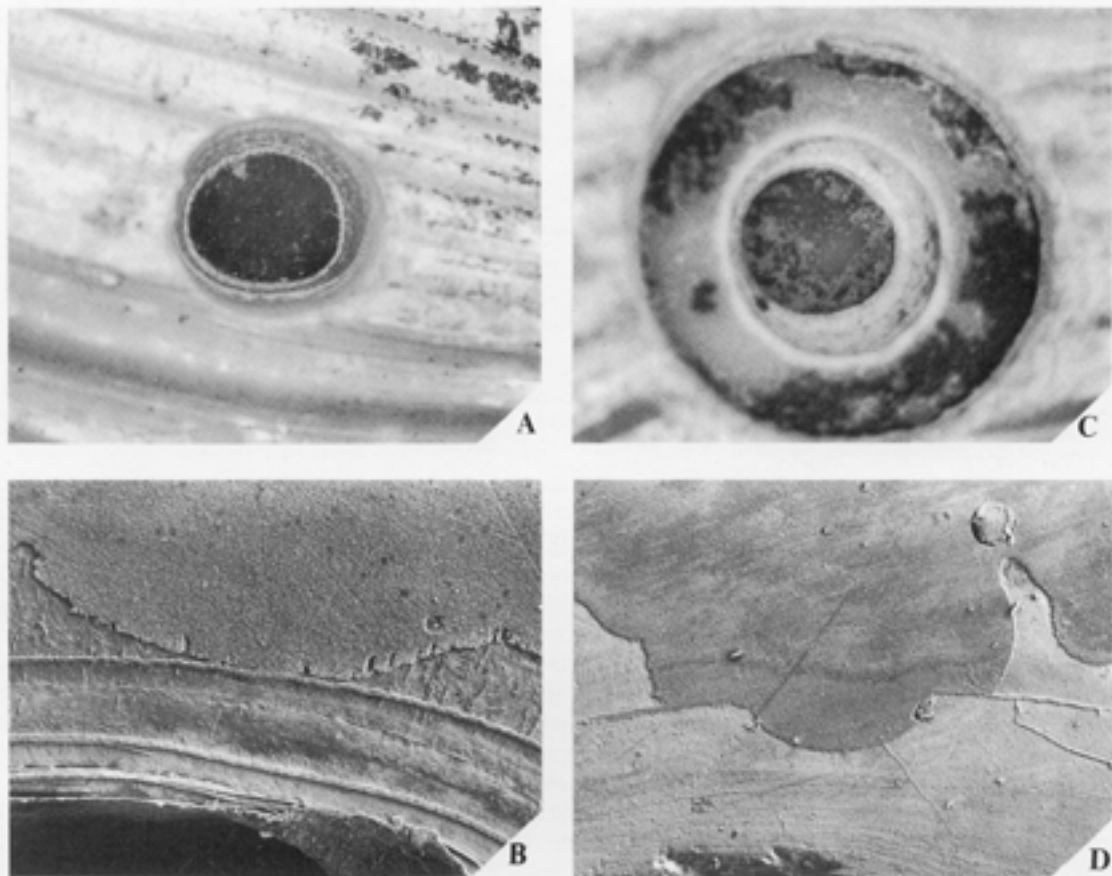
WHAT IS THE PRIMARY FUNCTION OF THE SHEETS?

Defensive value

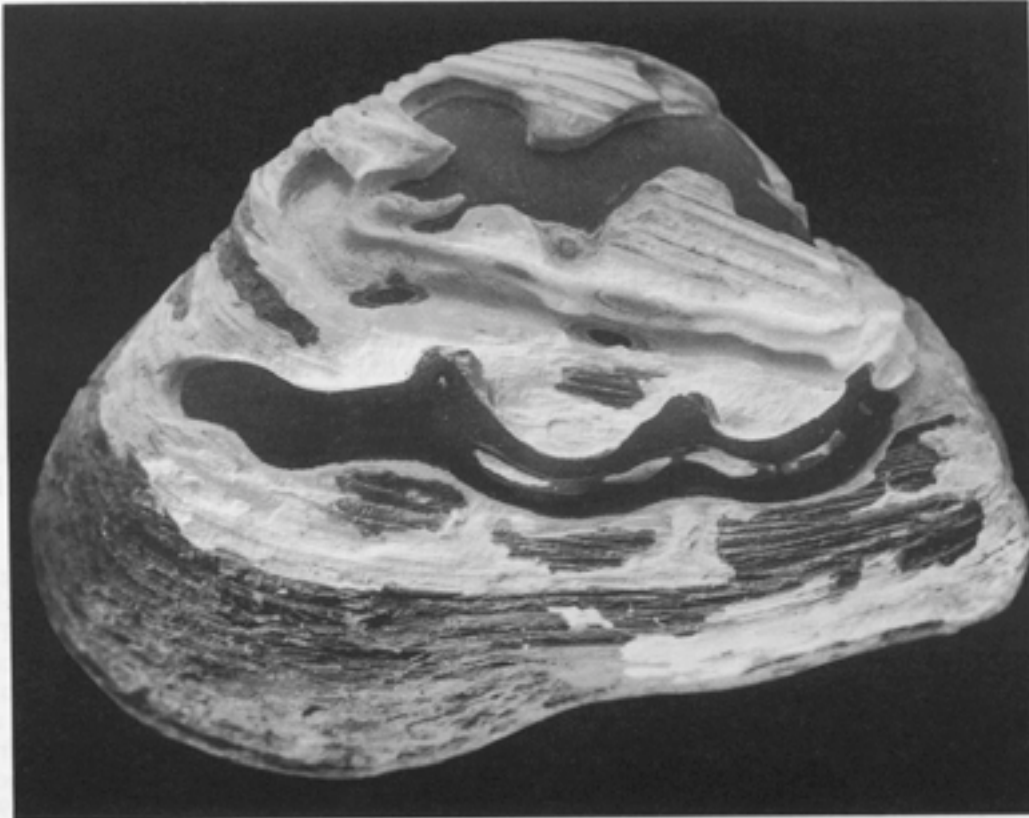
It has long been suggested that conchiolin sheets have a defensive value against boring predators. Jeffreys (1865, p. 65) noted that in *C. gibba*, 'the shell is subject to the attacks of predatory molluscs, which do not always succeed in perforating it; in such cases the white outside layer only is removed, exposing the succeeding layers, which are of a firmer texture and coffee coloured ...'. Since then, this possibility has been explored by many authors (e.g. Ziegelmeier 1954; Fischer 1963; Lewy and Samtleben 1979; Morton 1990).

Evidence for the defensive value of the conchiolin sheets

There seems to be little doubt that the conchiolin sheets of corbulids act as a defence against boring predators. The above authors illustrated numerous examples of corbulid shells scarred by incomplete boreholes which terminate at such sheets (see also Text-fig. 3). Carriker (1981) recounted that both naticids and muricids bore largely by using a chemical secretion of acids, enzymes and



TEXT-FIG 3. Failed predatory boreholes in Recent *Corbula crassa* Reeve; Hong Kong. A-B, termination of a borehole at MCL. A, plan view; SM X.24545; $\times 14$. B, cross section; SM X.24528; $\times 22$. C-D, boreholes which pass through the MCL (with a restricted diameter) but terminate at a subsequent conchiolin sheet. C, plan view; SM X.24546; $\times 14$. D, cross section; SM X.24528; $\times 32$.



TEXT-FIG. 4. Non-predatory borings in a Recent *Corbula crassa* Reeve in which the damage is restricted to the outer shell layers by the MCL; SM X.24554; Hong Kong; $\times 5$.

chelators delivered by the accessory boring organ (ABO). Gabriel (1981) experimented on the effectiveness of ABO secretion on various bivalve shell microstructures, and found that those with a high organic content are least susceptible, whilst Harper and Skelton (1993b) showed experimentally that mytilids deprived of their thick periostraca (of similar composition to the conchiolin sheets) are much more vulnerable to muricid boring; they speculated that infaunal bivalves with thick periostraca might gain a similar protection from naticid gastropods. It is thus evident that the conchiolin sheets are more resistant to the action of ABO secretion than the calcareous parts of the shell, and hence act as a barrier. This is further evidenced by the observation that where the borer successfully breaches a conchiolin sheet the borehole produced is frequently of reduced diameter (see Text-fig. 2C-D).

Taylor (1990) examined the effect of similar sheets in the oyster *Saccostrea cucullata* on their muricid predators in Hong Kong. Taylor demonstrated that ninety five per cent of failed boreholes terminate at the sheets, and that even those which are successful in penetrating are of notably reduced diameter; he also discovered that muricids studied in the act of boring were most frequently in the process of boring through the sheet, implying that boring the conchiolin sheet is a more time consuming process than boring the calcareous parts of the shell.

Analysis by Kelley (1988) showed that patterns of naticid predation of Miocene corbulids do not fit the elaborate models of predicted foraging proposed by Kitchell *et al.* (1981). Kelley explained this by the presence of the conchiolin sheets. However, Anderson *et al.* (1991) and Anderson (1992)

suggested that other factors (e.g. small prey size, small sample sizes and environmental factors) have led to these unpredictable patterns and indeed claimed that the conchiolin sheets do not retard boring. Evidently Anderson and co-workers were unaware of the work of Gabriel (1981), Taylor (1990) and Morton (1990). Arguments over whether predation of corbulids is stereotypic or non-stereotypic are not the primary concern of this paper, although its conclusions may have some bearing on that debate.

Alternative hypotheses

Several alternative hypotheses may be advanced for the primary function of the conchiolin sheets.

1. *Retarding shell solution.* Corbulids are frequently associated with low salinity and cold bottom water conditions, both of which may be undersaturated with respect to calcium carbonate and likely to cause shell dissolution (Lewy and Samtleben 1979; Maslin 1989). The presence of thick organic sheets within the calcareous valve may retard acidic attack and loss of shell material. Previous studies have invoked this selective advantage for the thick periostracum and homologous conchiolin sheets in the freshwater unionids, margaritiferids and corbiculids (Tevesz and Carter 1980; Kat 1983; Isaji 1993).

2. *Assistance with hermetic sealing.* Members of the Corbulidae are renowned for their physiological tolerance; for example they may survive short periods of low oxygen levels (Lewy and Samtleben 1979). Morton (1990) noted that *Corbula crassa* survives in the highly polluted waters of Tolo Channel in Hong Kong, whilst other bivalves have disappeared. Tolerance of physiologically 'difficult' conditions appears to have persisted throughout the evolutionary history of the group; Hallam (1976) uses the Jurassic *Corbulolimima* as an indicator of low brachyhaline conditions and they are often found in monotypic assemblages (e.g. *Corbula* bed in the Thanet Sands). Apart from the low metabolic requirements of these sluggish animals, part of their success must be ascribed to the ability to produce a tight hermetic seal when the valves are closed. Lewy and Samtleben (1979) noted that, when closed, the ventral edge of the smaller left valve is placed within the groove in the right valve in which the MCL crops out (Text-fig. 1), thus forming an 'elastic gasket, permitting hermetic closure of the valves'. It seems likely that the elastic nature of the conchiolin sheet would enhance a tight seal.

3. *Protection against non-predatory borers.* The activities of non-predatory boring organisms (e.g. worms, sponges, forams, algae and fungi) may severely weaken calcareous shells (Kent 1981). As with predatory boring, the conchiolin sheets appear to retard the boring activity and confine damage to the outer shell layer (Text-fig. 4). Korrinda (1951) regarded the analogous conchiolin sheets in *Ostrea edulis* as affording protection from damage by polydorid worms.

4. *Prevention of crack propagation.* Anderson (1992) suggested that the conchiolin sheets prevent the propagation of cracks within the shell and may, therefore, be defensive against crushing predation. However, it has not been demonstrated that the sheets do function in this way and there is little evidence of shell repair in Recent or fossil corbulids (but see Robba and Ostinelli 1975) nor are there any published accounts of corbulids being important in the diets of crustaceans. Study of Recent corbulids did not reveal examples in which cracks had been deflected along the conchiolin sheets.

Discriminating between competing hypotheses

With the exception of the last, evidence can be cited in support of each of the above putative functions for the conchiolin sheets, but are these more important than their defensive value? The hypothesis tested here is that conchiolin sheets in corbulids evolved as a direct response to boring

predation and that other benefits derived from these sheets are secondary. Three different approaches have been used: (i) charting the success rate of gastropod borehole attack on corbulids over geological time; (ii) using various microstructural, morphological and taphonomic features to trace the evolutionary history of conchiolin sheets; and (iii) examining the geographical distribution of conchiolin sheets in Recent corbulids. The first and second methods hinge upon determining if pre-Albian corbulids possessed conchiolin sheets or whether their appearance post-dates the evolution of boring in the gastropods. If it can be demonstrated that conchiolin sheets are found in corbulids before the onslaught from boring gastropods, it implies that any defensive value against these predators is secondary. The third method assumes that the selection pressure for the various functions will vary latitudinally. Dudley and Vermeij (1978) found that the boring frequency in low latitude turrillids is approximately three times that in higher latitudes, a general trend which was confirmed by Allmon *et al.* (1990). Although Vermeij *et al.* (1989) observed an equatorward decrease in boring predation of bivalves, their data were limited to small sample sizes with few temperate taxa and tropical taxa, largely from Panama. Taylor and Taylor (1977) found that the diversity of predatory gastropods in the eastern Atlantic increased equatorwards. Both these observations suggest that selection pressure favouring defensive adaptations against boring predators increases towards the tropics. Conversely, selection pressure favouring anti-shell dissolution is strongest poleward, as calcium carbonate is most soluble in cold water.

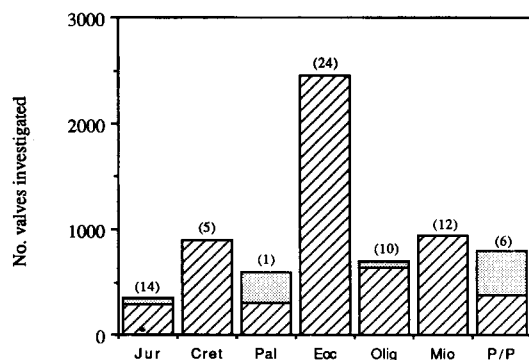
MATERIALS AND METHODS

Borehole survey

This survey was run similarly to that conducted by Allmon *et al.* (1990) in their investigation of the evolutionary history of drilling and peeling of turrillids.

The collections of the Sedgwick Museum, University of Cambridge (SM) were scoured for specimens belonging to the family Corbulidae. The computer listings (Price 1984) were searched for the generic and subgeneric names *Aloidis*, *Anisocorbula*, *Bicorbula*, *Caryocorbula*, *Corbula*, *Corbulomima*, *Eocallista*, *Jurassicorbula*, *Lentidium* and *Varicorbula*. Despite large holdings of corbulids, the sample sizes for the Paleocene, Oligocene, Pliocene and Pleistocene were comparatively small and thus were supplemented by examining the collections of The Natural History Museum (London) (Text-fig. 5). Internal and external moulds were rejected, as were

TEXT-FIG. 5. The number of corbulid specimens from each geological time interval examined for this study. Specimens from the Sedgwick Museum (Cambridge) are depicted by striped shading and those from The Natural History Museum (London) by dotted shading. The numbers in brackets refers to the number of species represented in each time interval.



individuals which had split along the conchiolin sheet in the manner described by Lewy and Samtleben (1979). The latter were discarded because de Cauwer (1985) has observed that taphonomic splitting along the MCL of valves bearing failed boreholes results in the production of

two 'valves': one bearing a complete borehole, the other apparently unscarred, leading to serious distortion of palaeoecological interpretations. Split valves were identified by their smooth reflective external surfaces which lack appreciable ornament or, on internal surfaces, by the absence of the adductor musculature. Specimens in blocks were used only as qualitative evidence, as it is not possible to determine whether these boreholes perforate the valve or not.

After this winnowing procedure, the remaining valves were retained for closer inspection. Each valve was examined for signs of boreholes, both complete and incomplete. Doubtful holes were rejected. For each scarred valve, the following were recorded: valve height, whether the valves were articulated or single, number of boreholes present, whether each of these was complete or incomplete, and whether it occurred on the right or left valve. The diameter of the boreholes was measured using vernier calipers, their position was marked on a species outline, and borehole morphology noted.

For each species, it was then possible to note the number of bored and unbored valves. Inevitably, any study which is heavily dependent on museum collections will be charged with biases. Collector bias may alter severely the frequency of bored and unbored specimens represented in a collection; relative abundances may be skewed by the number of boreholes being enhanced or reduced by collectors who regard their presence as novelty or blemish. However, these problems are minimized by the large number of individuals examined, the large number of different contributors and the small size of bivalves, many of which were collected in large lots.

Other authors have published information on boreholes in corbulids. These data were also considered, but there are considerable problems with utilizing this information when it is unclear exactly how the data were acquired or how derived information was calculated (de Cauwer 1985). Only data which had been collected in a manner similar to the above were used.

Geographical distribution of conchiolin sheets

Specimens of sixteen species of Recent corbulids, selected from as wide a geographical range as possible, were extracted from the collections of The Natural History Museum (London). These were blocked in epoxy resin, cut along the maximum growth axis, polished and then etched slightly in dilute hydrochloric acid. They were then gold-sputtered for routine scanning electron microscopy (SEM), using a JEOL JSM-820. Blocks were then examined for the presence or absence of conchiolin sheets, and where present their distribution, appearance, number and thickness were recorded.

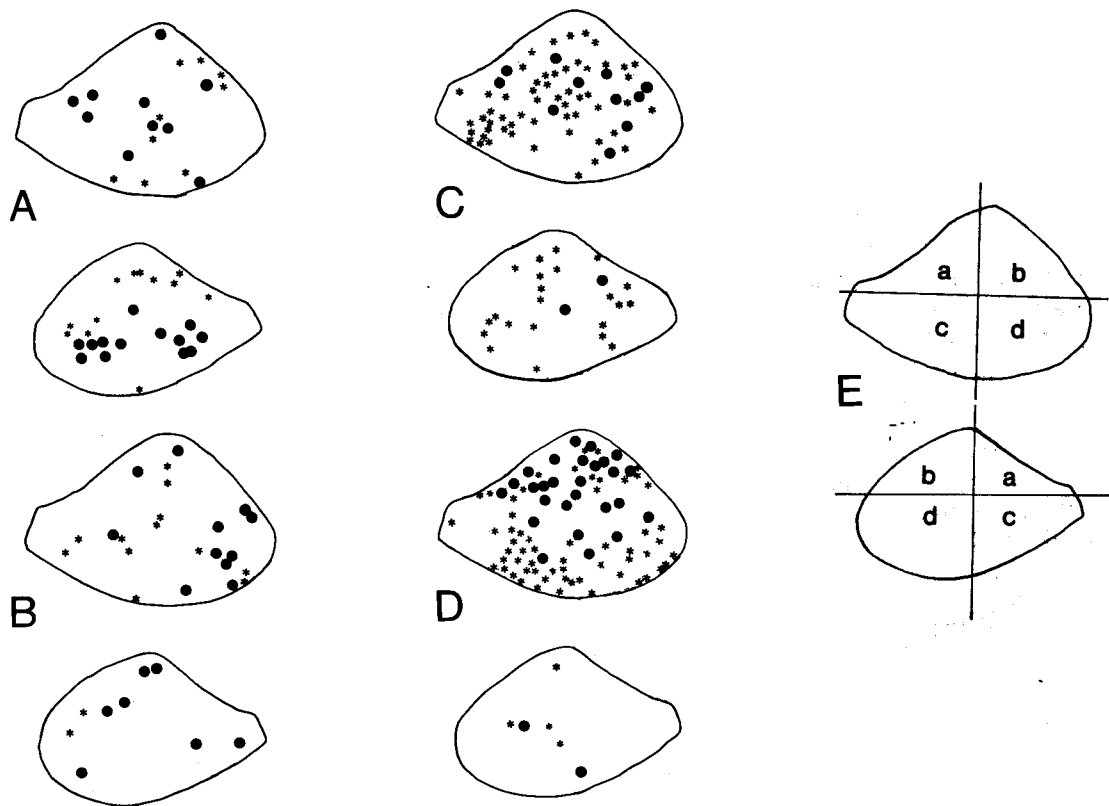
Temporal appearance of the conchiolin sheets

Three different methods have been used to determine whether fossil specimens possessed conchiolin sheets.

Direct microstructural evidence. Selected specimens from a range of geological ages were prepared for SEM in the manner described above and the same observations recorded. Additionally, some of the blocks were cut into thin slices, polished and carbon coated for X-ray micro-analysis (LINK 10000).

Taphonomic evidence. The presence of taphonomic splitting provides a good indication of the presence of the MCL. For each species examined, the occurrence of individuals in which splitting had occurred was noted. De Cauwer (1985) took the rather gloomy view that taphonomic splitting seriously limited the potential of palaeoecological studies of corbulids, but in this case it can be utilized in a positive way.

Morphological evidence. The occurrence of the MCL may be inferred by the presence of a co-marginal furrow in the right valve which runs ventrally to the pallial line (Text-fig. 1). This furrow marks the point on the internal surface where the MCL crops out, and also where the ventral margin



TEXT-FIG. 6. The positions of successful (*) and failed (●) boreholes in the four most preyed upon taxa. A, *Corbula regulbiensis* Morris; Paleocene; data from the Sedgwick Museum only. B, *C. alabamiensis* Lea; Eocene. C, *C. pisum* Sowerby; Eocene. D, *C. gibba* (Olivi); Miocene. E, the division of the corbulid valves into four sectors; the areas covered by each sector are a = 21 per cent, b = 22 per cent, c = 26 per cent and d = 31 per cent.

of the left valve resides during adduction (Lewy and Samtleben 1979). Each of the species examined during the borehole survey were inspected and the presence or absence of the furrow noted. Although Lewy and Samtleben used the furrow to indicate the presence of the MCL in Cretaceous corbulids, to do so on the basis of their Recent spatial coincidence may not be sound.

All mounted specimens used for SEM are now held in the Sedgwick Museum Cambridge (SM X.24504–SM X.24544, SM X.24554).

RESULTS AND ANALYSES

Borehole survey

After rejection of unsuitable material, a total of 6834 valves belonging to 72 species were examined. The raw data derived from this survey are presented in Appendix 1. Additional data culled from previous work are shown in Appendix 2. Except for the work of Taylor *et al.* (1983) on the Albian Blackdown Greensand, there is no overlap between the species and localities explored in the present study and those of previous studies. Since Taylor *et al.* made some of their observations on Sedgwick Museum material, my data set is a sub-set of theirs and thus, in the ensuing analysis, their data for this time have been used instead.

null hypothesis, thus agreeing with previous assertions that naticid predation of corbulids is non-stereotyped (Kelley 1988).

Most of the boreholes examined had the paraboloid shape of the type created either by naticids (Carriker and Yochelson 1968) or marginellids (Ponder and Taylor 1992). Relatively few were more straight sided of the type generally attributed to muricids (Carriker and Yochelson 1969), although as pointed out by de Cauwer (1985), muricid holes passing through a conchiolin sheet have a restricted diameter giving the borehole a stepped appearance which may be mistaken for naticid (or marginellid) predation. As corbulids are infaunal burrowers their principal gastropod predators are liable to be naticids or marginellids, although, since they only reach shallow depths it is not unlikely that if wholly or partially exhumed they may fall prey to epifaunal muricids. Morgan (1972) showed that dogwhelks deprived of their normal epifaunal prey (mussels and barnacles) attack infaunal cockles. It is interesting to note that Taylor (1970) identified muricid holes in Eocene *Bicorbula gallica* and that these were concentrated towards the posterior (i.e. closest to the sediment/water interface), although Morton (1990) recorded that Taylor by then believed these to be naticid borings.

Temporal changes in boring. Although it would be optimal to gauge changing boring rate by calculating the predation rate (PR), a measure of the number of boreholes per bivalved individual, as used by some other authors (e.g. Taylor *et al.* 1983), it is impractical here as most of the specimens in this study were disarticulated. A more practical approach has been to use boring frequency (BF), the percentage of valves examined bearing either complete or incomplete boreholes (some authors, e.g. de Cauwer (1985), use a different definition of this parameter, using only the percentage of valves displaying complete boreholes). Text-figure 7 plots the BF over geological time. Each species from each locality is plotted as a single point. I chose not to plot a single mean BF for each period, as used by Allmon *et al.* (1990), as the value obtained at each locality is liable to depend on a number of factors: predator presence, presence of other more preferable prey, as well as the susceptibility of the corbulids themselves. Vermeij (1982) pointed out that different localities and environments will produce different BF values for the same taxa.

No boreholes were found in pre-Albian corbulids. Albian boreholes were noted from the Blackdown Greensand as well as in blocked samples of the Gault containing *Corbula gaultina* (e.g. SM B.13693–13699). There is a significant difference (two tailed *t*-tests, $P < 0.01$) between the boring frequencies noted for Early and Late Cretaceous corbulids. Although the Early Cretaceous values come solely from the Blackdown Greensand (other Early Cretaceous samples pre-date the Albian) it should be noted that according to Taylor *et al.* (1983) corbulids are both the most abundant bivalve family and the most frequently attacked prey in that fauna.

In the Tertiary, BF shows wide variation with many species apparently suffering little predation and others where the pressure was more extreme. The highest BF was recorded in the Eocene *Corbula costata* from the Barton Clay at forty eight per cent.

The Permutation Test (Siegel and Castellan 1988) was used to test for significant differences between recorded BF for each geological time-interval. There was no significant difference (at the five per cent level) between the BF of any consecutive interval, except for between the Eocene and Oligocene. This significant difference is probably due to the small Oligocene data set, although it is of note that Allmon *et al.* (1990) also found an Oligocene drop in BF although again the sample size is low.

Failed boreholes and multiply bored valves. All boreholes which terminated before reaching the internal surface of the valve were classified as failed. This study does not follow Kitchell *et al.* (1986) and Kelley (1988), in designating some complete boreholes as non-functional and thus also as failures. These authors designated complete boreholes in which the ratio of inner and outer borehole diameter is less than 0.5 as non functional on the basis of experimental work by Kitchell *et al.* (1986), which showed that *Terebra dislocata* could not feed through such a restricted opening. It is not yet known, however, how general this value is nor whether it is applicable here. In any case, in natural

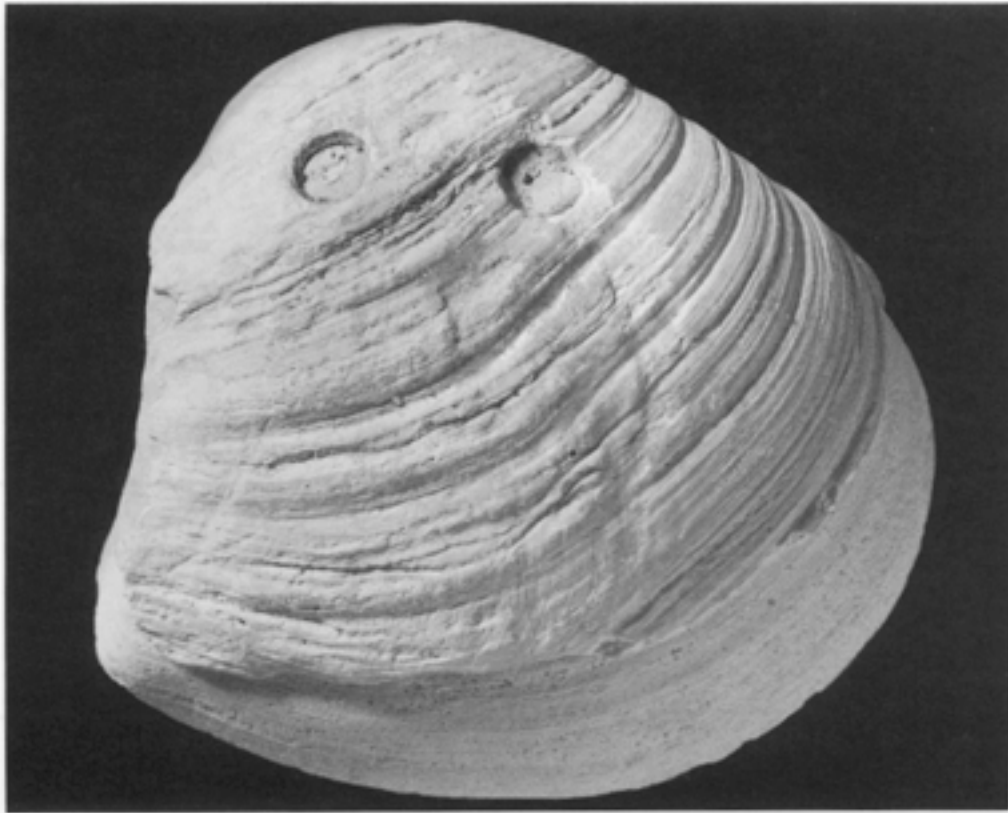
TABLE 1. Failure rate of boreholes calculated as by Vermeij (1987) and Vermeij *et al.* (1989). Those marked by symbols have been calculated from previously published data: ‡ = Anderson *et al.* (1991), * = Vermeij (1987), † = Cauwer (1985) and § = Adegoke and Tevesz (1974).

	Species	Locality	Failure rate
Plio/Pleistocene	<i>Varicorbula caloosae</i> (Dall)	Sarasoto	0.12‡
	<i>V. caloosae</i>	Davis	0.07‡
	<i>V. caloosae</i>	Forsberg	0.03‡
	<i>V. caloosae</i>	Punta Gorda	0.13‡
	<i>Corbula gibba</i> (Olivi)	Nicosia	0.40
	<i>C. inaequalis</i> Say	South Carolina	0.23
	<i>Carycorbula</i> spp.	Virginia	0.53*
Miocene	<i>C. carinata</i> Dujardin	Bordeaux	0.34
	<i>C. gibba</i>	Gironde	0.54
	<i>C. gibba</i>	Mellesdorf	0.86†
	<i>C. sericea</i> (Dall)	Bowden	0.33
Oligocene	<i>C. vectensis</i> Forbes	Isle of Wight	0.00
Eocene	<i>C. alabamiensis</i> Lea	Alabama	0.58
	<i>C. costata</i> (Sowerby)	Barton Beds	0.85
	<i>C. cuspidata</i> Sowerby	Barton Beds	0.20
	<i>C. cuspidata</i>	Headon Beds	0.19
	<i>C. murchisoniana</i> Lea	Alabama	0.53
	<i>C. pisum</i> Sowerby	Barton Beds	0.14
	<i>C. pisum</i>	Headon Beds	0.41
	<i>C. brabantina</i> Vincent	Oedelem	0.10†
	<i>C. rugosa</i> Lamarck	Parnes	0.33†
	<i>C. rugosa</i>	Grignon	0.41
	<i>V. amekiensis</i> (Eames)	Nigeria	0.11§
Paleocene	<i>C. regulbiensis</i> Morris	Thanet Sands	0.52
Cretaceous	<i>C. crassiplica</i> (Gabb)	Coon Creek (Camp.)	0.22†
	<i>C. crassiplica</i>	Mercers Hill (Camp.)	0.34†
	<i>C. substriatula</i> d'Orbigny	Vaals (Camp.)	0.23†
	<i>Corbula elegans</i> Sowerby	Blackdown (Albian)	0.00

conditions, even such a small complete perforation may be fatal even if it is abandoned, such as by metabolite leakage either attracting other predators or weakening the bivalve.

A total of 190 failed boreholes was observed. It is probable that some of the complete boreholes which occur close to the ventral edge of the right valve could have passed harmlessly through without penetrating flesh, and thus were also failures. However, it is not possible to be certain of these and, in any case, these failures cannot be attributed to the presence of conchiolin sheets. Table 1 lists failure rate for each of the major prey species studied. Following Vermeij (1987) and Vermeij *et al.* (1989) failure rate is expressed as a proportion (number of incomplete boreholes to total number of boreholes). In only *Corbula elegans* and *C. vectensis* were no failed boreholes observed; although failures were observed in the former by Taylor *et al.* (1983), they do not give sufficient data to calculate a proportion.

Most failed boreholes were shallow, penetrating less than half of the valve thickness. Most were flat bottomed lacking the characteristic central boss of incomplete naticid holes noted by Carriker and Yochelson (1968) and in many of these, termination of the hole coincides with intersection with

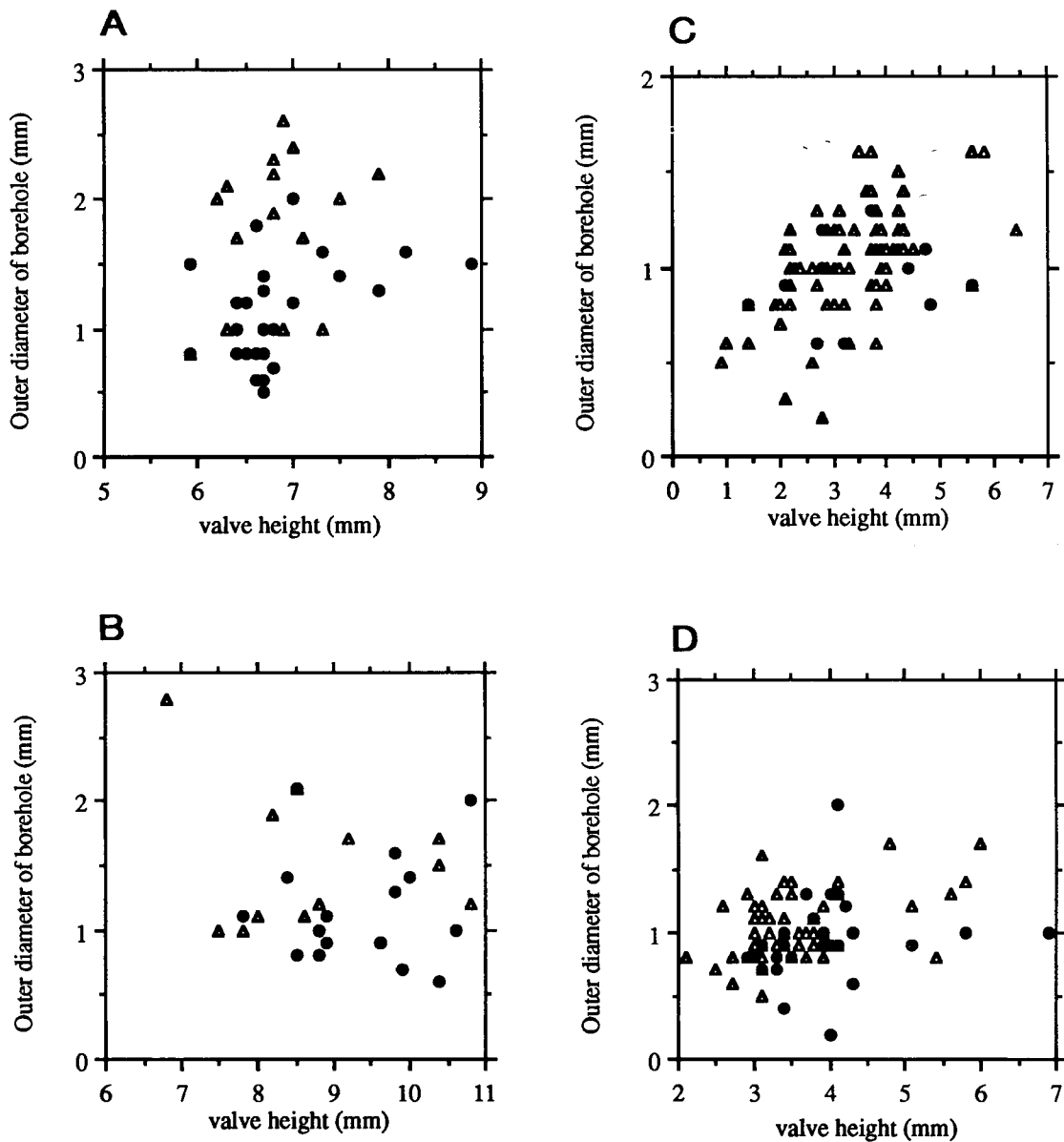


TEXT-FIG. 8. *Corbula idonea* bearing two failed boreholes; SM C.34210; Maryland; Miocene; the floor of the holes are flat bottomed rather than bossed, and are terminated at the level of the MCL, indicated by taphonomic splitting; $\times 3$.

a conchiolin sheet (Text-fig. 8). In other cases, boreholes terminated in the calcareous part of the shell having passed through, and been much restricted, by the conchiolin sheets.

Taking into account the preference for boring the right valve, the data from the seven species with more than ten failed boreholes were analysed by χ^2 -test taking the null hypothesis that failure occurs equally on right and left valves. Contrary to de Cauwer's (1985) assertion that failures occur more frequently on the left valve, no significant difference was found at the five per cent level. In order to determine whether failed boreholes occur randomly or are concentrated over specific parts of the valves, the tests for stereotyped borehole positioning used earlier were repeated this time using only the data for failed boreholes. No significant departures from the null hypothesis were found for three of the species but for Miocene *Corbula gibba* there were significantly higher numbers of failed boreholes in the more dorsal sectors ($P < 0.01$).

Kelley (1988) suggested that most failed boreholes resulted from small predators attempting prey items which were too large. There is no evidence for such over-ambition here. Using Wiltse's (1980) idea that predator size may be gauged from borehole size, the outer diameter of successful boreholes was plotted against valve height for the four most preyed upon species (Text-fig. 9). Although the correlation coefficients are not high, it does seem generally that larger prey was taken by the larger gastropods (although these larger predators will also take smaller items). Plotting the same information for failed boreholes reveals no notable differences and no evidence that they occur as smaller boreholes in larger prey. Failure was clearly due to another factor.



TEXT-FIG. 9. Valve height of victim plotted against the outer borehole diameter of successful (triangles) and failed (circles) boreholes. A, *Corbula regulbiensis* Morris; Paleocene; data from the Sedgwick Museum only; $\log y = 1.4 \log x - 0.9$, $r = 0.3$. B, *C. alabamiensis* Lea; Eocene; $\log y = -0.29 \log x + 0.43$, $r = 0.13$. C, *C. pisum* Sowerby; Eocene; $\log y = 0.49 \log x - 0.25$, $r = 0.5$. D, *C. gibba* (Olivi); Miocene; $\log y = 0.5 \log x - 0.26$, $r = 0.3$.

Has the proportion of failed attacks changed over geological time? Statistical analysis by the Permutation Test reveals no significant difference (at the five per cent level). The probability of failure was as high in the Cretaceous as in the subsequent periods. Indeed, from the Albian Blackdown Greensand, sixty six per cent of boreholes observed in *Corbula truncata* were failed, and

TABLE 2. The distribution of conchiolin sheets in Recent corbulids taken from a wide geographical range.

Species	Locality	Valve height (mm)	No. of major sheets	Maximum sheet thickness (μm)
60°–40°				
<i>Corbula gibba</i> (Olivi) SM X.24530	Millport, Scotland	8.5	1	< 10
<i>C. nucleus</i> Lamarck SM X.24540	Naples, Italy	7.5	1	30
<i>A. mediterranea</i> da Costa SM X.24531	S. of Rome, Italy	7.0	1	5
40°–20°				
<i>C. sp.</i> SM X.24537	Victoria, Australia	12.8	1	\leq 10
<i>C. sp.</i> SM X.24543	Suez	16.0	0	—
<i>C. crassa</i> Reeve SM X.24528	Hong Kong	—	2	18
<i>C. porcina</i> Lamarck SM X.24535	Montevideo, Uruguay	14.3	0	—
<i>Notocorbula zealandica</i> Quoy and Gaimard SM X.24532	Doubtless Bay, New Zealand	8.1	3	10
<i>Anisocorbula venusta</i> (Gould) SM X.24539	Honshu, Japan	6.0	4	10
<i>Varicorbula notalis</i> (Hinds) SM X.24545	Kyushu, Japan	4.8	1	8
<i>C. truncata</i> (Hinds) SM X.24531	Port Jackson, Australia	18.9	3	10
20°–0°				
<i>C. acutangular</i> Gray SM X.24533	Aden	7.1	3+	< 10
<i>C. sp.</i> SM X.24536	Queensland, Australia	10.7	1	12.5
<i>Aloidis dautzenbergi</i> (Lamarck) SM X.24538	Sierra Leone	11.0	2	10
<i>A. sulcata</i> (Lamarck) SM X.24541	Sierra Leone	15.1	1	30
<i>A. trigona</i> Hinds SM X.24542	Sierra Leone	9.5	1	10

from the same lithology Taylor *et al.* (1983) reported a single specimen of *C. elegans* bearing six incomplete boreholes.

Relatively few of the holed valves (seven per cent) had more than one borehole per valve. The vast majority of these multiply bored valves had only two boreholes with a maximum of three in two specimens. Kitchell *et al.* (1986) reserve the term 'multiple boreholes' for valves punctured by more than one complete perforation. Only two examples of this phenomenon were found, both in individuals of Miocene *Corbula gibba* bearing two complete holes each (both of which would have been deemed functional by Kitchell *et al.* 1986). A broader definition of 'multiple boreholes' is more useful when applied to an articulated specimen bearing more than one borehole (successful or failed) because these give an indication of the number of predation attempts per individual. Unfortunately, taphonomic and preparation processes limit this information; most holed specimens were disarticulated. However, of the eighty articulate bivalved specimens which did bear holes only seven were bored more than once, implying that few corbulids experienced more than one attack.

Geographical patterns in conchiolin sheets

The results of the survey of conchiolin sheets in Recent corbulids are shown in Table 2. In only two of the species did the specimens examined apparently lack conchiolin sheets (*Corbula sp.* from Suez, and *C. porcina* from Uruguay). In all others the basic distribution of major and subsidiary sheets was as described by Morton (1990) for *C. crassa*. It might be anticipated that major sheets would be more numerous in larger (and hence thicker) individuals, but this is not supported here. There is no clear latitudinal trend in the numbers of sheets observed, and no evidence that higher latitude taxa are better endowed. Although several of the low latitude specimens do show more conchiolin layers than those from higher latitudes, this is not statistically significant.

TABLE 3. Results of the direct microstructural survey of the preservation of conchiolin sheets in fossil corbulids. See also Plate 1.

Species	Age	Specimen details	Description of sheets
<i>Corbula gibba</i> (Olivi)	Holocene	Holland, SM X.24529	MCL very thin, < 10 μm (Pl. 1, fig. 1)
<i>C. striata</i> Walker and Boys	Pliocene	Suffolk, UK, SM X.24526	MCL present, <i>c.</i> 10 μm
<i>C. inaequalis</i> Say	Pliocene	S. Carolina, USA, SM X.24525	MCL present, < 10 μm
<i>C. carinata</i> Dujardin	Miocene	Bordeaux, France, SM X.24524	At least three major sheets, > 10 μm (Pl. 1, fig. 2)
<i>C. gibba</i>	Miocene	Bordeaux, France, SM X.24523	MCL very thin, < 10 μm
<i>C. sericea</i> (Dall)	Miocene	Jamaica, SM X.24522	None observed
<i>C. vectensis</i> Forbes	Oligocene	Isle of Wight, UK, SM X.24521	None observed
<i>C. alabamiensis</i> Lea	Eocene	Alabama, USA, SM X.24520	At least three major sheets, up to 20 μm (Pl. 1, fig. 5)
<i>C. costata</i> (Sowerby)	Eocene	Barton, UK, SM X.24519	At least four major sheets, > 10 μm
<i>C. cuspidata</i> Sowerby	Eocene	Barton, UK, SM X.24518	MCL visible to naked eye, > 10 μm
<i>C. ficus</i> (Solander)	Eocene	Barton, UK, SM X.24517	At least three major sheets, MCL visible to the naked eye, > 10 μm (Pl. 1, fig. 3)
<i>C. murchisoniana</i> Lea	Eocene	Alabama, USA, SM X.24516	MCL visible to the naked eye, > 20 μm (Pl. 1, fig. 4)
<i>C. pisum</i> Sowerby	Eocene	Barton, UK, SM X.24515	Vestiges of thin MCL < 5 μm
<i>C. regulbiensis</i> Morris	Paleocene	Thanet, UK, SM X.24514	MCL present, <i>c.</i> 10 μm
<i>C. crassiplica</i> (Gabb)	Cretaceous (Maastrichtian)	Georgia, USA, SM X.24527	MCL present, <i>c.</i> 10 μm
<i>C. angulata</i> (Phillips)	Cretaceous (Neocomian)	Speeton, UK, SM X.24513	None observed
<i>C. elegans</i> Sowerby	Cretaceous (Albian)	Blackdown, UK, SM X.24512	Silicified material, no sheet preservation
<i>C. gaultina</i> Pictet and Campiche	Cretaceous (Albian)	Folkestone, UK, SM X.24511	None observed
<i>C. striatula</i> Sowerby	Cretaceous (Albian)	Atherfield, UK, SM X.24510	None observed
<i>C. truncata</i> Sowerby	Cretaceous (Albian)	Blackdown, UK, SM X.24509	Silicified material, no sheet preservation
<i>C. chilmarkensis</i> Cox	Jurassic (Portlandian)	Tisbury, UK, SM X.24508	Neomorphosed, no sheet preservation
<i>C. fallax</i> Contejean	Jurassic (Kimmeridgian)	Market Rasen, UK, SM X.24507	Neomorphosed, no sheet preservation
<i>C. hulliana</i> Morris	Jurassic (Forest Marble)	Kirtlington, UK, SM X.24506	Neomorphosed, no sheet preservation
<i>Jurassicorbula edwardi</i> (Sharpe)	Jurassic (Kimmeridgian)	Santa Cruz, Portugal, SM X.24505	Well preserved microstructure but no sign of sheets
<i>J. edwardi</i>	Jurassic (Kimmeridgian)	Praia Areia Branca, Portugal, SM X.24504	Well preserved microstructure but no sign of sheets

Appearance of the conchiolin sheets in fossil corbulids

Direct microstructural evidence. With good preservation it is possible to recognize the presence of conchiolin sheets, but this is not true for specimens in which the aragonite has been replaced by either drusy calcite or silica. In some cut specimens, the MCL (at least) is visible to the naked eye as a dark brown line within the shell (e.g. Eocene *Corbula ficus* SM X.24517b) but in the majority of specimens it was only identifiable by SEM. Care must be taken not to confuse possible conchiolin sheets with myostracal layers. The latter are distinguishable by their prismatic structure and more curved trajectories, which terminate at the pallial and adductor muscle scars. Conchiolin sheets are in contrast frequently amorphous or sometimes granular, often of varying width, and coalesce with one another. Table 3 records the results of the SEM survey and Plate 1 displays some of the evidence for preserved conchiolin sheets. In Tertiary material at least, one sheet (the MCL) was clear and in some species (e.g. Miocene *Corbula carinata* and *C. alabamiensis*) there are multiple sheets. Sheets were less easy to recognize in *C. gibba* and no sign of their presence was found in Oligocene *C. vectensis*. X-ray micro-analysis of the sheets in Eocene *C. ficus* reveals that they are preserved in calcium carbonate but have an iron signature not found in the crossed lamellar aragonite on either side of the MCL. The oldest conchiolin sheets were noted in Maastrichtian *C. crassiplica* (Pl. 1, fig. 6). Unfortunately, early Cretaceous *C. elegans* and *C. truncata* from the Blackdown Greensand, as noted by Taylor *et al.* (1983), were silicified with no relict microstructure, but other early Cretaceous specimens of *C. gaultina* and *C. striatula* did have preserved microstructure but had no sign of conchiolin sheets. Most Jurassic specimens lacked original mineralogy and structure, but some specimens of *Jurassicorbula edwardsii* collected by Fürsich and Werner from the Kimmeridgian of Portugal show fine preservation of the aragonite microstructure, but again no sign of conchiolin sheets.

Indirect methods. Species, in which the presence of conchiolin sheets may be inferred from the presence of an internal furrow or by taphonomic splitting, are marked accordingly in Appendix 1. For all Tertiary and Late Cretaceous taxa for which a significant number of specimens were examined, conchiolin sheets were suggested by one or, more often, both indicators, providing strong evidence for the presence of the MCL. Many Early Cretaceous specimens were furrowed, as was noted by Lewy and Samtleben (1979) for *Corbula elegans*, but, despite examination of 854 individuals, no positive sign of taphonomic splitting was apparent. There was no evidence of either indicator from the Jurassic.

INTERPRETATIONS

The results from each of the three approaches have been interpreted as follows.

Borehole survey

Recent levels of gastropod predation on corbulids were reached by the Late Cretaceous, very early in the history of boring. These findings agree with the previous studies of de Cauwer (1985) and Allmon *et al.* (1990), but not those of Kelley and Hansen (1993) who found that boring frequency remained low throughout the Cretaceous, rising sharply at the K-T boundary. Likelihood of borehole failure has not increased significantly over geological time.

Geographical distribution of conchiolin sheets

There is no evidence that corbulids which inhabit colder waters have better developed conchiolin sheets as an adaptation against shell dissolution. Although some high latitude taxa do have numerous and thick sheets, there is no statistically significant equatorward increase in their development.

Temporal distribution

Amalgamating both the direct and indirect evidence, it is clear that conchiolin sheets in corbulids were not present in the Jurassic but had become well developed by the Late Cretaceous. Evidence for the conchiolin sheet in Early Cretaceous corbulids is equivocal, restricted to inference from the furrowed right valve. As noted earlier, this is the weakest criterion for recognition of the MCL and, in isolation, cannot be taken as positive indication of its presence. It is probable that, in these taxa, thin conchiolin sheets were present but that they were not thick enough either to be detected by SEM or to cause taphonomic splitting. Selection pressures favouring the evolution of conchiolin sheets, as an adaptation to retard shell dissolution and non-predatory borers and to prevent crack propagation, have been operational since at least the early Mesozoic with no increase in intensity at the beginning of the Cretaceous. However, pressure to acquire defences from predatory borers rose sharply at that time. The first well developed MCL coincides with this increase in predation pressure and it is thus suggested that conchiolin sheets evolved as a primary adaptation to that threat. It is likely that earlier corbulids did possess some vestiges of organic layers in their shells but these are not uncommon in other bivalves (personal observation) and it is unlikely that such thin sheets could have provided an effective barrier against borers or dissolution. Once acquired, however, well developed conchiolin sheets would have had additional value in these other ways. They may also have had a profound effect on the evolution of corbulid overall morphology by allowing the valves to become grossly discordant. Coincidence of the MCL with the furrow into which the left valve fits, greatly facilitates the hermetic seal during adduction (Lewy and Samtleben 1979). Early corbulids (prior to the appearance of the MCL) are notably less inequivalve and less discordant than their descendants. Vermeij (1987) regarded discordance in bivalves itself as a defensive adaptation, providing a wide expanse of valve margin which may be damaged without harming the hermetic seal. However, Yonge (1946) observed that this grossly inequivalve shape has contributed to the poor burrowing ability of these bivalves and hence has precluded escape as an effective defence.

It might be expected that early gastropod borers were inefficient predators and the high rate of failure sustained in the Cretaceous reflects this, but that later failures were due to enhanced prey defences. However, as noted by Taylor *et al.* (1983), the earliest known Albian borings already reveal well established predatory behaviours, such as preference for the right valve. Failure rate has remained relatively constant over geological time and so any 'improvement' in corbulid defence must have occurred as part of an 'arms race' in tandem with increased predator efficiency rather than by the sudden evolution of a wonder trait.

DISCUSSION

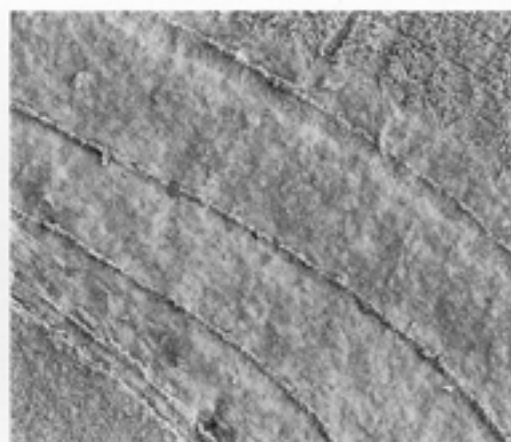
In the evolution of prey taxa, predation failure is an important process; high failure rates in species which display variability in their defences is likely to lead to selection of anti-predatory traits (Vermeij 1982). With particular reference to boring predation, Vermeij suggested that naticid gastropods seldom fail to complete their attack once they have seized their prey, and therefore the

EXPLANATION OF PLATE 1

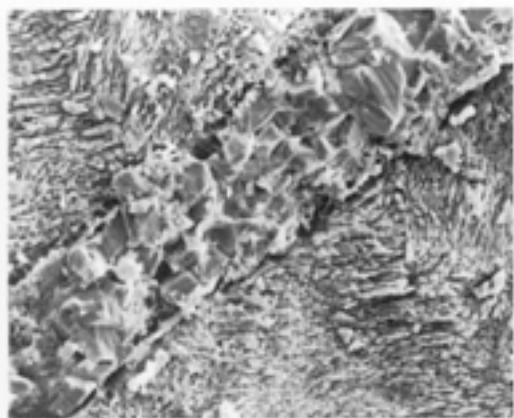
Figs 1-6. Preservation of conchiolin sheets in fossil corbulids. 1, *Corbula gibba* (Olivi); SM X.24529; Holocene; shell banks, Westerschelde, Holland; $\times 250$. 2, *C. carinata* Dujardin; SM X.24524; Miocene; Bordeaux, France; $\times 80$. 3, *C. ficus* (Solander); SM X.24517; Barton Beds, Eocene; Barton, UK; $\times 800$. 4, *C. murchisoniana* Lea; SM X.24516; Claiborne Formation, Eocene; Alabama, USA; $\times 230$. 5, *C. alabamiensis* Lea; SM X.24520; Claiborne Formation, Eocene; Alabama, USA; $\times 900$. 6, *C. crassiplica* (Gabb); SM X.24527; Maastrichtian; Georgia, USA; $\times 130$.



1



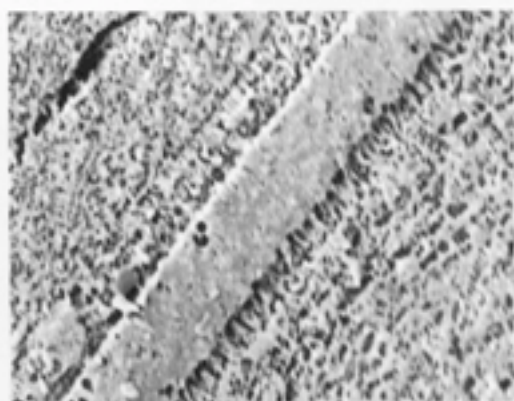
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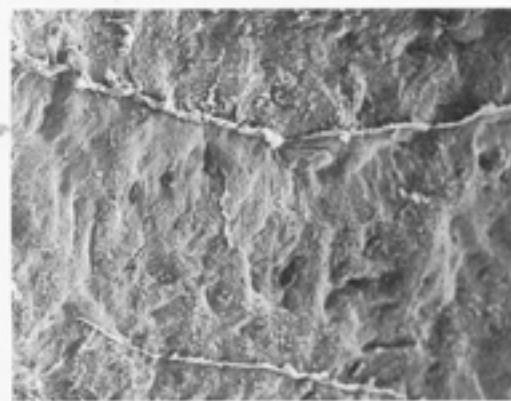
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5



6

HARPER, corbulid conchiolin sheets

chief line of defence against these predators is evasion of detection and of engulfment by the gastropod foot. Being slow burrowers, however, corbulids cannot escape and thus must rely on passive constructional defences, which retard the boring process to make them unprofitable prey. As de Cauwer (1985) pointed out, the high number of failed boreholes in corbulids attests not only to their success in foiling predation attempts but also to their initial vulnerability to attack (although it may also reflect longevity). But are corbulids really more resistant to attack than most other bivalves and how important are conchiolin sheets in their defence?

Vermeij (1987) and Vermeij *et al.* (1989) calculated the proportion of boring attempts that end in failure, and used this as an index of the effectiveness of the prey's defences. There are several flaws to this approach when applied to small sample sizes; failure may be related to factors other than prey defence (e.g. changing environmental conditions and predation or competition affecting the would-be predator itself) and it takes no account of attacks terminated before their traces are readily detectable to the investigator. Nevertheless corbulids do tend to show high values for this parameter. Vermeij (1987, table 11.5) provided data for the proportions of failed boreholes in a number of infaunal bivalves of Plio-Pleistocene, Miocene and Eocene age. In order to ascertain whether corbulids of the same ages were more or less susceptible to successful predation, the data in Table 1 were compared with Vermeij's non-corbulid data using the Permutation Test. Significantly higher failure rates in corbulids were discovered for the Miocene and Eocene (both at the five per cent level) but not for the Plio-Pleistocene. Although Morton (1990) considered that *Corbula crassa* is 'virtually immune from gastropod predation' in Tolo Channel, his study was restricted to live individuals which had evaded death and he did not record the incidence of complete boreholes in empty shells. Conchiolin sheets do not confer complete defence; sixty five per cent of all boreholes in the current survey were successful.

Conchiolin sheets may not be the only means by which corbulids gain defence. Possession of (i) a thickened periostracum and (ii) thickened valves may also slow boring and therefore promote failure.

Corbulids do possess thick periostraca; values of over 100 μm have been recorded for both *Corbula gibba* and *C. crassa* (Harper, unpublished data). I have found no evidence for the periostracum being thicker on the left valve than on the right, as suggested by de Cauwer (1985), although that of the right was often more abraded, particularly on the older part of the shell. This latter observation might explain the frequently expressed preference for boring the right valve.

Kelley (1989) reported that in the Miocene *C. idonea* there was an eight per cent increase in thickness over a three million year period, which she attributed to predation pressure. Crossed and complex crossed lamellar aragonite microstructures have a low organic content (Taylor and Layman 1972) and are thus metabolically cheap and rapid to lay down (Gabriel 1981), ideal for thick shells. These microstructures also fared well against Gabriel's simulated ABO attack, despite their low organic content. However, the case for increased shell thickness as a defence against boring predators, although appealing, is far from proven. Stereotyped borehole positioning in the umbonal region means that the borers often select the thicker part of the shell (Harper and Skelton 1993b), and Kabat (1990) noted that naticids have no known mechanism for gauging prey thickness. Boggs *et al.* (1984) experimentally showed that the naticid *Polinices* was unable to detect and select *Mercenaria* with artificially thinned valves.

In recent years there has been much debate over whether naticid predation of corbulids occurs less frequently and less predictably than suggested by the models of Kitchell *et al.* (1981), whether attacks fail more often than with other prey and what role the conchiolin sheets play in these anomalies (Kitchell *et al.* 1986; Kelley 1988, 1989; Anderson *et al.* 1991; Anderson 1992). It seems unnecessary to consider anomalous predation patterns and high failure rate together; the two need not be related. Given the interest in corbulid predation, there is a surprising lack of experimental information on how long it takes various gastropods to detect, bore and consume corbulid prey, and no assessment of the energy yield gained from these prey. Does the amount of energy gained from consuming a corbulid outweigh difficulties in detection and boring? Additionally, previous studies on muricids boring bivalve prey have shown that stereotypic predatory behaviour results from

experienced individual predators and that inexperienced individuals do not feed in a predictable pattern (Hughes and Dunkin 1984); the possibility of experience being equally important for naticids needs to be addressed.

The presence of conchiolin sheets may affect some aspects of predation but not others. Although conchiolin sheets do cause a high failure rate, they are unlikely to explain the non-stereotypic borehole positioning reported by Kelley (1988). The morphology of the failed boreholes studied suggests that most terminate at the MCL. Since the MCL covers the entire valve, there is no advantage to boring at random locations in order to try and avoid conchiolin patches.

A frequent objection to assigning defensive value to conchiolin sheets is that failure rate is often highly variable (Anderson *et al.* 1991; Anderson 1992). Although in this survey failure rate was zero to eighty five per cent, zero failures were recorded in only two taxa (*Corbula elegans* in which Taylor *et al.* (1983) do record high failure rates, and *C. vectensis* which has very thin valves) and in the remaining species failure was more common. Another reason why Anderson (1992) rejected the importance of conchiolin sheets is that anomalous predation is also found in bivalve taxa which lack them. Harper and Skelton (1993a) demonstrated a range of means by which bivalves are known to gain defence from the attentions of boring gastropods (shell microstructure, periostracal fabric, valve thickness, valve ornament, behavioural modification, acquired toxicity, camouflage and active escape). Possession of conchiolin sheets is just one possibility; various bodyplan constraints prevent some clades from evolving some defensive adaptations but preadapts them for others. Not all infaunal bivalves are preadapted for this particular defensive strategy.

Function of conchiolin sheets in other bivalve taxa

Well developed conchiolin sheets have been acquired independently in other bivalves but there is no requirement that they too should also have evolved in response to predation pressure. It is most unlikely that borers (either predators or endoliths) were responsible for their evolution in the unionoids. In his review of borers, Kabat (1990) documented few examples in freshwater habitats. It is more likely here that the sheets are a protective adaptation against shell dissolution, as suggested by Tevesz and Carter (1980), Kat (1983) and Isaji (1993).

A survey of Recent genera has revealed conchiolin sheets in some species of the ostreid genera *Alectryonella*, *Crassostrea*, *Ostrea*, *Saccostrea* and *Striostrea* as well as the gryphaeids *Hytissa* and *Neopycnodonte*, although they are frequently less well developed than those reported in *Saccostrea cucullata* (Taylor 1990). It is unclear whether conchiolin sheets are a synapomorphic character of the Ostreoidea (in which case we might expect them to be apparent by the Jurassic) or whether they were independently acquired in the Ostreidae and Gryphaeidae (in which case they would appear later and probably at separate times). What is the primary function of these sheets in oysters? Taylor (1990) demonstrated that the sheets in *Saccostrea cucullata* provided defence against boring muricid gastropods, whilst Korringa (1951) suggested their function in *Ostrea edulis* was to deter polydorid polychaete borings. According to Hudson and Palmer (1976), significant moments in oyster evolution occurred in euryhaline habitats, where selection pressure to acquire conchiolin sheets to prevent shell dissolution would have been high. Resolution of these questions could be achieved by conducting a study similar to that above. This should be easier than for corbulids, as oysters are predominantly composed of calcite rather than aragonite so there is no loss of information due to diagenetic dissolution and recrystallization. Positive identification of conchiolin sheets may be hampered, however, by the fact that many oyster shells contain fluid filled chambers and chalky layers (Korringa 1951), and there appears to be no morphological expression of the sheets such as the furrow in corbulids. If these problems can be overcome such a study may prove fruitful.

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REFERENCES

- ADEGOKE, O. S. and TEVESZ, M. J. 1974. Gastropod predation patterns in the Eocene of Nigeria. *Lethaia*, **7**, 17–24.
- ALLMON, W. D., NIEH, J. C. and NORRIS, R. D. 1990. Drilling and peeling of turrilline gastropods since the Late Cretaceous. *Palaeontology*, **33**, 595–611.
- ANDERSON, L. C. 1992. Naticid gastropod predation on corbulid bivalves: effects of physical factors, morphological features, and statistical artifacts. *Palaios*, **7**, 602–620.
- GEARY, D. H., NEHM, R. H. and ALLMON, W. D. 1991. A comparative study of naticid gastropod predation on *Varicorbula caloosae* and *Chione cancellata*, Plio-Pleistocene of Florida, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **85**, 29–46.
- ANSELL, A. D. 1969. Defensive adaptations to predation in the Mollusca. *Proceedings of the Symposium on Mollusca*, **2**, 487–512.
- ARUA, I. 1989. Gastropod predators and their dietary preference in an Eocene molluscan fauna from Nigeria. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **72**, 283–290.
- BOGGS, C. H., RICE, J. A., KITCHELL, J. A. and KITCHELL, J. F. 1984. Predation at a snail's pace: what's time to a gastropod? *Oecologia*, **62**, 13–17.
- BROMLEY, R. G. 1993. Predation habits of octopus past and present and a new ichnospecies. *Oichnus ovalis*. *Bulletin of the Geological Society of Denmark*, **40**, 167–173.
- CARRIKER, M. R. 1981. Shell penetration and feeding by naticacean and muricacean gastropods: a synthesis. *Malacologia*, **20**, 403–422.
- and YOCHELSON, E. 1968. Recent gastropod boreholes and Ordovician cylindrical borings. *Professional Papers of the United States Geological Survey*, **593B**, 1–26.
- CARTER, R. M. 1968. On the biology and palaeontology of some predators of bivalved Mollusca. *Palaeogeography, Palaeoclimatology and Palaeoecology*, **4**, 29–65.
- CAUWER, G. DE 1985. Gastropod predation on corbulid bivalves; palaeoecology or taphonomy? *Annales de la Société Royale Zoologique de Belgique*, **115**, 183–196.
- DUDLEY, E. C. and VERMEIJ, G. J. 1978. Predation in time and space: drilling in the gastropod. *Turritella*. *Paleobiology*, **4**, 436–441.
- FISCHER, P. H. 1963. Corbules fossiles perforées par des gastéropodes prédateurs. *Journal de Conchyliologies*, **103**, 29–31.
- FÜRSICH, F. T. and JABLONSKI, D. 1984. Late Triassic naticid drillholes: carnivorous gastropods gain a major adaptation but fail to radiate. *Science*, **224**, 78–80.
- GABRIEL, J. M. 1981. Differing resistance of various mollusc shell material to simulated whelk attack. *Journal of Zoology*, **194**, 363–369.
- GOULD, S. J. and VRBA, E. S. 1982. Exaptation – a missing term in the science of form. *Paleobiology*, **8**, 4–15.
- HALLAM, A. 1976. Stratigraphic distribution and ecology of European Jurassic bivalves. *Lethaia*, **9**, 245–259.
- HARPER, E. M. 1991. The role of predation in the evolution of the cemented habit in bivalves. *Palaeontology*, **34**, 455–460.
- and SKELTON, P. W. 1993a. The Mesozoic Marine Revolution and epifaunal bivalves. *Scripta Geologica, Special Issue*, **2**, 127–153.
- — 1993b. A defensive value of the thickened periostracum in the Mytiloidea. *The Veliger*, **36**, 36–42.
- HOFFMAN, A., PISERA, A. and RYSZKIEWICZ, M. 1974. Predation by muricid and naticid gastropods on the Lower Tortonian mollusks from the Korytnica clays. *Acta Geologica Polonica*, **24**, 249–260.
- HUDSON, J. D. and PALMER, T. J. 1976. A euryhaline oyster from the middle Jurassic and the origin of the true oysters. *Palaeontology*, **19**, 79–93.
- HUGHES, R. N. and DUNKIN, S. DE B. 1984. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.) feeding on mussels in the laboratory. *Journal of Experimental Marine Biology and Ecology*, **77**, 45–68.
- ISAJI, S. 1993. Formation of organic sheets in the inner shell layer of *Geloina* (Bivalvia: Corbiculidae): an adaptive response to shell dissolution. *The Veliger*, **36**, 166–173.
- JEFFREYS, J. G. 1865. *British conchology III*. John Van Voorst, London, 393 pp.
- KABAT, A. R. 1990. Predatory ecology of naticid gastropods with a review of shell boring. *Malacologia*, **32**, 155–193.

- KAT, P. W. 1983. Conchiolin layers among the Unionidae and Margaritiferidae (Bivalvia): microstructural characteristics and taxonomic implications. *Malacologia*, **24**, 298–311.
- KELLEY, P. H. 1988. Predation by Miocene gastropods of the Chesapeake Group: stereotyped and predictable. *Palaios*, **3**, 436–448.
- 1989. Evolutionary trends within bivalve prey of Chesapeake Group naticid gastropods. *Historical Biology*, **2**, 139–156.
- and HANSEN, T. A. 1993. Evolution of the naticid gastropod predator–prey system: an evaluation of the hypothesis of escalation. *Palaios*, **8**, 358–375.
- KENT, R. M. L. 1981. The effect of *Polydora ciliata* on the shell strength of *Mytilus edulis*. *Journal du Conseil International pour l'Exploration de la Mer*, **39**, 252–257.
- KITCHELL, J. A., BOGGS, C. H., KITCHELL, J. F. and RICE, J. A. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology*, **7**, 533–552.
- — — RICE, J. A., KITCHELL, J. F., HOFFMAN, A. and MARTINELL, A. 1986. Anomalies in naticid predatory behavior: a critique and experimental observations. *Malacologia*, **27**, 291–298.
- KORRINGA, P. 1951. On the nature and function of 'chalky' deposits in the shell of *Ostrea edulis*. *Proceedings of the California Academy of Sciences, Series 4*, **27**, 133–158.
- LEWY, Z. and SAMTLEBEN, C. 1979. Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia*, **12**, 341–351.
- LOGAN, A. 1974. Morphology and life habits of the Recent cementing bivalve *Spondylus americanus* Hermann from the Bermuda Platform. *Bulletin of Marine Science*, **24**, 568–594.
- MASLIN, J. L. 1989. The salinity tolerance of *Corbula trigona* (Bivalvia: Corbulidae) from a west-African lagoon and its variations. *Archiv für Hydrobiologie*, **117**, 205–223.
- MOORE, R. C. 1969. *Treatise of invertebrate paleontology, Part N (1–3)*. University of Kansas and Geological Society of America, Lawrence, Kansas and Boulder, Colorado, 952 pp.
- MORGAN, P. R. 1972. *Nucella lapillus* (L.) as a predator of edible cockles. *Journal of Experimental Marine Biology and Ecology*, **8**, 45–52.
- MORTON, B. 1990. The biology and functional morphology of *Corbula crassa* (Bivalvia: Corbulidae) with special reference to shell structure and formation. 1055–1073. In MORTON, B. (ed.). *Proceedings of the second international marine biological workshop: the marine flora and fauna of Hong Kong and Southern China, Hong Kong, 1986*. Hong Kong University Press, Hong Kong, 1268 pp.
- PONDER, W. F. and TAYLOR, J. D. 1992. Predatory shell drilling by two species of *Austroginalla* (Gastropoda: Marginellidae). *Journal of Zoology*, **228**, 317–328.
- PRICE, D. 1984. Computer-based storage and retrieval of palaeontological data at the Sedgwick Museum, Cambridge, England. *Palaeontology*, **27**, 393–405.
- ROBBA, E. and OSTINELLI, F. 1975. Studi paleoecologici sul Pliocene ligure, I. Testimonianze di predazione sui molluschi Plioceni di Albenga. *Rivista Italiana Paleontologia*, **81**, 309–372.
- SIEGEL, S. and CASTELLAN, N. J. 1988. *Nonparametric statistics for the behavioral sciences*. McGraw Hill, New York, 399 pp.
- SPEDEEN, I. G. 1970. The type Fox Hills Formation, Cretaceous (Maestrichtian), South Dakota. Part 2: systematics of the Bivalvia. *Bulletin of the Peabody Museum of Natural History*, **33**, 1–222.
- STANLEY, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Memoir of the Geological Society of America*, **125**, 1–296.
- TAYLOR, J. D. 1970. Feeding habits of predatory gastropods in a Tertiary (Eocene) molluscan assemblage from the Paris Basin. *Palaeontology*, **13**, 254–260.
- 1990. Field observations of prey selection by the muricid gastropods *Thais clavigera* and *Morula musiva* feeding on the intertidal oyster *Saccostrea cucullata*. 837–855. In MORTON, B. S. (ed.). *Proceedings of the second international marine biological workshop: the marine flora and fauna of Hong Kong and Southern China, Hong Kong, 1986*. Hong Kong University Press, Hong Kong, 1268 pp.
- CLEEVELY, R. J. and MORRIS, N. J. 1983. Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. *Palaeontology*, **26**, 521–533.
- KENNEDY, W. J. and HALL, A. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea-Trigoniacea. *Bulletin of the British Museum (Natural History), Zoology Series, Supplement*, **3**, 1–125.
- — — 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea, Conclusions. *Bulletin of the British Museum (Natural History), Zoology Series*, **22**, 225–294.
- and LAYMAN, M. 1972. The mechanical properties of bivalve (Mollusca) shell structures. *Palaeontology*, **15**, 73–87.

- TAYLOR, J. D. and TAYLOR, C. N. 1977. Latitudinal distribution of predatory gastropods on the eastern Atlantic shelf. *Journal of Biogeography*, **4**, 73–81.
- TEVESZ, M. J. and CARTER, J. G. 1980. Environmental relationships of shell form and structure of unionacean bivalves. 295–322. In RHOADS, D. C. and LUTZ, R. A. (eds.). *Skeletal growth of aquatic organisms*. Plenum Press, New York and London, 750 pp.
- VERMEIJ, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **2**, 245–258.
- 1982. Unsuccessful predation and evolution. *The American Naturalist*, **120**, 701–720.
- 1983. Traces and trends in predation with special reference to bivalved animals. *Palaeontology*, **26**, 455–465.
- 1987. *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton, New Jersey, 527 pp.
- DUDLEY, E. C. and ZIPSER, E. 1989. Successful and unsuccessful drilling predation in Recent pelecypods. *The Veliger*, **32**, 266–273.
- VOKES, H. W. 1945. Supraspecific groups of the pelecypod family Corbulidae. *Bulletin of the American Museum of Natural History*, **86**, 1–32.
- WILTSE, L. W. 1980. Predation by juvenile *Polinices duplicatus* (Say) on *Gemma* (Totten). *Journal of Experimental Marine Biology and Ecology*, **42**, 187–199.
- YONGE, C. M. 1946. On the habits and adaptations of *Aloidis* (*Corbula*) *gibba*. *Journal of the Marine Biological Association*, **26**, 358–376.
- ZIEGELMEIER, E. 1954. Beobachtungen über den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda Prosobranchia). *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **5**, 1–33.

ELIZABETH M. HARPER

Department of Earth Sciences
Downing Street
Cambridge CB2 3EQ, UK

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APPENDIX 1

Raw data on boring frequencies and stratigraphical information for the corbulids studied. [F] and [T] indicate species in which an internal furrow, and taphonomic splitting, respectively, have been observed. Information in round brackets refers to valve preference; X = no preference, R = preference for the right valve where $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$.

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Jurassic					
<i>C. attenuata</i> Lycett	Forest Marble, Minchinhampton, UK	101	0	—	—
<i>C. bayani</i> de Loriol	Portland Clay, Swindon, UK	10	0	—	—
<i>C. buckmani</i> Lycett	Great Oolite, Minchinhampton, UK	26	0	—	—
<i>C. chilmarkensis</i> Cox	Portland Oolite, Portland, UK	18	0	—	—
<i>C. deshayesea</i> Skeat	Jutland, Denmark	9	0	—	—
<i>C. fallax</i> Contejean	Kimmeridge Clay, Market Rasen, UK	32	0	—	—
<i>C. hulliana</i> Morris	Great Oolite, Kirtlington, UK	29	0	—	—
<i>C. involuta</i> Münster	Forest Marble, Laycock, UK	2	0	—	—
<i>C. islipiensis</i> Lycett	Forest Marble, Laycock, UK	1	0	—	—
<i>C. lyrata</i> Sowerby	Kutch, India	6	0	—	—
<i>C. macneilli</i> Morris	Oxford Clay, Studley, UK	26	0	—	—
<i>C. pectinata</i> Sowerby	Kutch, India	50	0	—	—
<i>C. sp.</i>	Various	26	0	—	—
<i>Corbulomima suprajurensis</i> (d'Orbigny)	Kimmeridgian, Santa Cruz, Portugal	2	0	—	—

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
<i>Jurassicorbula edwardii</i> (Sharpe)	Kimmeridgian, Santa Cruz, Portugal	4	0	—	—
Also examined: blocks of <i>C. hebreatica</i> Tate (Great Estuarine Group) and <i>C. alata</i> Sowerby (Purbeck Beds, Swanage, UK).					
Cretaceous					
<i>C. angulata</i> (Phillips)	Neocomian, Speeton Clay, Speeton, UK	50	0	—	—
<i>C. elegans</i> Sowerby [F]	Albian, Blackdown, UK	667	18(R***)	18	0
<i>C. gaultina</i> Pictet and Campiche	Gault, Folkstone, UK	7	0	—	—
<i>C. striatula</i> Sowerby [F]	Aptian, Lower Greensand, Atherfield, UK	127	0	—	—
<i>C. truncata</i> [F]	Albian, Blackdown, UK	53	9(X)	3	6
<i>C. truncata</i>	Cenomanian, Dunscombe and Chard, UK	4	0	—	—
Also examined: <i>C. crassiplica</i> (Gabb) [F, T] (Coon Creek, Washington, Maastrichtian); <i>C. sp</i> [F, T] (Gosau, Upper Cretaceous) and <i>C. truncata</i> [F] (Bracquegrives, Belgium, Albian).					
Paleocene					
<i>C. regulbiensis</i> Morris [F, T]	Thanet Sands, Herne Bay, Kent, UK	592	77(X)	37	40
Eocene					
<i>C. alabamiensis</i> Lea [F, T]	Claiborne Formation, Alabama, USA	231	31(R*)	13	18
<i>C. aldrichi</i> Meyer [F, T]	Woods Bluff, Alabama, USA	29	6(R*)	4	2
<i>C. ampullacea</i> (Deshayes)	Paris Basin, Grignon, France	1	0	—	—
<i>C. anantina</i> (Lamarck)	Paris Basin, Grignon, France	3	0	—	—
<i>C. arnouldi</i> Woods	Negritos, Peru	54	1	1	0
<i>C. angulata</i> (Lamarck)	Paris Basin, Grignon, France	5	0	—	—
<i>C. bicarinata</i> Conrad	Mississippi, USA	14	0	—	—
<i>C. costata</i> (Sowerby) [F, T]	Barton Clay, Barton, UK	27	13(R*)	2	11
<i>C. cuspidata</i> Sowerby [F, T]	London Clay, Portsmouth, UK	11	0	0	0
<i>C. cuspidata</i> [F, T]	Bracklesham Beds, Barton, UK	21	3	2	1
<i>C. cuspidata</i> [F, T]	Barton Clay, Hampshire, UK	169	15(X)	12	3
<i>C. cuspidata</i> [F, T]	Headon Beds, Hampshire, UK	140	21(X)	17	4
<i>C. densata</i> Conrad	Mississippi, USA	4	0	—	—
<i>C. exarata</i> (Deshayes)	Paris Basin, France	1	0	—	—
<i>C. ficus</i> (Solander) [F, T]	Barton Clay, Barton, UK	44	4	1	3
<i>C. gallica</i> (Lamarck)	Paris Basin, Grignon, France	15	0	—	—
<i>C. gallica</i>	Barton Beds, Barton, UK	27	0	—	—
<i>C. lamarckii</i> Deshayes	Barton Beds, Bunny Beacon, UK	7	0	—	—
<i>C. longirostris</i> Deshayes [F, T]	Barton Beds, Barton, UK	31	1	1	0
<i>C. murchinsonia</i> Lea [F, T]	Claiborne, Alabama, USA	119	17(R**)	8	9
<i>C. nastua</i> Conrad [F, T]	Claiborne, Alabama, USA	13	3	1	2
<i>C. nitida</i> Sowerby [F, T]	Headon Beds, Brockenhurst UK	6	1	1	0
<i>C. oniscus</i> Conrad [F]	Claiborne, Alabama, USA	45	2	2	0

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
<i>C. peruviana</i> Woods	Negritos, Peru	54	1	0	0
<i>C. pisum</i> Sowerby [F]	London Clay, Portsmouth, UK	182	8	6	2
<i>C. pisum</i> [F]	Headon Beds, Hampshire, UK	15	2	2	0
<i>C. pisum</i> [F]	Barton Beds, Barton, UK	664	74(R***)	64	10
<i>C. pisum</i> [F]	Headon Beds, Hampshire, UK	394	17(R*)	10	7
<i>C. revoluta</i> (Brocchi) [F]	Barton Beds, Barton, UK	45	4	3	1
<i>C. striata</i> Deshayes [F]	Bracklesham Beds, Barton, UK	18	0	—	—
<i>C. striata</i> [F]	Barton Clay, Barton, UK	47	3	2	1
<i>C. waringi</i> Woods	Negritos, Peru	8	0	—	—
Oligocene					
<i>C. alta</i> Conrad	Vicksburg, Mississippi, USA	7	0	—	—
<i>C. descendens</i> Forbes [F]	Isle of Wight, UK	42	0	—	—
<i>C. engonata</i> Conrad	Vicksburg, Mississippi, USA	13	0	—	—
<i>C. gibba</i> (Olivi) [F]	Berg, Belgium	42	1	0	1
<i>C. gibba</i> [F]	Isle of Wight, UK	42	0	—	—
<i>C. laqueata</i> Conrad [F, T]	Vicksburg, Mississippi, USA	27	1	1	0
<i>C. pisum</i> Sowerby	Isle of Wight, UK	11	0	—	—
<i>C. rotunda</i> Sowerby	Kassel, Germany	2	0	—	—
<i>C. rugosa</i> Lamarck	Kassel, Germany	5	0	—	—
<i>C. subpisum</i> Sowerby	Isle of Wight, UK	10	1	1	0
<i>C. vectensis</i> Forbes [F, T]	Isle of Wight, UK	497	11(X)	11	0
Miocene					
<i>C. canaliculata</i> Hutton [F, T]	Canterbury, New Zealand	4	1	1	0
<i>C. carinata</i> Dujardin [F, T]	Bordeaux, France	387	32(X)	21	11
<i>C. elevata</i> Conrad	Maryland, USA	6	0	—	—
<i>C. funiakensis</i> Gardner	Chipola Formation, Florida, USA	6	1	0	1
<i>C. gibba</i> (Olivi) [F, T]	Gironde, France	416	91	59	32
<i>C. heterogena</i> Dall	Bowden, Jamaica	5	0	—	—
<i>C. idonea</i> Conrad [F, T]	Chesapeake Group, Maryland, USA	8	2	0	2
<i>C. radiatula</i> Dall [F]	Chipola Formation, Florida, USA	10	2	1	1
<i>C. revoluta</i> (Brocchi) [F, T]	Ponteleroy, France	41	3	1	0
<i>C. seminella</i> Dall	Chipola Formation, Florida, USA	13	1	1	0
<i>C. sericea</i> (Dall) [F, T]	Bowden, Jamaica	45	15	10	5
<i>C. waltonensis</i> Dall	Chipola Formation, Florida, USA	6	0	—	—
Pliocene					
<i>c. gibba</i> (Olivi) [F, T]	Coralline Crag, Suffolk, UK	15	0	—	—
<i>C. gibba</i> [F, T]	Antwerp, Belgium	91	0	—	—
<i>C. gibba</i> [F, T]	Nicosia, Cyprus	106	0	—	—
<i>C. gibba</i> [F, T]	Piedmont, Italy	282	20(X)	12	8
<i>C. inaequalis</i> Say [F, T]	South Carolina, USA	76	13(X)	10	3
<i>C. macilenta</i> Hutton [F, T]	Wanganui, New Zealand	4	1	1	0

Species	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
<i>C. revoluta</i> (Brocchi) [F]	Piedmont, Italy	3	0	—	—
<i>C. rotundata</i> Sowerby	Anvers, Belgium	6	0	—	—
<i>C. sp.</i>	Various	12	0	—	—
<i>C. striata</i> Walker and Boys [F, T]	Coralline Crag, Suffolk, UK	148	8	5	0
<i>C. striata</i> [F, T]	Piedmont, Italy	48	6	1	5
Pleistocene					
<i>C. gibba</i> (Olivi) [F, T]	Red Crag, Suffolk, UK	46	0	—	—
<i>C. gibba</i> [F, T]	Weybourne Crag, Suffolk, UK	43	2	2	0
<i>C. striata</i> Walker and Boys	Red Crag, Suffolk, UK	23	3	2	1

APPENDIX 2

Data from previously published works. 1, Taylor *et al.* (1983); 2, de Cauwer (1985); 3, Speden (1970); 4, Taylor (1970); 5, Adegoke and Tevesz (1974); 6, Arua (1989); 7, Kelley (1989); 8, Hoffman *et al.* (1974); 9, Robba and Ostinelli (1975); 10, Anderson *et al.* (1991).

Species	Author	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Cretaceous						
<i>Corbula elegans</i> Sowerby	1	Albian, Blackdown Greensand, UK	712	42	?	?
<i>C. truncata</i> Sowerby	1	Albian, Blackdown Greensand, UK	145	7	?	?
<i>C. crassiplica</i> (Gabb)	2	Campanian, Coon Creek, Tennessee, USA	294	57	48	9
<i>C. crassiplica</i>	2	Campanian, Mercers Mill, Georgia, USA	331	96	74	22
<i>C. substriatula</i> d'Orbigny	2	Campanian, Vaals, The Netherlands	484	99	70	29
<i>Corbulamella gregarea</i> Meek and Hayden	3	Maastrichtian, Fox Hills Formation, South Dakota, USA	332	115	?	?
Eocene						
<i>Bicorbula gallica</i> (Lamarck)	4	Lutetian, Damery, France	27	5	?	?
<i>C. brabantina</i> Vincent	2	Lutetian, Oedelem, Belgium	315	139	131	8
<i>C. rugosa</i> Lamarck	4	Lutetian, Damery, France	179	27	?	?
<i>C. rugosa</i>	2	Lutetian, Grignon, France	524	146	121	25
<i>C. rugosa</i>	2	Lutetian, Parnes, France	578	128	104	24
<i>V. amekiensis</i> (Eames)	5	Lutetian, Ameki Formation, Nigeria	89	28	25	3
<i>V. amekiensis</i>	6	Lutetian, Ameki Formation, Nigeria	403	20	?	?
Miocene						
<i>C. idonea</i> Conrad	7	Chesapeake Group, Maryland, USA	361	20	?	?
<i>C. gibba</i> (Olivi)	8	Korytnica Clays, Poland	928	251	?	?
<i>C. gibba</i>	2	Mellesdorf, Austria	443	90	87	3

Species	Author	Locality	Number of specimens examined	No. bored valves	No. of successful boreholes	No. of failed boreholes
Plio/Pleistocene						
<i>C. gibba</i>	9	Italy	804	126	?	?
<i>Varicorbula caloosae</i> (Dall)	10	Sarasota, USA	?	43	38	5
<i>V. caloosae</i>	10	Davis, USA	?	42	39	3
<i>V. caloosae</i>	10	Forsberg, USA	?	29	28	1
<i>V. caloosae</i>	10	Punta Gorda, USA	?	31	27	4