A COMPUTER AIDED PALAEOECOLOGICAL STUDY OF SELECTED RED CRAG (LOWER PLEISTOCENE) GASTROPODS.

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C.N.A.A.

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To my family.

Frontispiece

Top: the Red Crag, Bawdsey Cliffs.

Bottom: imbricate structure in the shelly sands, Buckenay Farm.

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A COMPUTER AIDED PALAEOECOLOGICAL STUDY OF SELECTED RED CRAG (LOWER PLEISTOCENE) GASTROPODS.

M. D. Harrison.

Abstract.

The thesis sets out to study the palaeoecology and palaeoethology of the Buccinidae, Muricidae, Naticidae and Turritellidae families of gastropods from the Red Crag (Lower Pleistocene), with particular reference to interactive fauna. The Red Crag is a fully marine deposit and contains large numbers of molluscan fossils. The methods of study include much use of the computer as a tool to the Palaeontologist.

The shell shape of Nucella lapillus (L.) is studied and used as a palaeoenvironmental indicator showing that the rocky coasts of the Red Crag were not exposed to severe wave action. Neptunea contraria (L.) shell shape is analysed using Raupian parameters with a computer program and the variation in shape is recorded. A study of the encrusting organisms on the gastropod shells is undertaken and the strange phenomenon of uncoiling is explained by the overgrowth of soft bodied encrusting annelids.

A study of the diets of the hole boring muricid and naticid gastropods shows the muricids to have favoured the shallow burrowing and coarse sediment dwelling bivalves Astarte, Glycymeris and the gastropod Turritella. The naticids however favoured the bivalves Spisula and Macoma which inhabited finer grained sediments. Rates of predation in these prey are shown to be comparable to those of the present day. The distribution of borehole loci is studied using a new method of producing composite diagrams of bored bivalve populations and testing these distributions for randomness. This shows that the muricids drilled Astarte in random positions while Glycymeris was bored preferentially on the dorsal half of their valves. Naticids demonstrated great stereotypy in their drilling habits boring Macoma in the centre of their valves and Spisula close to their umbones.

Octopus predation is recorded on Nucella lapillus and predation on gastropods by crabs is studied with a discussion on the problems associated with the interpretation of aperture breaks in gastropods. From the information amassed on predation a primitive invertebrate food web is constructed.

PART I

INTRODUCTION.

CH.1 The Red Crag.

CH.2 Previous work and aims.

CHAPTER 1.

The Red Crag.

1.1 Location and age.

Crag is a local East Anglian term for shelly sand and the Red Crag is thus named after its very striking brick red colour (see frontispiece).

The Red Crag is exposed in Suffolk and north-east Essex (see fig. 1.1), the main exposures being centred on the three estuaries of the rivers Deben, Orwell and Stour. Outcrops have been reported further afield, for example at Netly Heath near Guildford in Surrey (Sherlock 1976, p.41) but such outcrops are small and of debatable age. Subsurface occurrences of the Red Crag have been recorded in boreholes at Ludham in Norfolk (TM 385199) by West (1961) and at Stradbroke in Suffolk (TM 122738) by Beck et al. (1972). From the Ludham borehole deposits older than the Ludhamian stage of the Pleistocene were correlated with surface outcrops of the Red Crag using forams and from this the term Preludhamian was coined (West 1961). Montfrans (1971) established that the Preludhamian had normal magnetic polarity and is therefore older than 1.6 m.a.

The Red Crag is transgressive and lies unconformably on the Chalk (Cretaceous), London Clay (Eocene) and Coralline Crag (Pliocene). It is in turn unconformably overlain by the Norwich Crag (Lower Pleistocene) (West and Norton 1974).

Early workers considered the Red Crag along with the Coralline Crag to be a Pliocene deposit (Wood 1848-82, Harmer 1899). In 1955 however King placed the Plio-Pleistocene boundary between the Coralline Crag and the Red Crag and since then the Red Crag has been considered to be

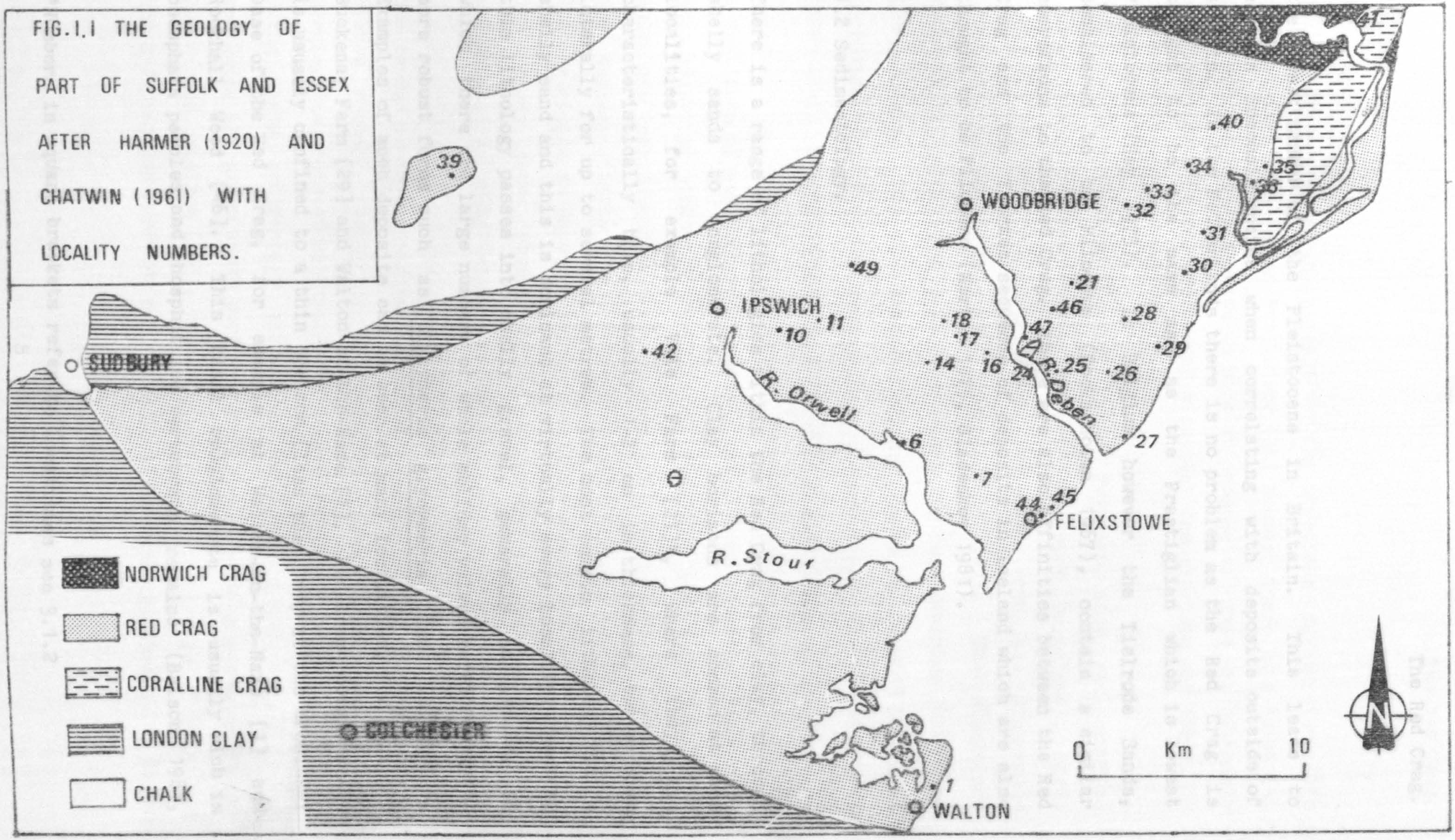


FIG.1.1 THE GEOLOGY OF PART OF SUFFOLK AND ESSEX AFTER HARMER (1920) AND CHATWIN (1961) WITH LOCALITY NUMBERS.

the lowest member of the Pleistocene in Britain. This leads to certain inconsistencies when correlating with deposits outside of Britain. In the Netherlands there is no problem as the Red Crag is thought to be the same age as the Praetiglian which is lowest Pleistocene (Hey 1975). In Belgium however the Tielrode Sands, considered to be Pliocene (Boekschoten 1967), contain a similar macrofauna to the Red Crag. There are also affinities between the Red Crag and the Tjornes sequence of deposits in Iceland which are also thought to be Pliocene (Norton 1975, Gladenkov 1981).

1.2 Sedimentology.

There is a range of lithologies within the Red Crag from clay, through shelly sands to conglomerate. Clay horizons are common at most localities, for example Vale Farm [21]*, where they are characteristically thin, usually 1-2 cm in thickness, but persist laterally for up to several metres. The most common lithology is a shelly sand and this is dominant at virtually every locality. Locally this lithology passes into shelly gravel, generally in lenses, in which there are large numbers of whole mollusc valves particularly of more robust forms such as <u>Glycymeris glycymeris</u> Linne (Bivalvia). Examples of such deposits can be seen at many localities, for instance Buckenay Farm [29] and Walton-on-the-Naze [1]. Red Crag conglomerate is usually confined to a thin horizon (less than 1m), at the erosional base of the Red Crag, for example at Walton-on-the-Naze [1] and Rockhall Wood [46]. This basal conglomerate is usually rich in phosphate pebbles and phosphatised vertebrate remains (Balson 1981,

*Numbers in square brackets refer to localities see 3.1.2

p.21). It was commercially exploited for phosphate during the 19th century (see 1.5). At Battisford [39] however there is a thick (at least 5m) conglomerate which is poor in phosphate. This unconformably overlies the Chalk and represents a coastal deposit (Spencer 1980).

A thin section study of the shelly sand revealed many well rounded quartz clasts (approximately 65% of the rock by volume). Shell fragments account for approximately 5-10% of the rock and Glauconite (coating the quartz clasts) approximately 1-3%. The clasts are cemented by sparry calcite which accounts for the remaining 20-25% of the deposit. The clay contains similar clasts to the sand making up approximately 15% of the rock. These clasts float in a matrix of brown clay. Sparry calcite is rare in this lithology.

A multitude of sedimentary structures are present in the Red Crag. Not least of these is trough cross stratification, good examples of which are conspicuous at Virtue's Farm [28], Waldringfield Heath [18] and Bawdsey Cliffs [27]. Broken shell fragments are often stacked into imbricate structures, which is well developed at Newbourn [16]. Herringbone cross stratification is present at Capel Green [32] and channels at Waldringfield Heath [18].

The trough cross stratification is the result of a submarine dune system probably built up by easterly gales (Dixon 1977a) and the herringbone cross stratification strongly suggests a tidal influence. Using these sedimentary structures Humphreys (1979, pp. 11-13) estimates the water depth during deposition to be within the range of 0-30m and Boatman (1977, p. 159) also estimates depths of 5-30m for the Red Crag Sea based on sedimentary structures. Humphreys (1979, p.

25) found that the predominant dune building current direction was from the east and north-east.

It will already be evident that the Red Crag is extremely fossiliferous, containing many specimens and fragments of a rich fauna. This includes echinoids, brachiopods, corals and occasional vertebrate remains as well as a multitude of molluscs. The abundant gastropod and bivalve species have been laboriously catalogued by Wood (1848-82) and Harmer (1914-25). Shells are readily collectable at many localities especially Walton-on-the-Naze [1], Stratton Hall [6], Waldringfield Heath [18], Bawdsey Cliffs [27] and Buckenay Farm [29]. As well as body fossils, traces of life are preserved in the sediments of the Red Crag. Echinoid burrowing traces, which look like those of the modern genus *Echinocardium* (Reineck 1968 and Schafer 1972, p.310), are not uncommon and the vertical dwelling tubes of marine worms are common at many localities, for example Vale Farm [21].

1.3 Diagenesis.

During the Pleistocene glaciations the sea level fluctuations must have caused the submergence and re-emergence of the Red Crag deposits. They are nowhere much higher than present day sea level (Battisford [39] being the highest at approximately 45m O.D.) and relatively minor oscillations would have resulted in their submergence or emergence. Ice wedges at some sites, for example Vale Farm [21] and Walton-on-the-Naze [1] (Hall and White 1970), provide evidence of emergence during post Red Crag glacial eras. The overlying Norwich Crag, which is fully marine, is evidence of post Red Crag submergence.

Decalcification, especially of the higher parts of the Red Crag, has left external moulds of mollusc shells as the only fossil material; Kesgrave [49] and the uppermost horizons at the Waldringfield Heath [18] section show the best examples of this. The probable cause is the percolation of acidic water through the sand which prior to cementation was very porous. Rain water during some emergent stage of the Pleistocene is a probable agent for this. Fissures, now lined with powdery calcite, probably represent pathways for the decalcifying fluid and may have been formed after a certain amount of cementation had reduced the porosity of the sand.

The calcite cement was almost certainly derived from the decalcification of the Upper Red Crag. Within the cemented levels of the deposit the shells maintain their original structure and some are still aragonitic. There is little evidence of any dissolution at these levels and the cement is allochthonous (Humphreys 1979, p.33), there is no evidence to suggest a vadose cement and so it is assumed to be wholly phreatic.

As well as calcite, limonite is a common cement in the Red Crag. The iron was probably carried, under reducing conditions, by water percolating through the sand (Humphreys 1979, p. 35). The reduced iron compounds give the rock a grey appearance at depth and on fresh faces. Oxidation, on exposure to the atmosphere, gives the Red Crag its distinctive colour (Boatman 1977, p. 189).

1.4 Taphonomic considerations.

1.4.1 Some cautionary notes.

The evidence available to the palaeontologist at outcrop and the palaeoecological deductions which can be made from this evidence are subject to certain limitations. These are summarised by Ager (1963, p.10-11).

> "__Limitations of fossilization.__
>
> 1. The remains of most organisms are removed after death by scavengers, saprophytes, and bacterial decay.
> 2. The parts of an organism which do escape these processes are still very unlikely to be preserved as fossils.
> 3. Those that are preserved are likely to be removed by later erosion.
> 4. Only a minute proportion of those that survive are likely to be exposed at the surface or to come to the notice of a paleontologist.
>
> __Limitations of interpretation.__
>
> 5. Only certain environments are at all likely to be represented in the rocks.
> 6. Many, if not most, fossils are preserved in environments other than those in which they lived.
> 7. It is impossible to make provable deductions about the ecology of organisms which are now extinct.
> 8. The uniformitarian approach of interpreting past environments in the light of modern ones may not be valid, since geographical factors may have changed.

9. Similarly, the organisms themselves may have changed their habits and habitats with time."

It is to these considerations that the evidence gathered from the Red Crag must be subjected, and the limitations to deductions from the palaeoecology borne in mind.

Only in very exceptional situations do the soft parts of organisms become preserved in the fossil record, for example mammoths frozen in ice in Siberia. Usually all of the soft parts of an organism are eaten by predators and scavengers or are subjected to bacterial decay. This leaves only a small amount of material available for preservation: the skeletal material, bones and shells. Even this material is subject to biological destruction. Shells of oysters, for example, are composed of calcite needles or lamellae bound together by a network of organic material known as the organic matrix (Raup and Stanley 1978, p.15), the integrity of this gives the shell its strength. After death the shell is attacked by boring organisms: worms, sponges (Cliona for example), green algae, blue-green algae and fungi. These boring thalophytes and organisms degrade the structure of the shell, making it chalky and therefore more vulnerable to chemical and mechanical destruction (Schafer 1972). Rapid burial of material therefore increases its preservation potential.

Mechanical destruction causes much wear and breakage particularly in environments of high energy, such as the surf zone on a sea shore. This is of particular significance in relation to the less robust shells (Raup and Stanley 1978). There is therefore a bias in preservation potential towards the more robust shells and also towards those which live in low energy environments. Potential fossil material once buried can be removed in solution, yet another mechanism of potential fossil destruction.

The amount of any sedimentary rock unit exposed at the surface at any one time is only a very small percentage of the total amount of that rock unit either not exposed or having already been removed by erosion. Any material which has been preserved must then be exposed in this small percentage of rock available for inspection and then be observed by a palaeontologist in order that it may be included in a palaeoecological study. It is evident from the above arguement that preservation and collection of fossil material is the exception rather than the rule and that material which is collected and studied is a biased sample of the original living population or populations which it represents.

Pleistocene marine invertebrate faunas of California are only two thirds as large as the living fossilizable fauna in the same area (Durham 1967) and the Tertiary marine invertebrate faunas of California are even less well represented. This gives a rough idea of the amount of information that is being lost through poor preservation potential.

A cautionary note, when interpretating fossil assemblages, has recently been highlighted by Koch and Sohl (1983). When comparing fossil assemblages either spacially or through time, care must be taken not to overlook the differences which occur simply due to the quality of preservation. Localities containing fossil assemblages in different states of preservation may give misleading information purely due to the lack of preservation of a species or range of species at one locality and their preservation at another. In the Red Crag the fossil assemblage from the upper decalcified beds and one from the lower shelly sands could not validly be compared unless the very different states of preservation of the fossil assemblages in the two beds was taken into account.

1.4.2 Taphonomic problems in the Red Crag.

The poor preservation potential of certain groups of fauna has almost certainly resulted in their lack of representation or under representation in the Red Crag. Such a lack of fossil evidence is of particular significance in this study especially when it involves for instance the preservation of predators involved in the invertebrate food web. Star fish for example, which are prolific predators of bivalves in the present marine environment (Carter 1968), are seldom preserved whole in the fossil record (Schafer 1972, p.94) and they leave no feeding trace on their prey. Star fish were probably significant participants in the Red Crag invertebrate food web, but there is no fossil evidence to support this. Many species of fish also prey upon bivalves in the present marine environment and in doing so they break the bivalve shell into grit size pieces (Schafer 1972, p.159). This kind of predation can not be recognised in the fossil record although it too was probably an important factor in the Red Crag food web. The soft bodied encrusting organisms responsible for the uncoiling of the Red Crag gastropods (see chapter 7) are good examples of species being poorly represented in the fossil fauna. The only trace of these animals being the monstrous growth of the shells of their hosts.

The vast majority of the Red Crag bivalve and brachiopod valves are disarticulated and these with the univalve shells show evidence of wear caused by sedimentary transport (Pratje 1929, Dixon 1977 and Humphreys 1979). Many shells are fragmented. Some of this fragmentation was caused by predatory, scavenging and shell boring organisms. Further fragmentation is the result of diagenetic compression (Humphreys 1979, p.21) which can be distinguished from other breakage as the fragments of these valves can be associated with one another as they allow a "jig saw" fit with adjacent pieces. Much of the breakage however must have been due to sedimentary transport. There are examples of *in situ* faunas in the Red Crag, for example there are articulated *Mya truncata* in life position at Ramsholt Quay [24], but these are few and far between.

The Red Crag represents a depositional complex which was laid down largely by submarine dune systems and its fauna has been, to a certain extent, introduced from outside the depositional environment, a vital-lipostrate according to Schafer's (1972, p.479) classification. By analogy to present day faunas it can be seen that the shells of the Red Crag originated from a variety of marine environments. Rocky coast dwellers, such as *Nucella lapillus* and *Mytilus edulis*, account for 9.26% of the total fossil fauna in the Red Crag, and these can be mixed together with species indicative of the following environments: intertidal, for example *Cerastoderma edule* and *Mya arenaria*, these make up 4.72% of the total fauna; 0.74% of the fossil fauna is composed of species from an shallow infralittoral environment, *Calypraea chinensis* and *Emarginula crassa* being good examples; species from a sublittoral shell gravel environment, such as *Glycymeris glycymeris* and *Venus casina*, are the largest contributors to the fossil fauna at 11.83%; 6.66% of the fossil fauna are from a sublittoral muddy sand, for example Aporrhais pes-pelicani and Turritella communis; and 8.21% are indicative of a sublittoral clean sand, Natica catena and Colus gracilis for example. These percentages, which are of individuals, were calculated from data presented by Dixon (1977) and the remaining 58.58% of the fossil fauna is composed of extinct species or individuals which could not be identified.

These faunas were mixed together by various, tidal and storm generated, marine currents. The mixing of shells originating from a variety of environments along with the evidence of abrasion and fragmentation as outlined above indicate that sedimentary transport was a significant process in the Red Crag. Warme (1969) however suggests that shell material is not transported great distances even in environments of quite high energy and Schafer (1972, p.479) states that shells do not have to travel far in environments of high energy before they are destroyed. So although sedimentary transport was an active process in the Red Crag the valves of the specimens which have been preserved may not have been transported very far from their position of life.

Shells of different resistances to mechanical erosion, from the same environment, can be mis-represented in the fossil record. Whole shells of Nucella lapillus abound in the Red Crag whereas Mytilus edulis valves are nearly always fragmented, only the umbones and hingelines being preserved in identifiable fragments. Mytilus edulis forms a major part of the diet of Nucella lapillus in the present intertidal environment but, as whole valves of M. edulis are a rarity in the Red Crag, the boreholes of *Nucella lapillus*, if any were present, cannot be seen. There is therefore no evidence that *N. lapillus* preyed upon *M. edulis* during the Red Crag. So the faunas from the source environments contributing to the Red Crag fossil essemblage are probably mis-represented and some evidence has been lost.

Shells of differing resistance to mechanical erosion from different environments can be found deposited together in the Red Crag. The worn shells of *Nucella lapillus* and the plates of balanoid barnacles from rocky shores can be found together with the much more fragile and yet intact valves of *Macoma praetenuis* (see Appendix 3 for shell strength comparisons). The phenomenon of fossil faunas being composed of shells of different strengths has been recorded in recent sediments in the Solway Firth (Wilson 1967) where the shells of *Macoma* and *Scrobicularia plana* (from intertidal mudflats), showing little evidence of wear, have been deposited with the worn valves of *Cerastoderma edule* (originating from coarser grained sediments). Shells originating from high energy environments are more likely to encounter greater mechanical forces than those originating from low energy environments and therefore more likely to be broken.

Thin fragile shells are more likely to be broken than thick resistant ones. In an environment of deposition where the fossil material is likely to be recycled several times, the only examples of fragile shells to be preserved will be ones which have undergone little reworking, as these shells cannot survive much sedimentary transport. The ones that are preserved therefore are unlikely to show much evidence of abrasion. On the other hand durable shells can survive many cycles of erosion, transportation and deposition, and the preserved specimens of such shells will probably display a variety of degrees of abrasion, depending on how often they have been reworked. This is of particular relevance to the Red Crag where the nature of the sedimentary environment, the submarine dune systems, would dictate much sedimentary recycling. This is a probable cause of the above phenomenon of finding worn specimens of robust shelled species, such as Nucella lapillus, along with relatively unabraded specimens of fragile shelled species, such as Macoma praetenuis; the specimens of the former having been in several episodes of sedimentary transport and the latter only one or two. This points to a general preservation bias towards species with more resistant shells in the Red Crag.

Although shells preserved in the Red Crag originate from a variety of marine environments, there are some environments which are poorly represented. There are few specimens of the species indicative of esturine and intertidal mudflats, for example Scrobicularia plana (an intertidal mudflat dweller) is present in the Red Crag but is not common. The sparcity of the fossil fauna, originating from these environments, in the Red Crag, may be the result of taphonomic processes. Esturine and intertidal mud-flats may well have existed during the Red Crag even though they are poorly represented by the fossil fauna. Intertidal environments are areas in which preservation potential is poor, the sediments are constantly being reworked and the shells washed out of the sediment are subjected to much physical erosion in the surf zone. Sea birds are also responsible for the destruction of large numbers of the shells of molluscs in the present intertidal environment (Schafer 1972, p.414). A lack of input from the intertidal environment could also account for the poor representation of such a fauna in the Red Crag.

The question of differential preservation of bored and unbored bivalve shells is of particular significance to this study. A shell breakage experiment was carried out with bored and non-bored valves (see Appendix 3) and it is suggested that there is little difference in the resistance to abrasive mechanical forces between the two.

The differential sorting of the shells of bivalves in the Red Crag is a problem that was dealt with by sampling from the whole of outcrops and from many outcrops rather than from specific beds, although no sorting between outcrops and across outcrops has been observed. Any sorting of left and right-hand valves of any species is thus minimized and a count of the valves recovered showed an almost equal number of each for each species studied (see chapter 8, Table 8.3). The problem of differential sorting due to the hydrodynamic properties of different valves was highlighted by Lever and Thijssen (1968) in experiments with plastic replicas of bivalve shells. They discovered that the presence of a borehole gave the valves completely different hydraulic properties resulting in the concentration of the drilled valves in one area and the non-bored valves in another. This problem is again overcome, to some extent, in the Red Crag by sampling from the whole outcrop and from many outcrops, although differential sorting in the source environment, if remote from the environment of deposition, is a distinct possibility. The experiments of Lever and Thijssen (1968) were carried out on a beach in the surf zone and their results may not be applicable in sublittoral conditions. The Red Crag deposits are sublittoral and the species chosen for work on predation ratios are also from a sublittoral environment. In the light of this and the work of Warme (1969) and Schafer (1972, p.484) the problems of sorting outlined by Lever and Thijssen (1968) are probably not applicable to the Red Crag.

1.4.3 Problems of size distribution.

The way in which the size distribution of a living population is related to the size distribution of the population available for fossilization was described by Craig and Oertal (1966). In this paper they show how variation in growth rates, mortality rates and different breeding strategies in a living population can affect the size-frequency distribution of the population available for fossilization. Only catastrophic events preserve the actual size distribution of the living population and this is not the normal method of fossil recruitment.

Sedimentary transport can alter the size distribution of the material made available for fossilization by size sorting the sample. An example of this would be the winnowing of the smallest valves from a dead bivalve population by a weak current, leaving only the larger valves in the death assemblage (Fagerstrom 1964). The actual mechanical forces operating in sedimentary transport can also be size selective, with smaller individuals being more susceptible to breakage under certain circumstances. Chave (1964) in his tumbler experiments found that Spisula valves smaller than 1.6 inches were destroyed much more quickly than the larger Spisula valves (larger than 1.7inches). Fossil populations are likely to have had their size-frequency distribution changed, from the size-frequency distribution originally made available for fossilization, by the processes of sedimentary transport. Size-frequency distribution, in fossil populations with a right-hand skewed or normal distribution are often the result of sorting by sedimentary processes (Fagerstrom 1964).

Once buried the size-frequency of a fossil population can undergo still further modification. Hallam (1967) noted that small, thin shells were more likely to be disolved than larger ones.

The size distribution of a fossil population may undergo a final distortion during collection when the smaller specimens are less likely to be noticed and collected. It is clear that there is a great deal of potential alteration to the size-frequency distribution of a population during its transition from a live community to a sample of a fossil population in a laboratory. This potential distortion of the size-frequency distribution must be borne in mind in a palaeoecological study, particularly the bias against the preservation and collection of smaller individuals.

The frequency distributions of ratios of the dimensions of individuals from samples of a fossil population can be very useful, for example in the determination of environmental conditions (see chapter 5). If the ratio of any dimensions on individuals from a species or genus are independent of size, that is these ratios do not vary during ontogeny, the frequency distributions of these ratios will be less affected by the above phenomena of size-frequency distortion. Many mollusc shells maintain constant ratios of the dimensions of their shells throughout ontogeny, for example the length to length of aperture ratio in _Neptunea_ _contraria_ (see fig. 6.1). The measurement of these ratios can therefore be a useful exercise with samples from fossil populations of molluscs.

1.5 Commercial exploitation.

The Red Crag is often poorly cemented and friable making it an easily worked deposit. For this reason it has been exploited on a small scale by the local population. Some exposures are the result of this local working, Virtue's Farm [28] is the best example. The excavated Crag is used by farmers as a track surfacing material and for chicken scratchings.

On a larger scale there are a few companies which exploit the Red Crag deposits along with more recent sands and gravels. The largest of these, Wilding and Smith, work the Red Crag at Waldringfield Heath [18] and have produced the largest inland exposure at the present time. Similar but smaller excavations occur at Battisford [39] and Valley Farm [42]. The major use of the Red Crag is as ballast in road construction and similar projects.

The basal conglomerate of the Red Crag used to be exploited for the fertilizer industry, for its phosphate content. Commercial excavation began in 1847 reaching a peak of 1,000 tons per annum in 1855 (Reid 1890). Shortly after this the Cambridge Greensand deposits were discovered and the use of the Red Crag phosphates declined and these deposits are no longer being worked.

CHAPTER 2.

Previous work and aims.

2.1 Introduction.

The palaeoecology and palaeoethology of the more common Red Crag gastropods is studied. These are the Mesogastropoda and Neogastropoda in the families Buccinidae, Muricidae, Naticidae and Turritellidae. In this section the previous work relevant to this thesis is described.

A mention of past work on the Red Crag is made. The study of the gastropod shell shape in terms of the equiangular spiral is reported as parameters of this are used in a study of the shell shape of Neptunea contraria Linne. An account of sexual dimorphism is given in living representatives of the family of gastropods Buccinidae. Work on the shell shape of Nucella lapillus Linne in respect to its environment in the modern is described. The sparcity of information on the uncoiling phenomenon in gastropods is noted.

An introduction to the shell boring predatory gastropods is given with a description of the shape of the boreholes made by and the mechanism employed by living naticid and muricid gastropods. A short critique of composite diagrams of gastropod boreholes on bivalves by previous workers is given. Work on predator:prey size relationships in modern molluscs is noted. Studies on aperture damage in both living and fossil gastropods are listed.

2.2 Previous work on the Red Crag.

The monographs of Wood (1848-82) and Harmer (1914-25) provide lists of the various Mollusca to be found in the Red Crag. Much of the work since then has been concerned with dating the Crags and putting them into context with Plio-Pleistocene stratigraphy (Boswell 1952, King 1955, Norton 1967, Beck et al. 1972, Hey 1975, Cambridge 1977). Dixon (1977, pp. 23-49) gives an exhaustive literature review and this will not be repeated here. Palaeoecological work has been limited to Dixon (1977, 1977a) where he discussed the fauna related to different facies in the Red Crag. Boekschoten (1967) uses a few examples of Red Crag molluscs in his description of the palaeoecology of the Belgian Pliocene.

2.3 Gastropod shell shape.

2.3.1 The equiangular spiral.

A study of gastropod shell shape must start with an understanding of the equiangular spiral. A spiral is a curve whose radius of curvature continually increases as it recedes from the point of origin (Thompson 1961, p. 172). Such curves are common in nature for example the horns of ruminants and the shells of molluscs. In the equiangular spiral the whorls increase in breath in a steady and unchanging ratio. The ratio of the length of a radii vector cutting two whorls is equal to the ratio of any other radii cutting the same whorls of the spiral. Further more any number of radii vectors intersecting the spiral, form equal angles to the tangents of that spiral. The spirals of all mollusc shells fall into this category thus allowing the animal to grow without changing its shape. A more detailed account of the properties of the equiangular spiral can be found in Thompson (1961, pp. 176-180) and will not be repeated here.

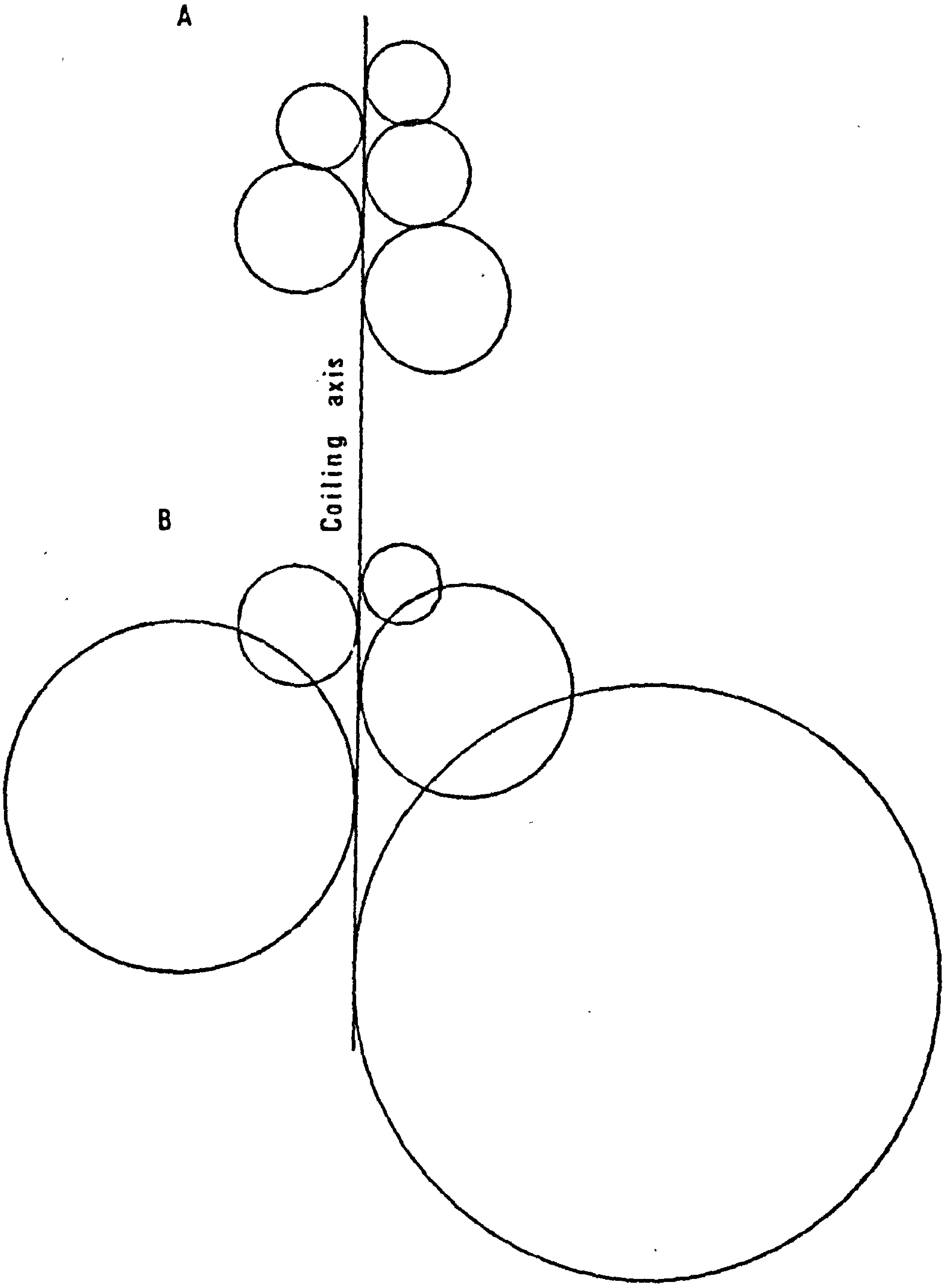
Raup (1962, 1966) worked on reproducing shapes resulting from the growth of equiangular spirals using a computer to simulate them. By varying the parameters he was able to generate the range of possible shapes and then observe the ones which occur in mollusc shells. The variables he used were whorl expansion rate (WER), translation and distance of the generating curve from the coiling axis.

WER is the ratio of the radius of a whorl to the preceding whorl. In gastropods of the Turritellidae family where successive whorls are only slightly larger than the previous one WER is low (see fig. 2.1a). In families like Naticidae however progressive whorls are much larger than previous ones and so WER is high (see fig. 2.1b).

Translation is the distance any whorl has progressed in a direction along the coiling axis with respect to the previous whorl. For example where coiling is in a single plane such as in Nautilus the amount of translation is nil, if the coiling progresses laterally along the coiling axis, describing a cone, then the value of translation is proportional to the degree of lateral progression. So a high spired gastropod such as those of the Turritellidae family demonstrate high values of translation (see fig. 2.1a) and low spired gastropods like those of the Naticidae family have low values of translation (see fig. 2.1b).

FIG. 2.1

Cross sections of two possible coils with different translation and whorl expansion rates



Distance of the generating curve from the coiling axis can be best explained diagrammatically (see fig. 2.2). In two planospirals A and B whorl expansion is equal and translation is zero so that each corresponding circle or whorl is the same diameter in both A and B, and they are contained in a single plane. The only difference being that in A the whorls are closer to the coiling axis than in B, resulting in the former overlapping and the latter forming an open spiral shape.

Raup's work was very important in providing recordable parameters which describe the shell form of gastropods. The only problem being that in these hypothetical cases the generating curve is a circle and this is not a common occurrence in nature. The final parameter needed to describe our coiled mollusc shell is the shape of the generating curve which in the case of gastropods is the edge of the aperture.

So assuming that WER, translation, distance from the coiling axis and the aperture shape are constant all that is needed to generate the whole shape af any gastropod is an outline of the aperture in relation to the coiling axis, a value for WER and a tick on the outer lip of the aperture representing the amount of translation. The tick being the point at which the highest part of the next whorl would intersect the present aperture (Raup 1961) (see fig. 2.3).

Raupian parameters are used in this thesis when describing the shell shape of Neptunea contraria.

FIG. 2.2
Cross sections of two planispiral coils with generating curves at different positions in respect to the coiling axis

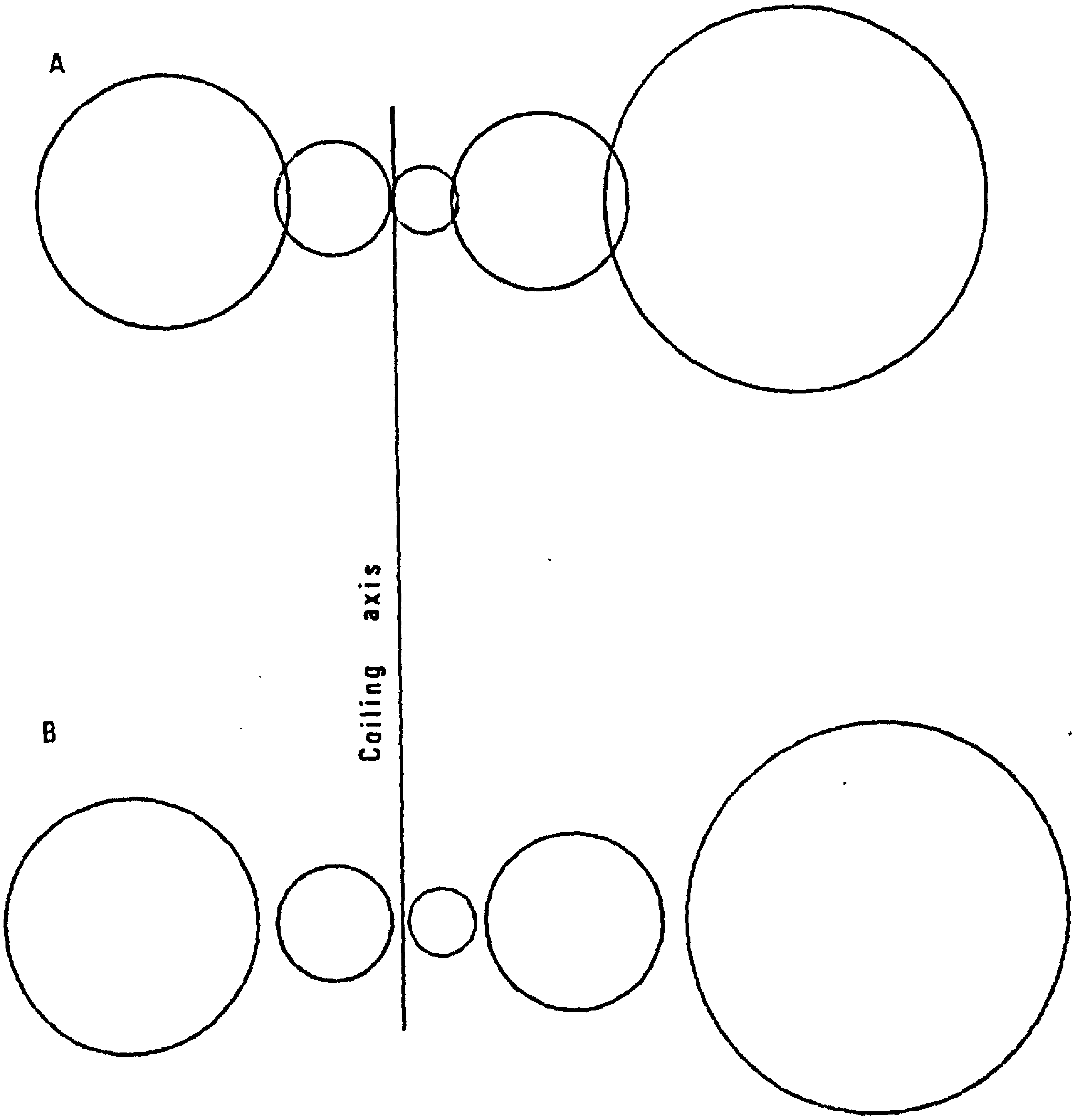
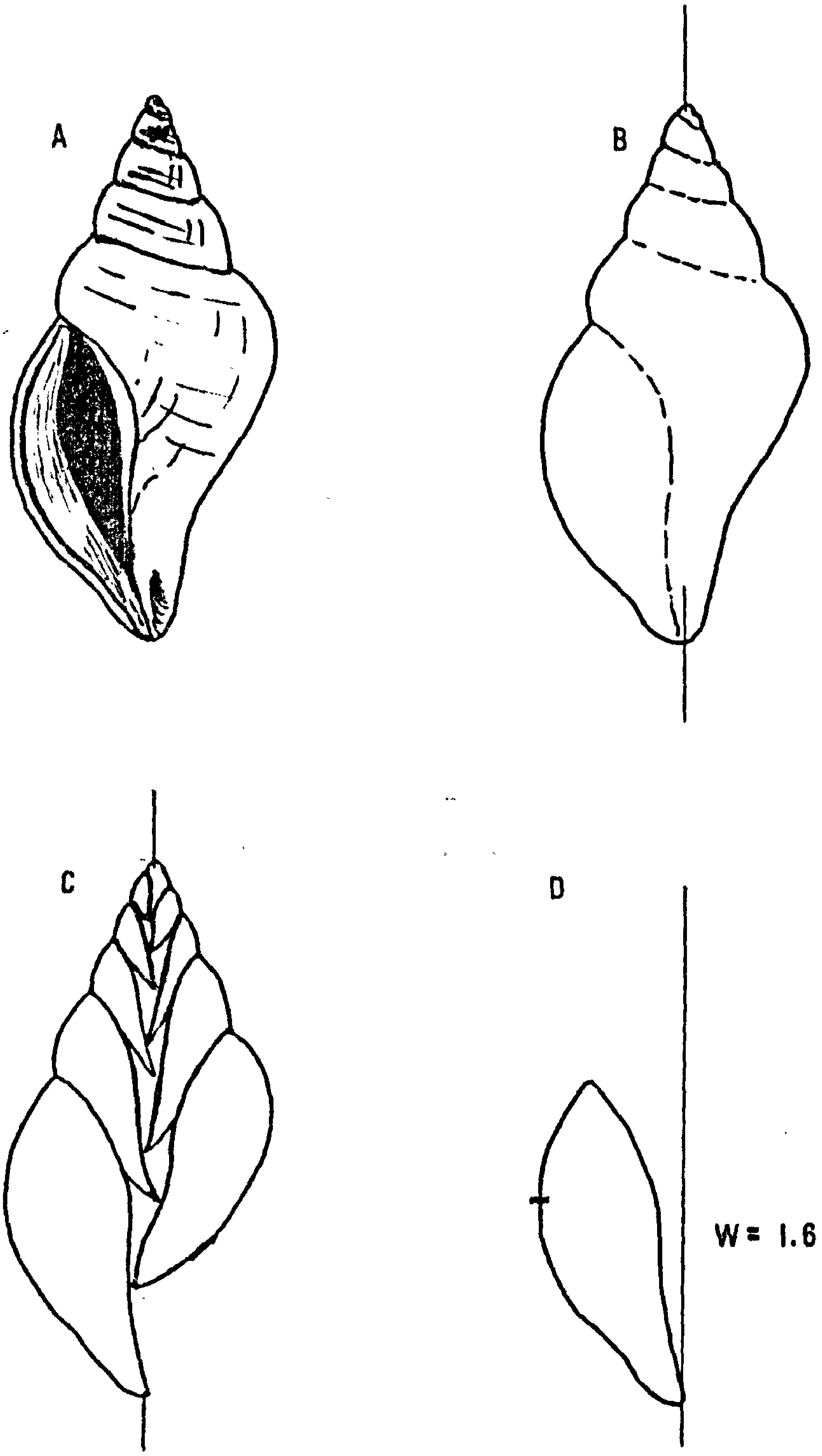


FIG. 2.3
Reconstruction of the basic gastropod form from its coiling characteristics. After Raup (1961).



Other workers who have contributed to the understanding of gastropod shell shape are Fukutomi (1953), Vermeij (1971) and Linsley (1977).

2.3.2 Sexual dimorphism.

Sohl (1969) draws attention to the potential of meeting sexual dimorphism in the fossil record when dealing with the Prosobranch gastropods. Most of these are separately sexed with only 10% of the 5,200 genera being hermaphrodites. If the anatomical variation in the sexes produces variation in the shell then this could be traced in the fossil record. He draws our attention however to the pitfalls of such interpretation in that size and shape variation can be the result of other factors regardless of sex. Variation in diet and environment (see 2.3.3) can cause variation in shell shape.

Buccinum undatum Linne an extant marine prosobranch of the Buccinidae family is separately sexed. Hallers-Tjabbes (1979) describes how the shell shape of this gastropod varies depending on sex. This is complicated by shape variation due to environmental factors but she was able none-the-less to show sexual dimorphism in the shell shape. Neptunea contraria of the same family as B. undatum is tested to see if a similar variation occurs.

2.3.3 Shell shape variation in Nucella lapillus.

Variation in the shell shape of N. lapillus was reported as long ago as 1895 by Cooke and has since been commented on by Colton (1922), Agersborg (1929), Moore (1936), Rees (1949), Staiger (1954, 57), Ebling et al. (1964), Kitching et al. (1966), Hoxmark (1970, 71), Largen (1971) and Crothers (1973, 74, 75, 75a). Cooke (1895) found that dog-whelks at exposed localities had shorter shells with wider apertures than those in sheltered areas. Colton (1922) described *N. lapillus* shells from sheltered localities with a plentiful food supply as being thicker than those from more exposed sites. Moore (1936) suggested that shell shape in *N. lapillus* was determined by dietary habits. Populations feeding mainly on *Mytilus edulis* had fatter shells (wider apertures) than those which fed mainly on barnacles.

Staiger (1954) discovered chromosome dimorphism in *N. lapillus* and suggested it was related to wave exposure. The form with 13 pairs of chromosomes living in the most exposed environments and the 18 paired form in the most sheltered. Intermediate habitats being shared by both karyotypes, where interbreeding between the two occurs (the relationship which links the two is commonly known as Robertsonian). Staiger (1957) attempted to link this to shell thickness and stated that as exposure to wave action increased shell thickness decreased. Hoxmark (1970, 71) in a study of shell thickness of *N. lapillus* claimed that factors, such as those suggested by Colton (1922) and Moore (1936) (see above), were responsible for shell thickness variation and chromosome dimorphism as well as exposure to wave action.

Ebling *et al.* (1964) and Kitching *et al.* (1966) studied variation in shell thickness and width of aperture in the dog-whelk. They found that the thinner shelled wider aperture form lived in more exposed positions than the thicker shelled variety. Their explanation of this was two fold: the thicker shelled form was more resistant to breakage due to crab predation; and the wider aperture form had greater powers of adhesion.

More recent work by Crothers (1973) again related shell shape in the dog-whelk to degree of exposure to wave action. Using Ballantine's (1961) Exposure Scale he found that, in modern _N. lapillus_, the length:length of aperture ratio (L/ LA) varied depending on the severity of exposure to wave action. The long slender shell, with high L/LA, being resident in sheltered localities and the squat shells, with low L/LA values, are found in exposed sites.

Ballantine's scale (1961) ranges from 1 (extremely exposed) to 8 (extremely sheltered). It is a biologically defined scale set up in Pembrokeshire, South Wales. The scale is based on the presence, absence and relative proportions of various intertidal species of invertebrates , algae and seaweeds. It is independent of substrate and seasonal variation. Examples of an exposed shore of value 1 on his scale are Grassholm, Skokholm and Skomer in the Dale area of Pembrokeshire (Ballantine 1961). At these stations the coasts are exposed to waves with a fetch of over 2,000 miles. On the other hand a very sheltered shore of value 8 on the same scale the coasts are exposed to waves with a fetch of less than 10 miles. Examples given by Ballantine (1961) are also in the Dale area and include Black Rock, Point Wood and Gann Quarry. Crothers (1973) used the same localities as Ballantine (1961) when he arrived at his conclusions on shell shape variation in dog-whelks as a response to wave exposure.

Each of the potential factors causing variation in the shape of _N. lapillus_ were acting during Red Crag times. There are shells of _N. lapillus_ which show evidence of crab predation (see chapter 9). There are also a few actual crab remains. The same prey were available to the dog-whelk; barnacles and _M. edulis_ have been recorded (Wood

1848-82, Darwin 1854, Dixon 1977, pers. obs.). N. lapillus is a rocky shore dweller and so was exposed to wave action during the Lower Pleistocene as it is now. There is no reason to suspect that chromosome dimorphism is a modern phenomenon in the dog-whelk. Dimorphism occurs when populations become genetically isolated (Staiger 1954). Rocky coastlines are often punctuated by bays, which if muddy form impassible barriers to N. lapillus. Since N. lapillus does not have a free swimming larvae (Staiger 1954) the mixing of populations across such a barrier is minimal resulting in genetically isolated communities. This would have been as true in the Lower Pleistocene as now.

Present day dog-whelks exhibit colour banding which is thought to be an environmental indicator (Fretter and Graham 1962, p. 513-514). The original colour of N. lapillus in the Red Crag has not been preserved.

To summarise, the concensus of opinion amongst the workers studying the shell shape of N. lapillus is that a range of forms exist, varying from those with a low L/ LA to those with a high L/ LA. The former living in areas of high exposure to wave action and the latter in areas of low exposure. Accepting this it should be possible to study fossil dog-whelks and ascertain the degree of wave action on an ancient coastline.

2.3.4 Uncoiling

Some specimens of the species *Neptunea contraria*, *Neptunea antiqua* Linne, *Neptunea despecta* Say, *Nucella lapillus* and *Turritella* spp. from the Red Crag demonstrate the unusual phenomenon of uncoiling. It is caused by the gastropod overgrowing an encrusting organism causing the coiling path to be disrupted and diverted. Commonly the encruster is not preserved leaving the hole as a trace. In extreme examples of this the final whorl can become separated from the previous one (see pl. 1A-C).

Cambridge (1975) reports monstrosities of *Nucella* and *Littorina* from the Norwich Crag; Blakes Pit, Bramerton, Norfolk (TG 301063). The monstrosities were due to encrusting barnacles, mainly *Balanus* spp. at the sutures of these gastropods. He goes on to say that present day *Littorina* and *Balanus* spp. live in the same environment but *Littorina* can deal with barnacle larvae and so there must have been another factor in play during the Norwich Crag as 23% of the *Littorina* spp. shells were monstorous. It is interesting to note that Cambridge (1975) reports that this phenomenon did not affect *Neptunea*.

Further reference to distorted *Littorina littorea*, *L. rudis* and *Thais (Nucella) lapillus* shells from the Norwich Crag can be found in Norton (1977) and Funnell *et al.* (1979). Again the distortions are caused by barnacle encrustation. It is suggested (Funnell *et al.* 1979) that the conditions of low salinity or ice, which persisted late into the spring, up to the time of cyprid settlement (this occurs in late March or early April in Boreal regions at present), enfeebled the gastropods.

There is no record of this unusual growth deviation in the literature regarding Neptunea, although Boekschoten (1967) figures a specimen of N. contraria from the Tielrode Sands (Pliocene), Belgium with a distorted suture due to the overgrowth of encrusting barnacles.

2.4 Predation.

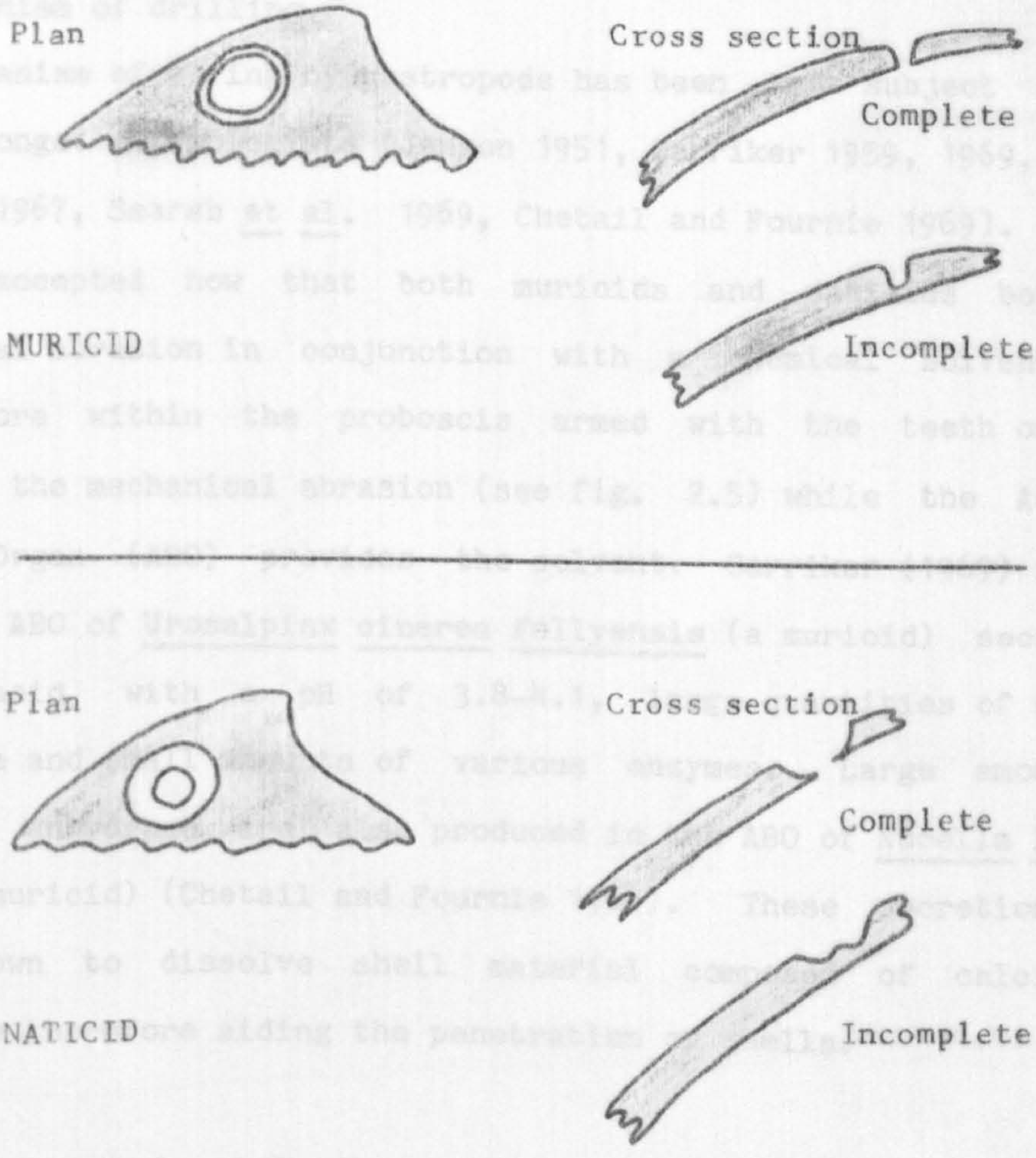
2.4.1 Introduction to boring gastropods.

Some predatory gastropods have the ability to bore holes through the shells of other invertebrates (Ziegelmeier 1954, Carriker 1955, Carter 1968) and these have been recorded from the Cretaceous (Albian) to the present day (Sohl 1969a, Taylor et al. 1980). There are three families of boring gastropods: the Cassididae, the Muricidae and the Naticidae (Taylor et al. 1980). Cassididae prey on echinoids while muricids and naticids bore, amongst other things, the shells of other molluscs. Many species of molluscs from the Crags of East Anglia show evidence of predation by boring gastropods. Muricid and naticid boreholes can be identified in the shells of both bivalves and gastropods.

a)Geometry of boreholes.

It is possible to tell from the shape of a borehole which family of predator was responsible (Fretter and Graham 1962, p. 248). The naticid gastropods produce holes which are counter sunk (see fig. 2.4 and pl. 3A) and muricids produce straight sided or slightly tapered holes. In badly worn specimens, especially thin shelled prey, it can be difficult to distinguish between the two types of bore while the

FIG. 2.4 THE GEOMETRY OF GASTROPOD BOREHOLES.



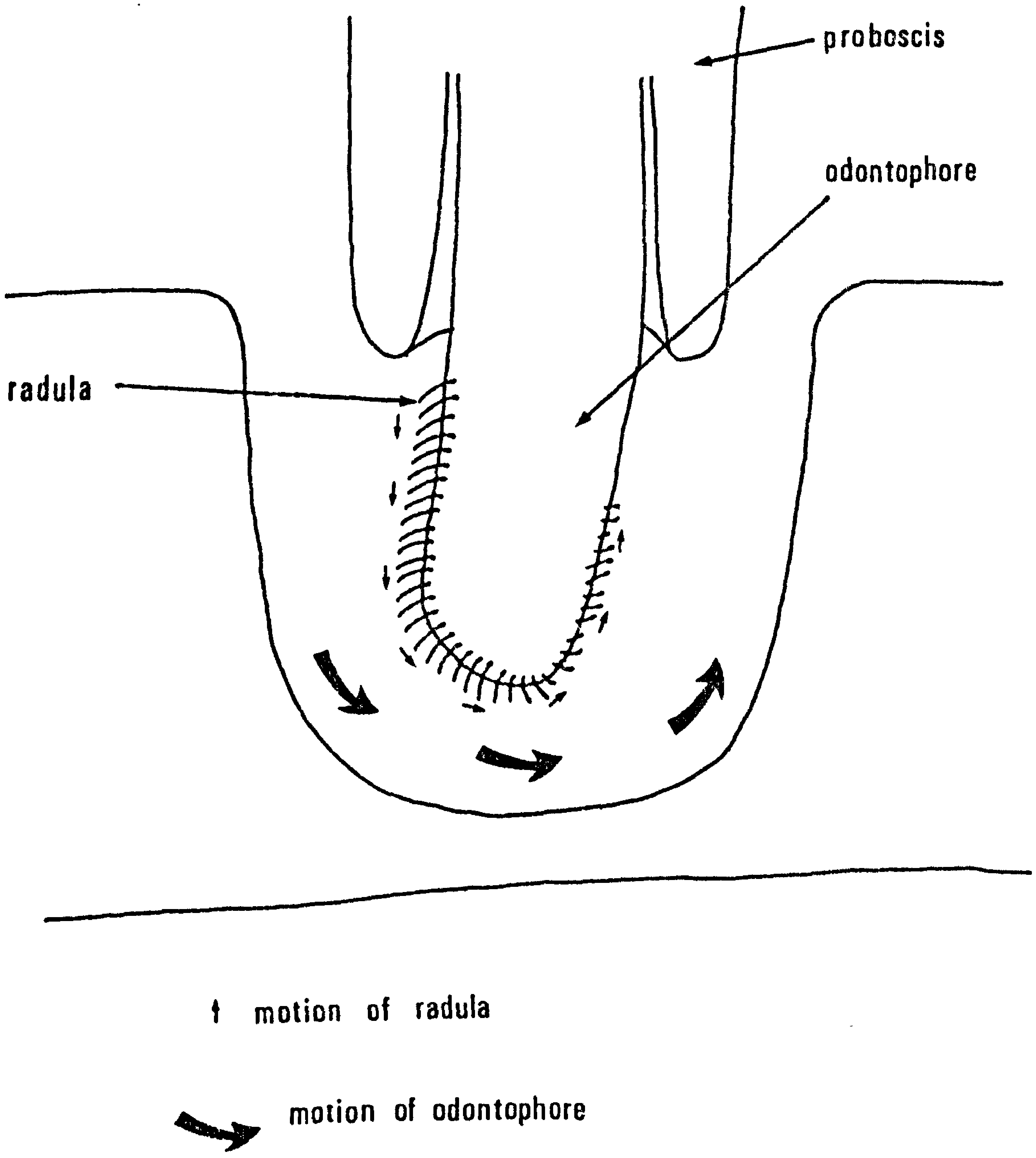
most distinctive examples are those boreholes which have failed to penetrate the shell completely. A failed naticid bore has a small boss in the centre (see pl. 3B and fig. 2.4). A failed muricid bore has a hemispherical termination and is easily distinguished from the former.

b) Mechanism of drilling.

The mechanism of boring by gastropods has been the subject of much work amongst malacologists (Jenson 1951, Carriker 1959, 1969, Pearson *et al.* 1967, Smarsh *et al.* 1969, Chetail and Fournie 1969). It is widely accepted now that both muricids and naticids bore using mechanical abrasion in conjunction with a chemical solvent. The odontophore within the proboscis armed with the teeth or radula provides the mechanical abrasion (see fig. 2.5) while the Accessory Boring Organ (ABO) provides the solvent. Carriker (1969) reported that the ABO of *Urosalpinx cinerea follyensis* (a muricid) secretes a viscid acid, with a pH of 3.8-4.1, large quantities of carbonic anhydrase and small amounts of various enzymes. Large amounts of carbonic anhydrase are also produced in the ABO of *Nucella lapillus* (also a muricid) (Chetail and Fournie 1969). These secretions have been shown to dissolve shell material composed of calcite and aragonite therefore aiding the penetration of shells.

Variation in the borehole shape between the two families of gastropod drills is a function of the different mechanisms employed. In both cases the proboscis is inserted into the bore after a period when the ABO occuppies the excavation. The radula are thus brought up against the working surface which has been attacked chemically. The shape of

FIG 2.5 The mechanism of boring (1) after Carriker and Van Zandt(1972)



the hole is dependent upon the way the proboscis is rotated during scraping by the odontophore (Smarsh _et_ _al_. 1969). Muricids rotate their proboscis about an axis which lies within the proboscis itself, producing a straight sided hole (see fig. 2.6). Naticids however rotate their proboscis about an axis outside the proboscis, so that the entire organ moves around the axis of rotation (Fretter and Graham 1962, p. 248). This results in a circular trough with a raised central mound or boss (see pl. 3B).

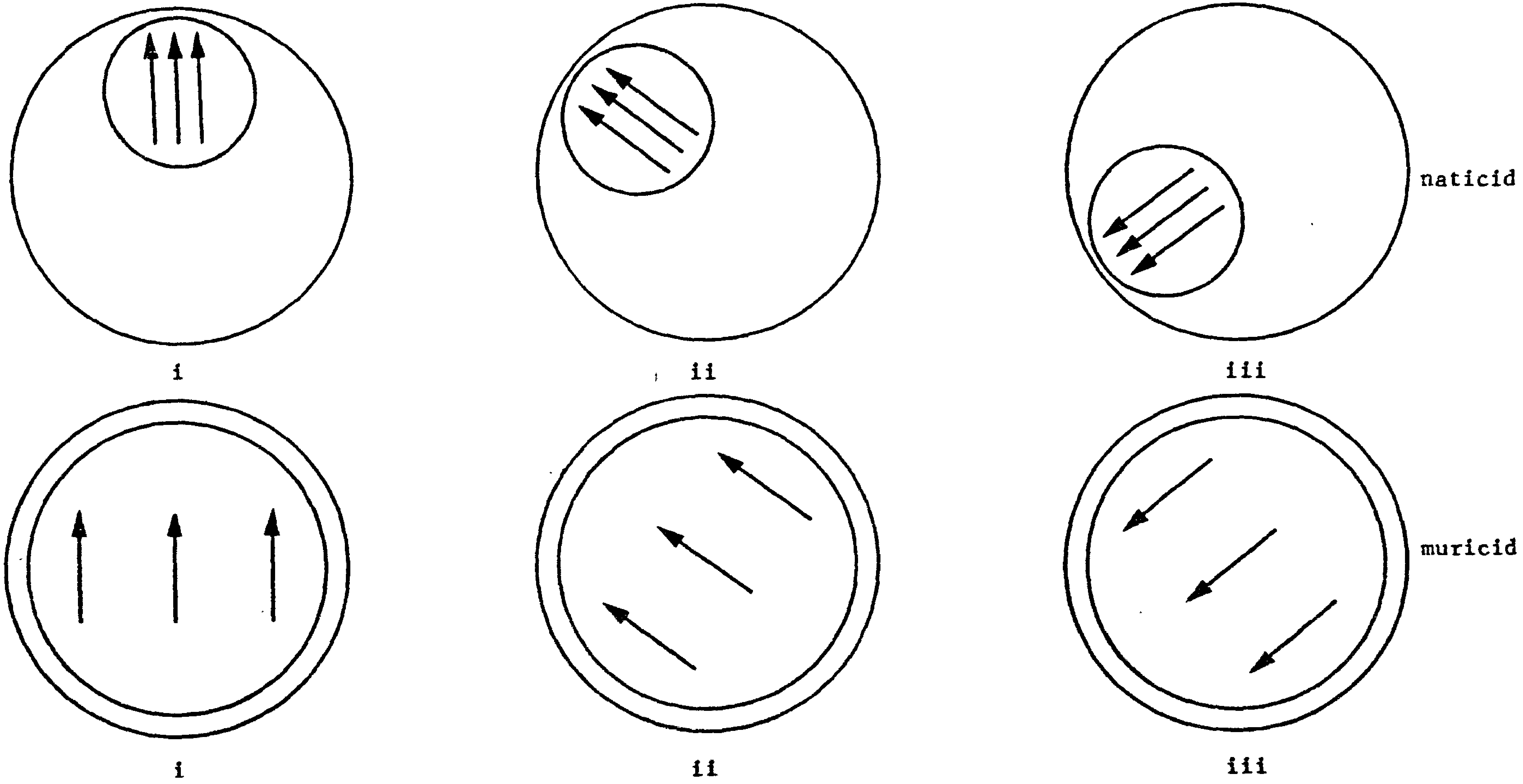
c) Composite diagrams.

Diagrams of bivalves showing the distribution of boreholes drilled by predatory gastropods are common in the literature (e.g. Ansell 1960, Reyment 1966, Sohl 1969a, Taylor 1970, Kojumdieva 1974, Negus 1975, Stump 1975, Thomas 1976). In most of these papers the problems of plotting boreholes from shells of different sizes and shapes are not discussed at all. Where they are (Stump 1975, Thomas 1976) the resultant diagrams do not reflect the shape of the shell; Stump (1975) plotted the poles of boreholes on stereonets and Thomas (1976) plotted them on sectors of a circle.

Attempts to quantify any clustering of borehole loci on bivalves have been limited to the division of a composite diagram into sectors and counting the loci within each sector (Sohl 1969a, Taylor 1970). A remedy for this state of affairs is sought in this thesis and the computer is used to draw accurate composite diagrams and test the distribution of borehole loci for randomness.

FIG. 2.6 THE MECHANISM OF BORING (2)

Position of odontophore and direction of rasping at three sequential stages in both a naticid and muricid borehole.



d) Predator:prey size relationships.

The predator:prey size relationship can not be measured directly in the fossil record as it is impossible to tell which predator specimen was responsible for particular holes. If however the size of the borehole is directly proportional to the size of the predator then this measurement can be used as a substitute for predator size . From the work of Mace (1978) and Wiltse (1980) it appears that in modern naticids there is a strong correlation between size of predator and diameter of the borehole it drills.

Ansell (1960) found a strong positive correlation between the borehole diameter of Natica alderi (Forbes) and the size of its prey Venus striatula (Da costa) . The larger the prey the larger the predator. Reyment (1966, 1967) however found no such correlation in the material collected from the Niger delta. Kitchell et al. (1981) found that there was a stronger correlation of naticid borehole size to prey size when the prey were more mobile. No work on muricid borehole size has been uncovered in the literature.

The relationship of borehole diameter to prey size in the Red Crag is studied for the common bivalve prey of both naticid and muricid gastropods.

2.4.2 Aperture damage.

The predators of gastropods such as fish, lobsters and crabs often break the shell of their victim in order to extract the flesh. Breakage induced by crab predation has been reported by Ebling et al. (1964), Rossi and Parisi (1973), Vermeij (1976) and Zisper and Vermeij (1978). Zisper and Vermeij (1978) show that in tropical environments, where crabs have the largest claws, the final whorl of the gastropod prey is severed from the spire. Crabs in temperate climes (along with tropical crabs attacking large prey), break the gastropod shell at the outer lip of the aperture.

Crabs often attack prey which is too large for them and after a limited handling period they lose interest (Vermeij 1976). This causes non-lethal shell damage which is readily repaired and has no lasting detrimental affects on the gastropod (Zisper and Vermeij 1980). The scar from such an attack is a potential trace of predation available for fossilization. Such traces have been recorded in rocks as old as the Triassic (Vermeij _et al_. 1982).

There are alternative mechanisms which can produce non-lethal breakage in gastropod shells. Neilson (1975) reported such breakage in _Buccinum undatum_ caused by its own predation behaviour. _B. undatum_ preys on bivalves by inserting the lip of its aperture between their gaping valves preventing them from closing. Occasionally however they select a victim which is too big for them and which is strong enough to break the whelks shell when it snaps its valves shut.

There is the possibility that gastropods may suffer non-lethal shell damage due to the action of strong currents. Gastropods in high energy environments could be displaced by strong currents and be transported. This action could cause minor repairable breaks in the shell.

Repaired aperture damage is common in the gastropods of the Red Crag. This is studied and conclusions reached about the cause of breakage. The inference of non-lethal breakage is discussed (Schoener 1979).

2.5 Aims of the thesis.

The overall aim of the thesis is to study the palaeoecology and palaeoethology of selected families of Red Crag gastropods. The shell shape of Neptunea contraria is studied to establish the degree of variation and to see if this is related to sexual dimorphism. A study of the many specimens of Nucella lapillus endeavours to establish the severity of wave action on the east coast during the Red Crag. Whether the wave action was uniform or varied is also assessed. Uncoiling in gastropods and the responsible encrusting organisms are studied, an attempt is made to identify the soft-bodied encrusters which cause the uncoiling phenomenon. The palaeoecological implications of the various encrusting organisms are considered.

A study of gastropod predation boreholes is made, in order to establish something of the muricids and naticids of the Red Crag. An estimate of predation rates on the common prey of these gastropods will be attempted. An analysis of the size relationships of predator and prey will be undertaken.

The behaviour of the predators will be considered by studying the position of their boreholes on their prey. With this a new method of plotting composite diagrams of bored bivalves is sought with the aid of the computer. A technique to test the distribution of these boreholes over the shells of the bivalves is also sought with the aid of a computer program.

The predation on gastropods is studied and an attempt made to see what causes non-fatal aperture breaks in gastropods. From this it is hoped to draw a conclusion about crab predation on gastropods in the Red Crag. An attempt is to be made to construct a crude food web from the information gathered on predation.

The study aims to discover aspects of the conditions under which these gastropods lived, their behaviour and the behaviour of interactive fauna with these gastropods.

PART II

METHODS.

CH.3 Collecting and Measuring.

CH.4 Computing.

CHAPTER 3.

Collecting and Measuring.

3.1 Field sampling.
    3.1.1 Sampling plan.
    3.1.2 Numbering system.
    3.1.3 Sampling.

3.2 *Nucella lapillus* and Crothers' regression.

3.3 *Neptunea contraria* and shadow casting.

3.4 Approach to the distribution of boreholes.
    3.4.1 The average shell shape.
    3.4.2 Measurement of borehole position.
    3.4.3 Borehole loci and the Poisson distribution.
    3.4.4 A test for randomness.
    3.4.5 Predator:prey size relationships.

3.5 Estimating predation rates.
    3.5.1 In bivalves.
    3.5.2 In gastropods.

3.1 Field sampling.

3.1.1 Sampling plan.

The position of Red Crag outcrops were gathered from a number of sources: Dixon (1977), Spencer (1980) and Balson (pers. com.). The location of these outcrops are given in Table 3.1, the numbering system is discussed below (see 3.1.2). Altogether 32 localities were sampled, 31 in south-east Suffolk and 1 in north-east Essex. The Suffolk sites are concentrated to the east of Ipswich and Woodbridge, to the north of the River Orwell and south of Aldeburgh [41].

Due to the nature of the Red Crag the exposures of it vary in quality through time. Coastal exposure, such as Bawdsey [27] may be altered by storms. Inland exposures are periodically worked for example Waldringfield Heath [18] (see 1.5) revealing fresh faces. Smaller pits are prone to tipping and are occasionally filled in, Trimley [7] has been recently degraded due to this. It is therefore difficult to quantify the quality of exposure at a particular site but the state at the time of sampling (1979-81) is given on table 3.1 along with other useful information to the would be collector.

3.1.2 Numbering system.

The numbering system used in this study was inherited from Dixon (1977). His collection, which was made from many of the same localities as the one for this study, is now stored at the City of London Polytechnic. It was therefore thought logical to maintain Dixon's system for continuity and easy cross reference between the two collections. The collection for this thesis is also stored at the City of London Polytechnic, Department of Geology, Walburgh House,

Table 3.1 Red Crag localities, numbers after Dixon (1977).

NAME.	NUMBER.	GRID REFERENCE.	EXPOSURE AND COMMENTS.
Walton-on-the-Naze	1	TM 26582334	Good. Access from the car park on the cliff top.
Stratton Hall	6	TM 24752821	Good. Some recent tipping (1981).
Trimley	7	TM 28253730	Poor. In danger of disappearing due to tipping.
Purdis Farm	10	TM 21724314	Moderate.
Monument Farm	11	TM 22254339	Moderate.
Brightwell	14	TM 25014300	Moderate.
Newbourn	16	TM 27604330	Good.
Foxburrow Plantation	17	TM 26024397	Good.
Waldringfield Heath	18	TM 25754460	V. Good. Permission from Wilding and Smith Ltd, Brightwell, Ipswich.
Vale Farm	21	TM 31954554	Good. Permission from farmhouse on access track.
Ramsholt Quay	24	TM 30594162	Poor. Articulated *Mya*.
Ramsholt Quarry	25	TM 30774145	Poor.
Alderton	26	TM 32844121	Moderate.
Bawdsey	27	TM 34303830	V. Good.
Virtue's Farm	28	TM 34044340	Good. Roadside exposure.
Buckenay Farm	29	TM 35634241	V. Good. Permission from farmhouse on access road.
Hollesley Bay Colony	30	TM 36604486	V. Poor. Permission from Borstal.
Cauldwell Hall Farm	31	TM 37714581	Poor.
Capel Green	32	TM 37074945	Moderate.
Daffodil Wood	33	TM 37604951	Moderate.
Neutral Farm	34	TM 37155105	Poor.
Butley Mills	35	TM 39195087	Good. Permission from Orford Lodge in advance.
Orford Lodge	36	TM 39005088	Good. See above [35].
Battisford	39	TM 06135375	Good. Conglomerate.
Chillesford Church	40	TM 38285228	Good. Norwich Crag overlies Red Crag (nolonger exposed).
Aldeburgh Brick Pit	41	TM 45185713	Moderate. Working pit.

Valley Farm	42	TM 11544334	Poor. Working pit.
Felixstowe Cliffs	44	TM 30643465	Poor.
Felixstowe Cafe	45	TM 30763468	Moderate. Behind the cafe.
Rockhall Wood	46	TM 30234391	Moderate. Red Crag overlies the Coralline Crag.
Ramsholt Cliff	47	TM 30464183	Moderate. Permission from Sutton Hall.
Kesgrave	49	TM 22804640	Poor. Council tip.

Bigland Street, London E1, apart from the figured specimens which are held by the British Museum (Natural History).

Numbers missing from the list (see table 3.1) represent localities which have been destroyed or made inaccessible. Tattingstone [4], for example, was flooded by a reservoir prior to the commencement of this study. New localities, which have been exposed after the Dixon (1977) collection was made have been given numbers following the existing ones sequentially, for example Valley Farm [42].

The exact location of the sites sampled are given by four figure grid references (see table 3.1) and their relative positions to one another can be seen on fig. 1.1.

3.1.3 Sampling.

Sampling was conducted between the autumn of 1979 and the summer of 1981. It was concluded at an early stage that bulk sampling was not a feasible technique for this study; as quite large samples (6 kg) did not yield sufficient material for the proposed study. An attempt was made to dry sieve material on site in order to reduce even larger bulk samples (20 kg) to a reasonable amount of usable material. This was not successful and bulk sampling was abandoned in favour of a collection of whole or nearly whole mollusc shells. A conscious effort was made not to make a biased collection either in terms of size or colour.

During early collections for this study all of the sites on table 3.1 were sampled but the later collections were limited to the better sites; that is those which are labelled good and very good (see table 3.1). These later collections were purposely biased towards certain genera of mollusc and towards species which exhibit traces of predation. This collection was made in order to swell the numbers of certain genera and individuals which had been preyed upon, for improved statistical analysis.

3.2 *Nucella lapillus* and Crothers' regression.

Although in *N. lapillus* the lip of the aperture thickens at a certain size this is no proof of maturity (Cowell and Crothers 1970). For this reason all shells larger than 10mm in length were measured. This was the method adopted by Crothers (1973) and the inclusion of both mature and immature individuals did not affect his results.

The length (L) and length of aperture (LA) of each of the selected shells were measured to the nearest 0.1mm using vernier calipers (see fig. 3.1). A specially written FORTRAN program NUCELA processed the data both from individual sites and the total sample (see 4.2.2). In this program a linear regression equation, derived from the data of Crothers (1973) is used to determine Ballantine's Exposure Value (BEV).

LENGTH AND LENGTH OF APERTURE OF *NUCELLA LAPILLUS.*

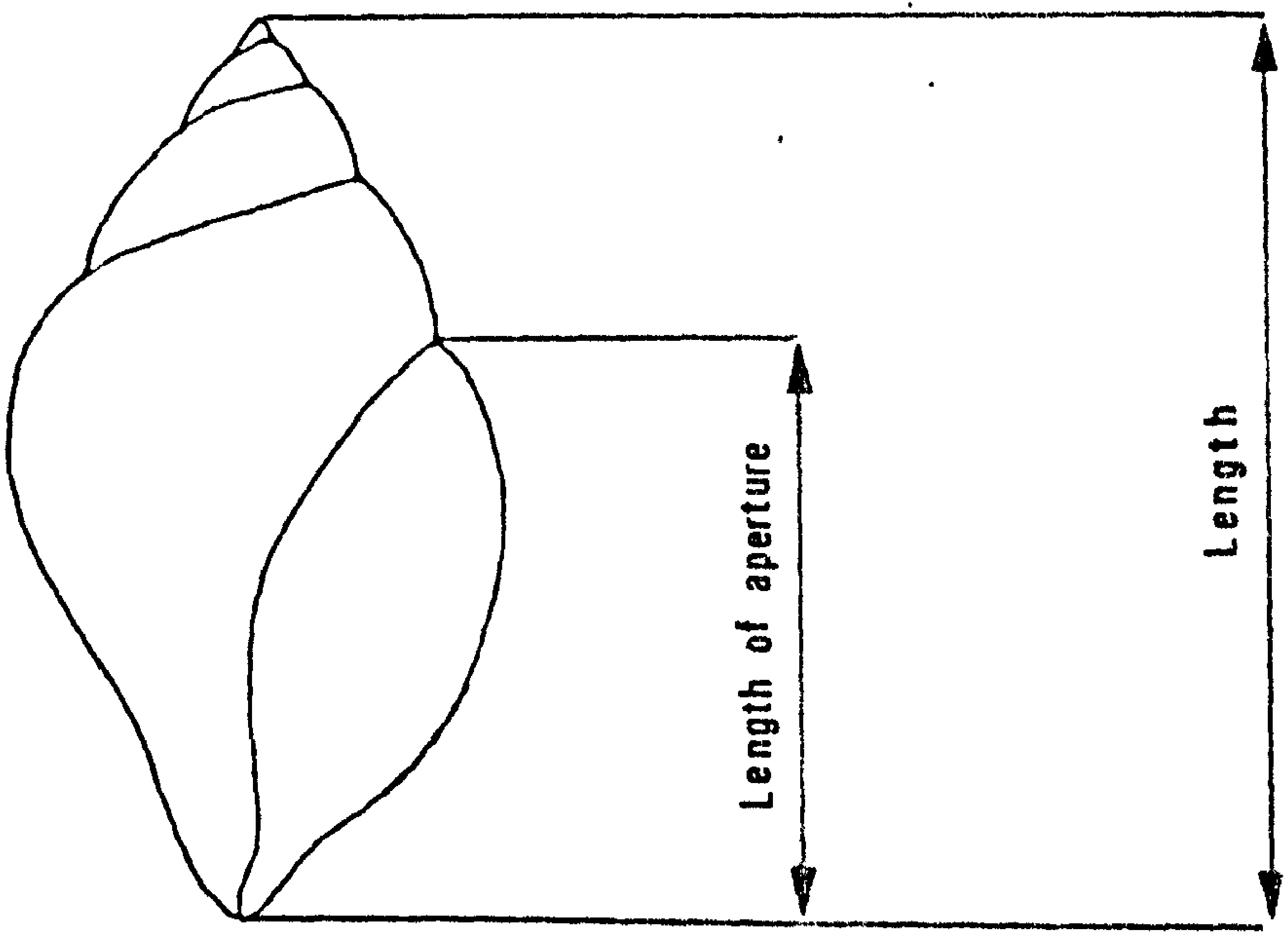


FIG. 3.1

RELATIONSHIP OF LENGTH DIVIDED BY LENGTH OF APERTURE TO BALLANTINE'S EXPOSURE SCALE (1961) IN *NUCELLA LAPILLUS*

AFTER CROTHERS (1973)

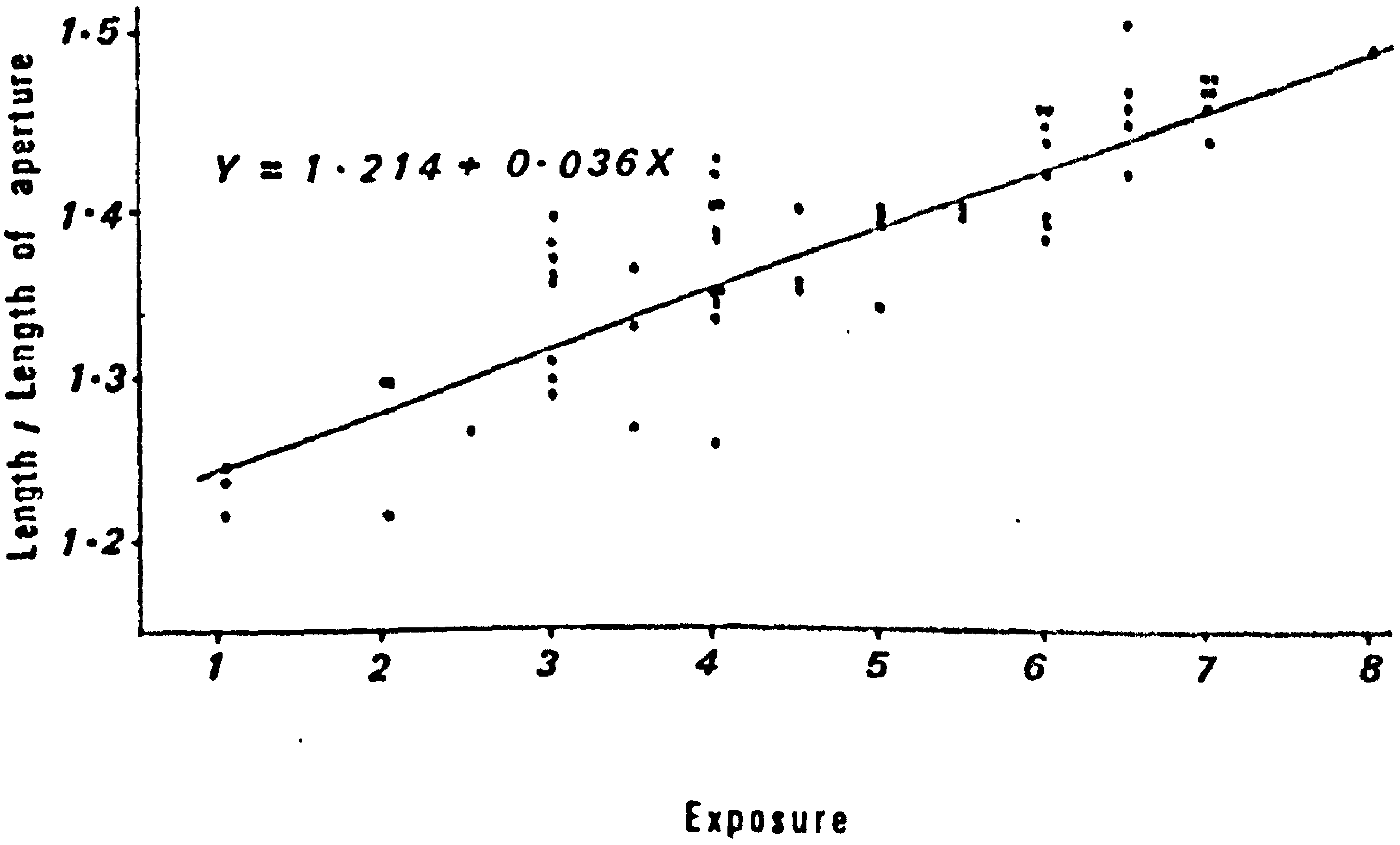


FIG. 3.2

Crothers' (1973) regression was for L/ LA on BEV (see fig. 3.2). His original data were not given but the means for each locality were. Since the number of specimens per sample was constant at 100 and no mention of a significant skewness in the distribution is made, it was felt that the calculation of the regression BEV on L/ LA using his mean values was valid. This recalculated regression (see fig. 3.3),

$X = (Y - 1.16)/ 0.047$,

where Y = L/ LA and X = BEV, is used in NUCELA.

A further computer program HISTO (see 4.2.1) was used to examine the distribution of length, length of aperture and L/ LA for the dog-whelk population of the Red Crag.

Length was plotted against length of aperture to ensure that there is a linear regression passing through the origin between the two variables, the computer program ORIGIN (see 4.2.7) was used for this.

Finally a visual inspection of the dog-whelk shells was undertaken to see if they had developed the shell sculpture described by Moore (1936), Rees (1949) and Largen (1971). Dog-whelks with this sculpture are known as the variety *N. lapillus imbricata* (Wood) and are indicative of subtidal or very sheltered conditions (Largen 1971).

RELATIONSHIP OF EXPOSURE TO L/LA AFTER CROTHERS(1973)

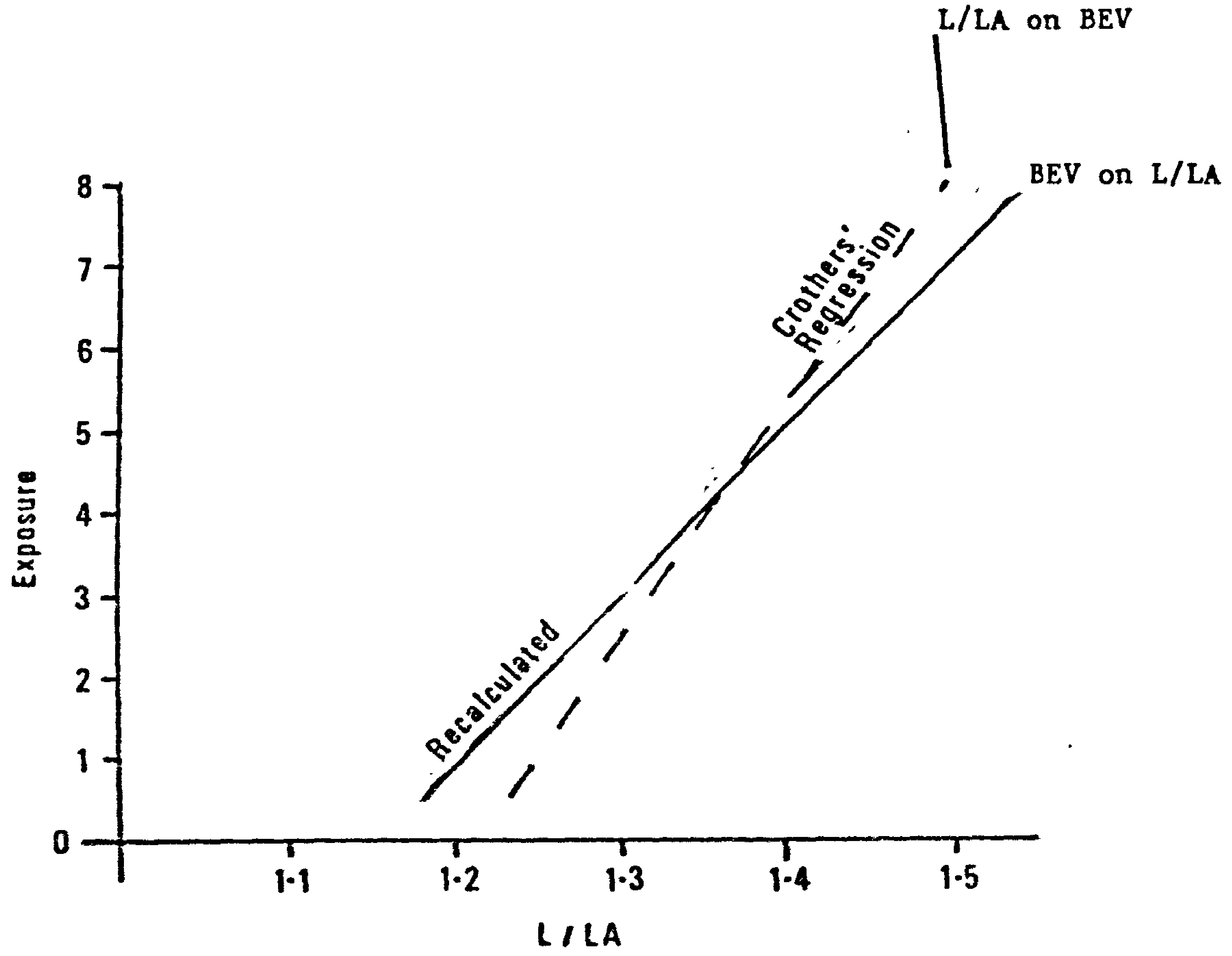


FIG.3.3

3.3 Neptunea contraria and shadow casting.

In an analysis of Neptunea contraria attempting to expose sexual dimorphism within the shell shape a method was needed for measuring the shell's Raupian parameters (see 2.3.1). To do this it was decided that the shell shape must be projected so that its complex three dimensional properties would be represented on a single plane. The most obvious way of achieving this is by aligning the gastropod shell in a certain position and photographing it. The photograph could then be measured.

A similar and somewhat less expensive method was decided upon, shadow casting. The shells of N. contraria were mounted, using Blu-tack, in a special orientation, on a frosted glass screen. A light source approximately 3m away projected their shadows onto the back of this screen. Their silhouettes could then be traced off or measured directly giving an accurate two dimensional picture of the shells.

Other methods of measuring the shell, that were considered, included sectioning. The main problem with this is that the shells are difficult to cut without breaking and it is difficult to cut the shell in a plane containing the coiling axis. There are more complicated methods of measuring the shells of gastropods, Hallers-Tjabbes (1979) describes a technique which involves the measuring of the length of the spiral trace of a series of points on the aperture. This is accomplished by placing the shell in a device which rotates the shell about its axis measuring lines down the spire. The shadow casting method was selected for its simplicity and its low cost.

The mounting of the shell is important as the coiling axis has to be parallel to the screen as does the plane of the aperture (see fig. 3.4). The aperture is not strictly in a single plane but describes a curved surface, the shells can however be mounted in a consistent way with their apertures close to parallel to the screen.

When testing the feasibility of this method shells were remounted and remeasured to see if they could be mounted in a consistent manner, the degree of variation was very small between two mounts of the same shell.

Shadow casting could be used to project other three dimensional shapes into a single plane for the purpose of easy measuring. Any spheroidal or elipsoidal object could be treated in the same way.

The measurements taken from the shadows of the shells of N. contraria can be seen on fig. 3.5. W1 and W2 are used to calculate the whorl expansion rate, t1, t2 and LA are used to calculate translation and the vectors a1 to a11 are used to represent the shape and position of the generating curve. All the calculations are performed by the computer program GASTRO (see 4.2.3). The measurements are stored in data files and they consist of all the information necessary to reconstruct the shell (see 2.3.1 and fig. 2.3).

Scatter diagrams produced by ORIGIN (see 4.2.7), histograms produced by HISTO (see 4.2.1) and diagrams produced by GASTRO (see 4.2.3) are used to analyse the variety of shapes of N. contraria from the Red Crag.

FIG. 3.4 Shadow casting.

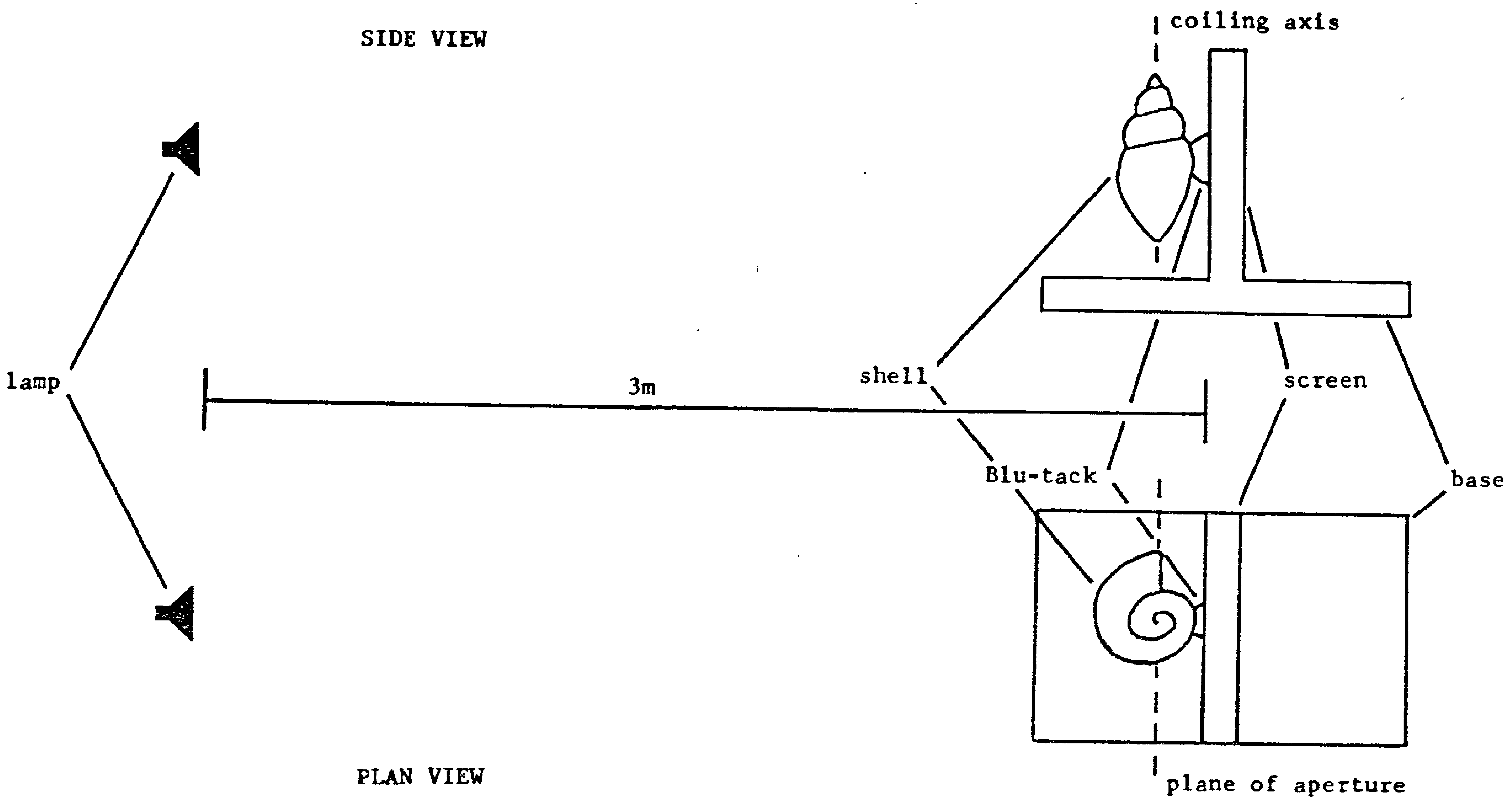
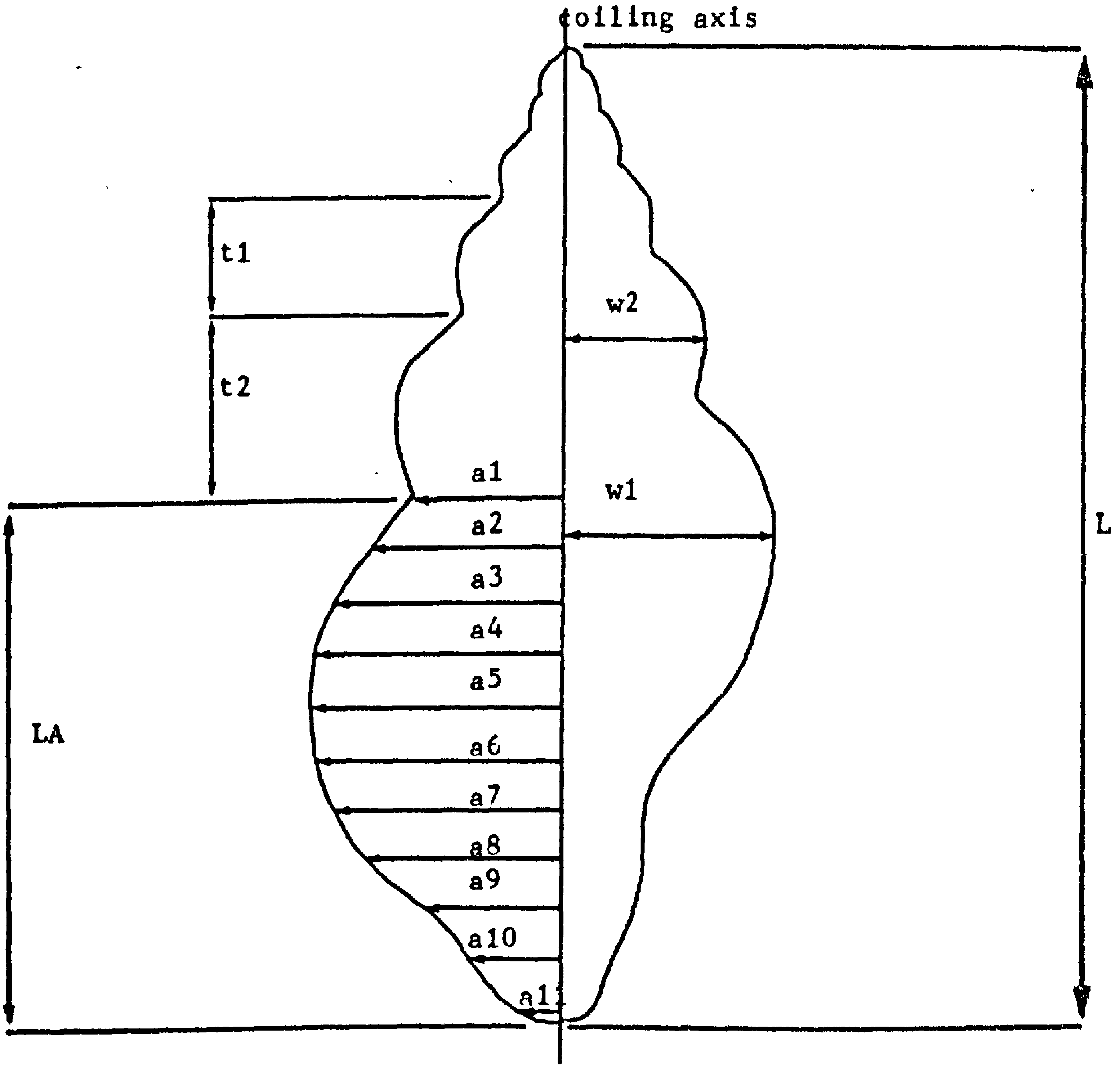


FIG. 3.5 Measurements taken from the shadow casts.



3.4 Approach to the distribution of boreholes.

The most obvious variation from a uniform distribution of predation borings on bivalves is one between valves, that is a preference for either left or right-hand valves. This can be tested using a chi square test as one would expect an equal number of boreholes to occur on both valves if there was no preference.

To study the distribution of predation boreholes over the area of the valves is a more involved process. The sample of shells under consideration are of varying sizes, with boreholes of varying diameters and often shells of varying shapes. So in order to gain a visual impression of the distribution of borehole loci it was decided to plot all of the bores from one genus on a single diagram. This involves the plotting of information from a three dimensional surface (the shell) onto a two dimensional one.

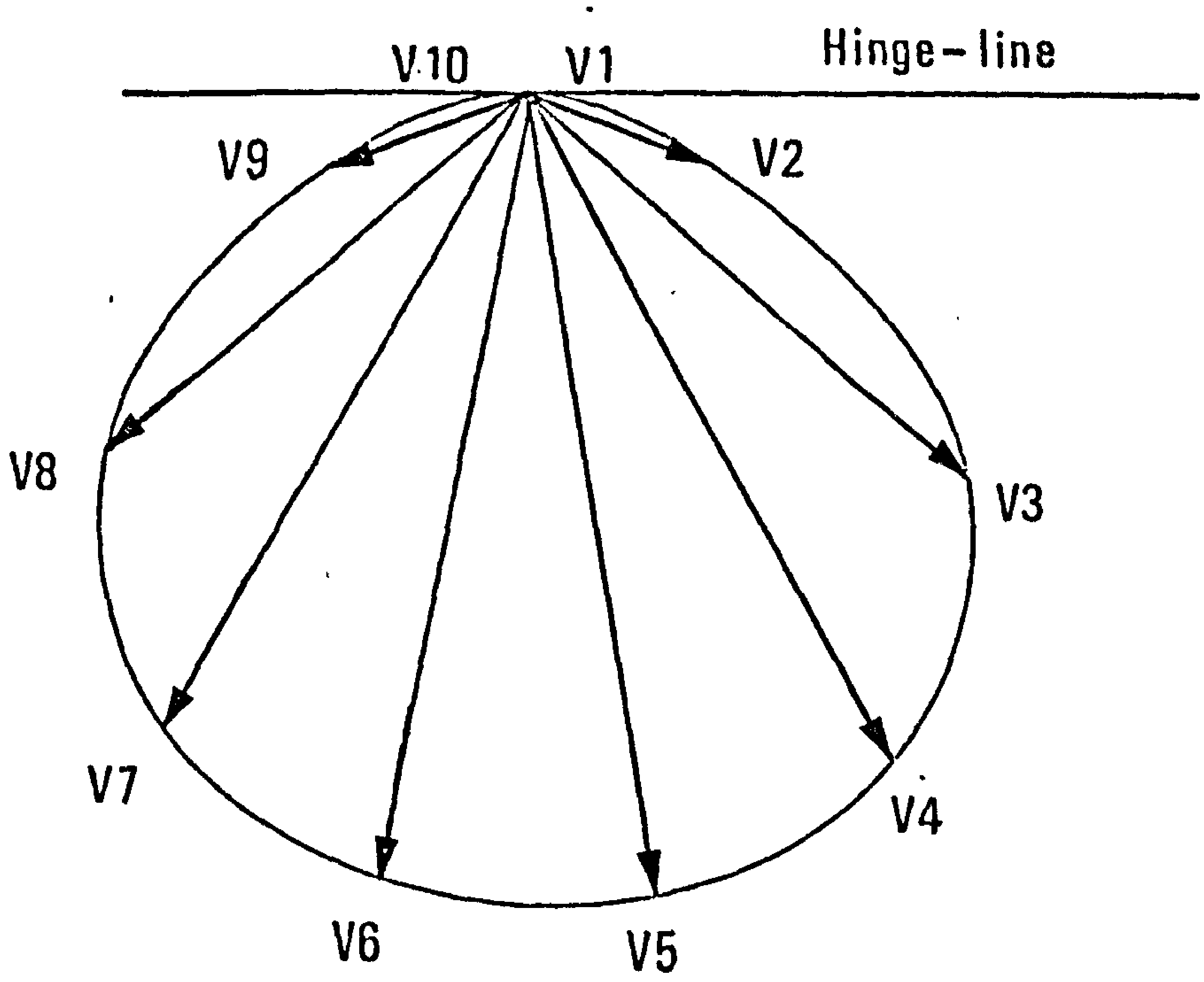
One idea for achieving this was to use the universal stage microscope and to plot the poles of each borehole on a stereonet. This method was abandoned for three main reasons: it was difficult to standardise the mounting of individual specimens so that the pole to the bore passed through the central point of rotation; the resultant stereograms gave little impression of shell shape; and boreholes clustered about the umbo were scattered on the stereogram even if in reality they were in very close proximity.

The method that was decided upon was one which treated the plan view of each valve as a two dimensional representation of the actual shape. This simplistic model was adopted because the resultant diagram is easily related to the shape of the bivalve and the distribution of boreholes could therefore be readily appreciated. For someone only vaguely familiar with bivalves it is not difficult to imagine the curvature of the valves from a two dimensional outline. Three of the genera used: Astarte, Glycymeris and Spisula have valve margins which lie in a single plane, the plane onto which the boreholes are projected. In Macoma however the valve margins are curved due to the pedal and siphonal gapes. The shell does however sit quite firmly on a single plane allowing the projection of borehole loci onto that plane, using a standard repeatable technique (see 3.4.2).

3.4.1 The average shell shape.

The method used to arrive at an average shell shape was as follows. Ten left-hand valves were taken at random from the sample of one genus (this was found to be the smallest adequate number). The outline of each of these was recorded as a series of ten vectors from the umbo of the shell to the margin at intervals of 20° from the hingeline, or some easily aligned dentition feature (see fig.3.6). The vector lengths were summed, for each angle, and divided by ten to give the average vectors. These were then drawn onto graph paper and the co-ordinates at the vector termini recorded (see fig. 3.7). To keep all of the co-ordinates positive the origin of the co-ordinate system was to the bottom left of the shape. These co-ordinates then formed the beginning of data files to be used by the computer program PREDAT (see 4.2.4) to draw composite diagrams on an average shell shape.

FIG. 3.6 The measuring system for the average shell.



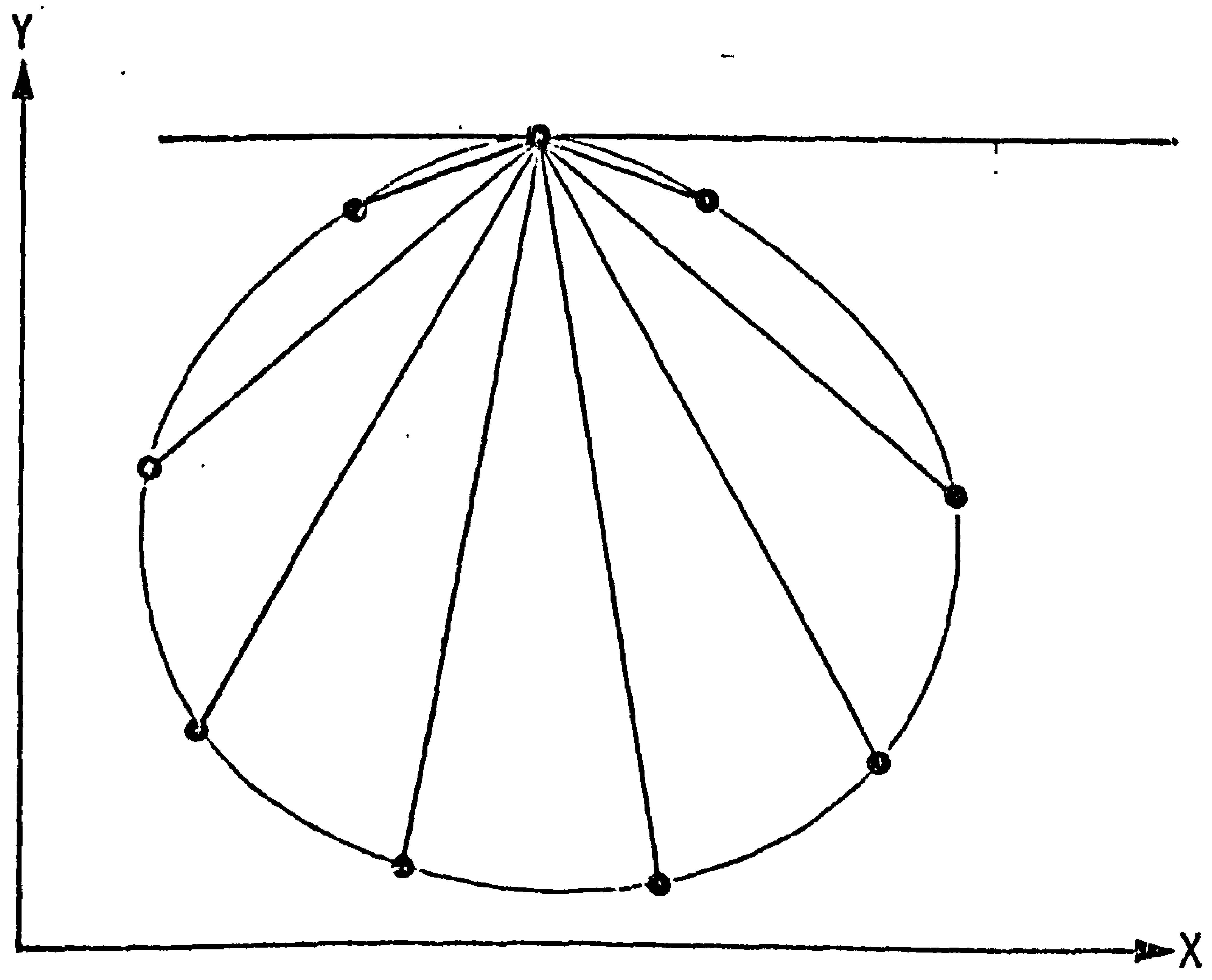


FIG. 3.7 The co-ordinate system for the average shell.

3.4.2 Measurement of borehole position.

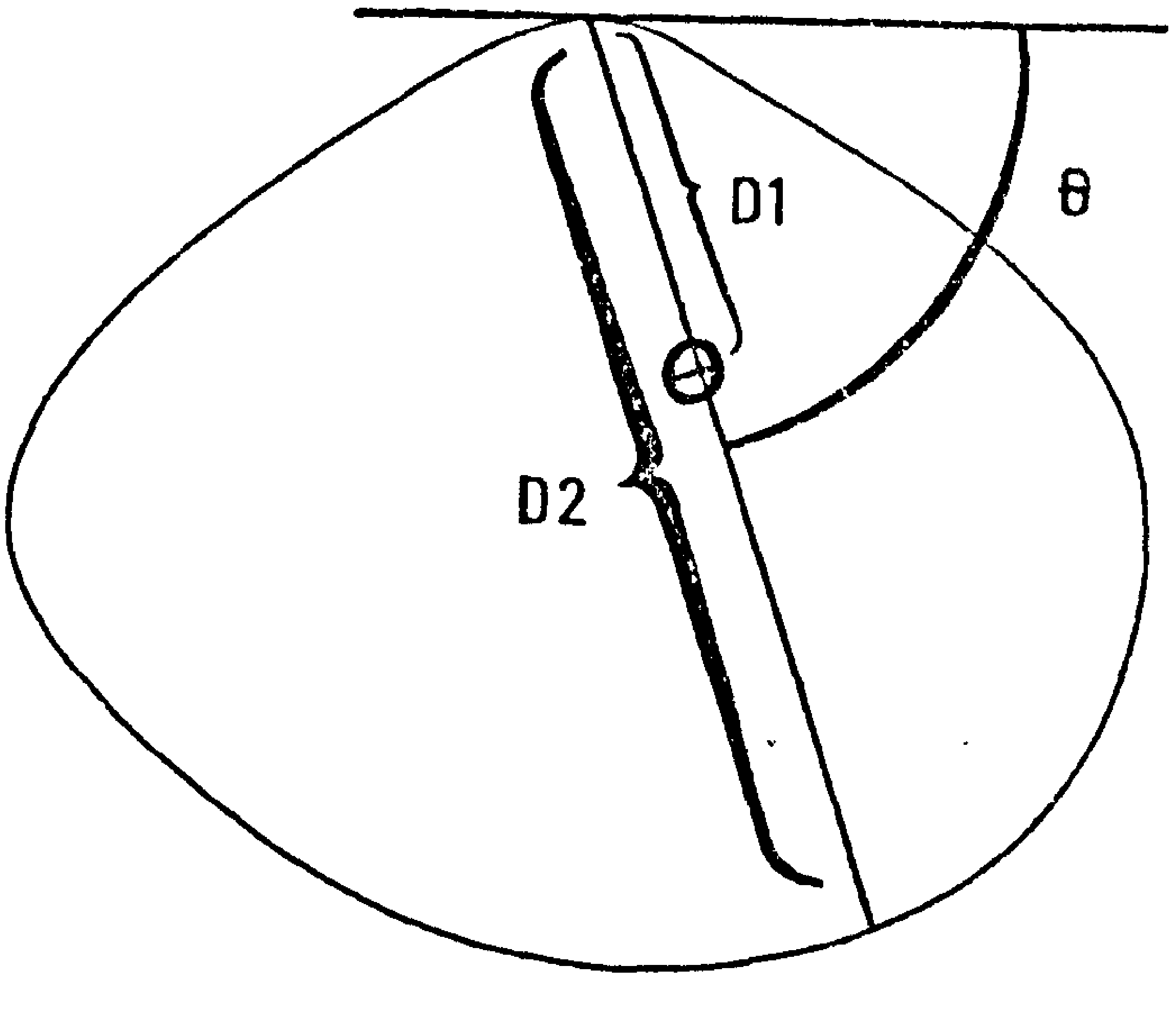
The rest of the data files for the program PREDAT are composed of information regarding the position of boreholes, their size and type. The first value is that of "N" which records the number of boreholes represented in the data file, this is followed by N lines of data each one representing one borehole.

e.g. L 2.9 10.4 110.0 1.15 M

Where L = left-hand valve, 2.9 is the distance from the umbo to the centre of the borehole, 10.4 is the distance to the shell margin from the umbo along the same line, 110.0 is the angle from the hingeline to the same line running through the borehole (in a clockwise direction) (see fig. 3.8), 1.15 is the inner diameter of the borehole and M stands for muricid. All the linear measurements are in mm and were measured to the nearest 0.1mm using vernier calipers, except for the borehole diameter which was measured using a travelling vernier microscope. The centre of the borehole was projected onto the measuring plane using a pin and was projected in such a way as to be normal to the measuring plane.

The measurement of borehole position on specimens of the gastropod Turritella was accomplished by measuring the distance from the apex to the centre of the borehole along a line parallel to the columella, the distance from the apex to the base and the angle from the aperture margin to the borehole (looking down the apex in a clockwise direction). There were problems with this method mainly due to the poor preservation of Turritella specimens. Often the apices were missing and commonly the apertures were damaged. It is possible however to measure some of the positions reasonably accurately by reconstruction of shell height because Turritella has a constant

FIG. 3.8 The measuring of a borehole position on a bivalve.



apical angle throughout ontogeny. In some cases however so little of the shell remained that the reconstruction was impossible.

3.4.3 Borehole loci and the Poisson distribution.

The first method to be considered to quantify the distribution of borehole loci was to divide the average shell shape up into a grid and compare the distribution with a Poisson distribution using a chi square test. To do this the boreholes on the right-hand valve were considered as being on left-hand ones by subtracting the angle to the borehole from 180° (see 3.4.2). This increased the number of boreholes on a single valve and simplified the statistical testing of the distribution. There proved to be problems with a comparison to the Poisson distribution as the grid squares at the margin were not covering an equal area to ones near the centre. A distorted grid was devised to give equal area squares composed of radial and concentric (parallel to growth lines) lines. Although this solved the problem of unequal areas within the grid there were still alot of very low and zero counts of boreholes in many of the squares which invalidated the chi square test.

Another approach would have been to use the multinomial distribution with a grid system, which would give the probability of finding the actual distribution assuming we were expecting a random distribution. It was felt however that a completely new approach was called for.

3.4.4 A test for randomness.

A new approach was needed to the problem and this was provided by using the computer to generate random distributions which could be compared to the actual distributions. To do this the problem was divided into two: the distribution in respect to distance from the umbo and the distribution in respect to angle from the hingeline.

If we treat the distance from the umbo to the borehole as a scaled radius where 0 distance is the umbo and 1 is the shell margin then the probability of any one distance to a borehole being less than a given value along this scale of 0 to 1 is $P\ (r > R) - A$.

Where R = the distance to the shell margin.

r = a given distance (to the borehole).

and A = the area of the shell.

That is $P\ (r < R) = KAr$.

where K = a constant.

and Ar is the area of the shell within r distance of the umbo.

$P\ (r < 1) = 1$

$KA1 = 1$

and $K = 1/\ A1$

so $P\ (r < R) = Ar/A1$

$$= \frac{2\pi r^2 \times \theta/2}{2\pi 1^2 \times \theta/2}$$

$$= r^2$$

where is the angle of the area within the shell shape.

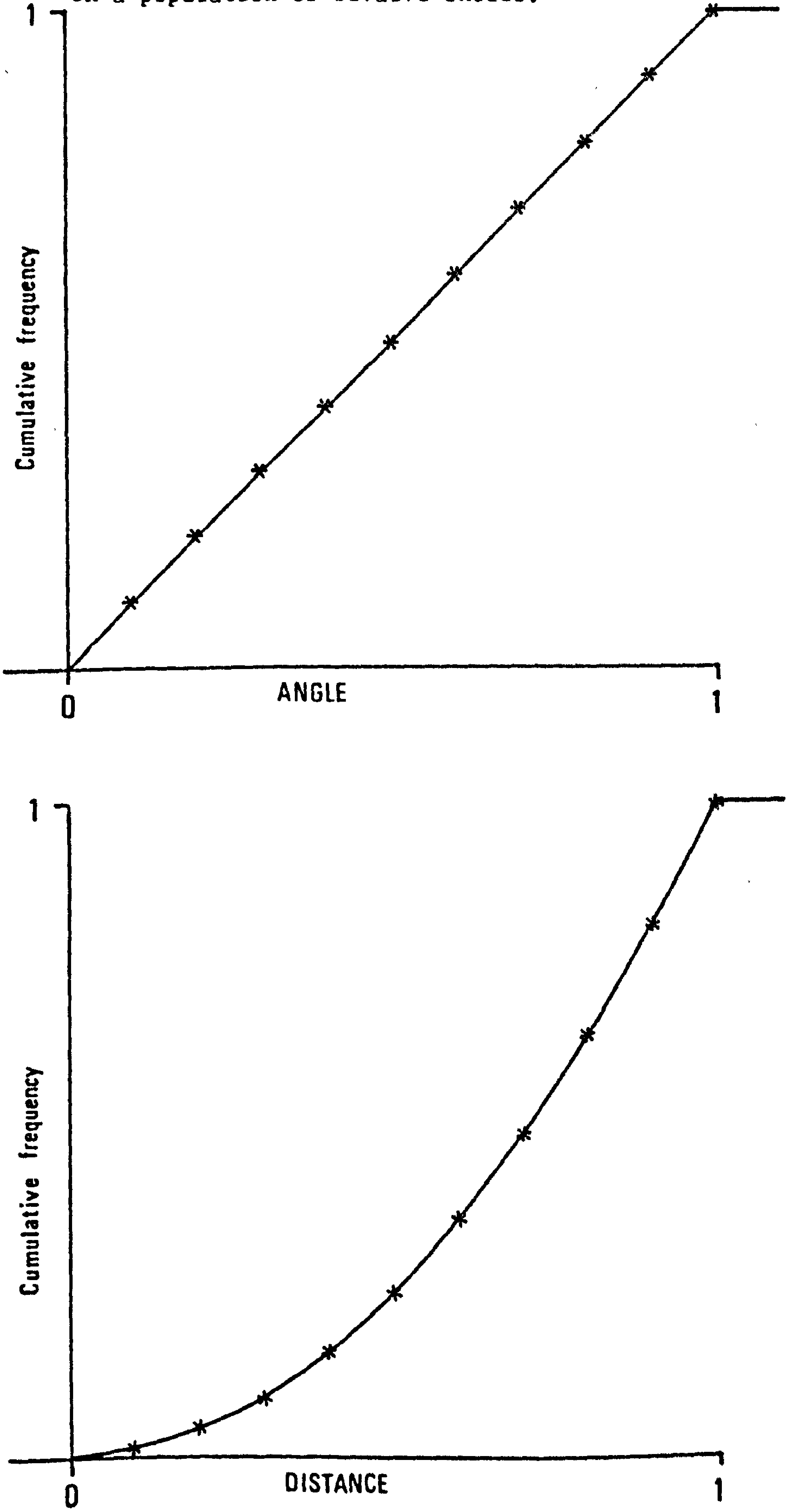
So the probability distribution function is as shown on fig. 3.9, where the cumulative frequency increases by the square of the linear distance from the umbo. The probability distribution function for the angular distribution of boreholes is more straightforward as each angular increment will cover an equal area so that there will be a linear relationship between angle and cumulative frequency (see fig. 3.9). So if our null hypothesis (Ho) is that boreholes are distributed randomly over the shell surface then our actual distribution should be close to the theoretical distribution function.

In this case assuming Ho to be true 20 sets of random observations are generated each of the same size as the actual distribution. These are plotted next to the actual distribution and visually compared so that an assessment can be made of their closeness to a random distribution.

3.4.5 Predator:prey size relationships.

The size of prey at the time of predation can be measured simply by taking a linear measurement from the shell, as successful boreholes are always fatal and therefore the size of the shell is the size at death. The length of the four common bivalve prey: *Astarte*, *Glycymeris*, *Macoma* and *Spisula* were recorded for this purpose. The size of the predator at the time of predation is not as easily measured but assuming the diameter of the borehole bares a relationship to the predator's size (Mace 1978) then a measure of this diameter will give some information of the relative sizes of the predators.

FIG. 3.9 The theoretical distribution of borehole positions on a population of bivalve shells.



Using the computer program HISTO (see 4.2.1) the size distribution of the bivalve prey can be studied. By comparing these distributions with ones for non-bored individuals and testing the difference between the means using the t distribution a conclusion can be reached on whether the predators favoured a particular size range or not. HISTO along with the t distribution test of the means is also used to study the size distribution of the predators (borehole diameter). Comparisons are made between size of boreholes on the four genera.

To test whether there is a relationship between size of prey a computer program ORIGIN was written (see 4.2.7). This produces a scatter diagram. The points from this diagram are ranked and a Spearman's rank co-efficient calculated. So the program produces a visual display of the distribution along with a statistic allowing a significance test to be performed. This was carried out on data for the four common bivalve prey genera preserved in the Red Crag. A similar correlation co-efficient was calculated for <u>Turritella</u> as was the analysis of the predator to prey size relationship. The comparison of bored to non-bored samples from the <u>Turritella</u> population was not feasible due to the poor preservation of this genus. When the shells of <u>Turritella</u> are incomplete it is not certain that the missing whorls of the shell did not contain predatory boreholes. The possibility of sedimentary sorting and or shell breakage creating a bias in the ratio of bored to non-bored valves is considered (see 1.4.2, 1.4.3 and Appendix 3).

3.5 Estimating predation rates.

All of the shells collected showing predation boreholes were separated and identified, a list of bivalve prey and one of gastropod prey were compiled. All of the gastropods in the collection from the families Muricidae and Naticidae were identified and a list of potential predators compiled.

3.5.1 In bivalves.

In the four commonly bored genera of bivalve, *Astarte*, *Glycymeris*, *Macoma* and *Spisula* the number of bored to non-bored individuals was calculated. Each bored valve was counted as one individual which had been preyed upon and every other valve was counted as one individual. A further collection of the bored valves of *Astarte* and *Macoma* was made in order to swell their numbers for statistical analysis. The proportion of bored valves, in the four above genera, which were the result of muricid or naticid activity was recorded and chi square tests performed to see if there was a significant preference for particular genera by the two families of predatory boring gastropods.

3.5.2 In gastropods.

The number of gastropods collected from the selected species was counted as was the number showing scars of non-lethal damage to the aperture of their shells. The number showing two separate non-lethal scars and so on. Therefore from this we can give the percentage of the total sample of a species which exhibit one or more shell repair scars, two or more repair scars and so on. The species used for this were *Neptunea contraria*, *Neptunea antiqua*, *Neptunea despecta*, *Buccinum undatum*, *Nucella lapillus*, *Nucella tetragona* and *Turritella* spp.

CHAPTER 4.

Computing.

4.1 Approach.

4.1.1 The language and the machine.

All the programs are written in FORTRAN which stands for FORmula TRANslation. FORTRAN was developed by the International Business Machine Corporation (IBM) in 1957 as a scientific language (Sammet 1969, p. 144). Most sciences use FORTRAN and Geology is no exception (Harbaugh and Bonham-Carter 1970, Davis 1973). In 1962 a more advanced form of the language FORTRAN IV was developed by IBM and is now the form of this language most commonly used in computing.

The Digital Equipment Corporation system 10 computer (DEC 10) was used to compile and run all of the programs written for this study. VDU terminals were used for input and lineprinters plus graphical devices (see 4.1.4) for output. The programs and data files were stored on magnetic discs.

The DEC 10 allows the use of some facilities not available on all other computers using FORTRAN IV. For example the DEC 10 allows alphanumeric strings to be entered within apostrophe marks: 'NAME' in place of 4HNAME which is standard FORTRAN IV format. It also allows the OPEN and CLOSE statements when dealing with data files, so that information can be exchanged with the program (see 4.1.2). These extensions of FORTRAN IV give rise to the FORTRAN 10 form of the language and this is the form used in this study (decsystem 10 FORTRAN programmer's reference manual 1977).

4.1.2 The use of data files.

As mentioned above the data were stored in 'files' which were kept on a magnetic disc. The data used were the measurements taken from the shells of the molluscs studied. The name of each of these data files reflected the information stored within it. Names of up to six characters are allowed, the first three denoted the species or genus to which the data referred, for example NUC being the abbreviation of Nucella lapillus and MAC for Macoma. The second three characters were used to label either what the data was to be used for or where the shells were collected from. For example NUCBUC.DAT being a data file containing the measurements of N. lapillus from BUCkenay Farm [29] or MACBOR.DAT a data file containing measurements of Macoma for analysis of BORehole position.

Wherever possible the data were stored in a consistent format to allow the use of sets of data with more than one program. Each data file has on the first line the integer value "N" which tells the program the number of lines of data to be read. Each line respresents the information about a single shell, therefore N equals the sample size.

When dealing with the measurements taken from the shadow casts of Neptunea contraria for example the format runs in this way. Firstly the aperture shape values are read for the whole sample, these are composed of 11 real numbers per line (one shell) representing the vectors a1 through a11 (see fig. 3.2). There are N lines of this data followed by N lines of data representing the other measurements taken from the shadow casts. Each of the latter lines contains 6 real numbers: W1, W2, T1, T2, L and LA (see fig. 3.2).

4.1.3 Processing and the interactive program.

As stated above the programs read data directly from data files already stored on disc. In addition to this they read information from a terminal (VDU) while it is running. This makes programs user interactive; a program can be given directions depending on what data it is using and for the specific purpose the user has in mind. To aid with the entering of information during running time the program prompts, that is it asks for information. A good example of this is a prompt that is near the beginning of every program written which asks for the name of the data file which it is to be read: ENTER NAME OF DATA FILE, 6 CHARACTERS. This kind of prompting and the interactive facility makes any program much more flexible. This type of interactive programming has become common since the advent of the micro-computer.

The usual features of FORTRAN are incorporated into the processing of the data: the use of iterative statements or DO LOOPS; the Boolean or IF statement; and SUBROUTINES for repeated procedures. These facilities give the power to a computer language, allowing tedious repetition to be accomplished very quickly.

The programs were written with many comment statements allowing easy reading of them for debugging and for the aid of other users.

4.1.4 Graphical output.

As well as output of the results on paper or a VDU most of the programs draw diagrams displaying the results graphically. HISTO, for example, draws a histogram and ORIGIN a scatter diagram (see 4.2.1 and 4.2.7). These diagrams are drawn by calls to the GINO-F library of subroutines. The finished diagrams can be output on a number of devices. Those available for this study were graphical VDUs such as the SIGMA 5680 and the IMLAC APDS4. Hard copies could be produced from the BENSON roller type plotter or the HEWLET PACARD flat bed plotter (HP7220). The computer drawn diagrams in this thesis were output on the HP7220. The device is chosen by a single CALL command within the program and must be altered if more than one machine is to be used.

The diagram labelling is produced by calls to the HERSHY library of subroutines which has several alphabet types (Gothic, italic etc.) and many symbols. This system allows the user to choose the size of the characters as well as the type of script.

4.1.5 Word processing and the typed output.

The thesis was typed onto the DEC 10 computer via a VDU terminal and corrected using the SOS editing system. It was stored in files which were submitted to a word processing package: RUNOFF. This package produces headings, leaves spaces, justifies each line, underlines and generally produces a polished typed report. RUNOFF was developed by the British Airways Management Services and Operational Research (Ashby 1977). The output was on a Diablo, daisy wheel type lineprinter.

4.2 Programs.

A listing of the programs used in this thesis are held with the thesis in the library, Department of Geography, Polytechnic of North London.

4.2.1 HISTO.

A program which selects the required data from a file, counts the data into classes and calculates the mean and standard deviation of the data. It draws a histogram with vertical lines representing the mean and two values of one standard deviation away from the mean. The graph is headed with a title and the sample size is printed.

The options available are:

i) To graph one column or a ratio of two columns.
iia) To select one of up to 11 columns for graphing.
iib) To select two of up to 11 columns for a ratio.
iii) To choose the number of classes for the histogram.

Input: is from a data file stored on disc. A single integer N is read from the first line of this file and then N lines of real numbers up to 11 columns wide. These are stored in a two dimensional array X which has a storage space of 300 x 11.

Structure: within the main body of the program there are a number of procedures. If two columns are selected at option "iib" the former is divided by the latter. The resultant data or the single column, if that has been selected at option "i", is sorted into ascending order. It is then divided into a number of classes (user selected at option "iii") and these are scaled to fit a predetermined diagram size. The mean and standard deviation of the column of data are calculated.

The mean value and one standard deviation are printed out on a VDU if required. The rest of the results are contained within the diagram which can be output on a number of graphical devices (see 4.1.4). The histogram is drawn with labelled axes and lines, representing the mean, plus one and minus one standard deviations from the mean, are drawn on. The title is written above the diagram along with the sample size.

When running the program is 31 Kwords long.

The main advantage to a computer drawn diagram of this kind as opposed to a hand drawn one is the ease with which the number of classes can be changed so that a number of histograms can be seen quickly for the same data. Any apparent skewness or bimodality can be visually tested by varying the number of classes to assess its reality. Another advantage is that large amounts of data can be graphed quickly and the usefulness of a given parameter readily determined.

4.2.2 NUCELA.

This program which is named after *Nucella lapillus* was designed and written to calculate Ballantine's Exposure Value (BEV) (see 2.3.3) using a regression equation (see 3.3) with measurements taken from samples of *N. lapillus*. These measurements were the length of the shell (L) and (LA) the length of the aperture (see fig. 3.3).

Input: after the value of N is read from a data file the values of L (i) and LA (i) are read from N lines of data (i = 1 to N). These data are stored in two one dimensional arrays L and LA.

Structure: the main structure of the program performs a number of calculations. L (i) is divided by LA (i), the resultant values are summed and divided by N to give the mean of this ratio. The standard deviation is calculated and from this the standard error of the mean is derived. The regression equation

$Y = (X - 1.16)/ 0.047$ is used to calculate the BEV.

Where X = Mean value of L/ LA and Y = BEV.

Output: the results are output on a VDU or lineprinter and consist of mean length, standard error of the mean and BEV. When running with a maximum array size of 300 the program is 11 Kwords long.

The program was modified to calculate the median value of L and consider the values above and below the median separately.

4.2.3 GASTRO.

This program analyses data compiled from the measurement of gastropod shadow casts (see 3.2). A selection of a specific parameter to be processed can be made and the selection of the maximum or minimum value of this parameter within the data. Certain features of the aperture can be studied. The program can average all of the parameters to produce a picture of the average shell shape for the sample. A diagram representing the shell shape of a particular individual is drawn.

Options:

i) The maximum, minimum of a parameter or the average of all of the

parameters.

* ii) One of the following:

Whorl expansion.

Translation.

Length.

Length of aperture.

Length divided by length of aperture.

Shape of aperture.

** iii) Where the aperture peaks in respect to its length or the width of the aperture in respect to its length.

Input: the name of a data file is entered while the program is running in response to a prompt. The data file must consist of single integer value N (the sample size) followed by N lines of real numbers 11 columns wide. This is stored in a two dimensional array APER, which is 300 x 11 in size. These data are the values of a1 to a11 taken from shadow casts (see 3.2), each line represents one individuals aperture.

Following this N lines of real data 6 columns wide are read. These are stored in one dimensional arrays W1, W2, T1, T2, L and LA; all 300 subscripts long. These are the dimensions measured from the shadow casts (see 3.2) and again one line represents all of these parameters

* Only if maximum or minimum is chosen in option i.

** Only if shape of aperture is chosen in option ii.

for one individual.

The options are read from the terminal while the program is running as single integer values. The title for the final plot is also entered while the program is running in response to a prompt and is stored in three one dimensional integer arrays 5 subscripts long.

Structure: firstly the whorl expansion rate (WER), WER = W1/ W2,
Translation (TRANS), TRANS = ((T2/ T1) T2)/ LA
and length divided by length of aperture (L/ LA) are calculated. If the average shell shape is selected (option i) all of the parameters are summed and divided by N. All of the APER values are summed and divided by N, giving 11 average aperture vectors, these are stored in the one dimensional array APER1. A call is then made to the subroutine DRAW. This subroutine scales all the parameters and produces a plot of the processed data it is provided with.

If the maximum or minimum of a parameter is required (option i) the program promts and asks which parameter is required (option ii). Acting on this information a call is made to the subroutine MAXMIN. This subroutine finds the maximum and minimum of the selected parameter. It records which of these two is required and returns the number of this individual to the main program. APER1 is loaded with the relevant values from APER and with this information a call is made to DRAW.

If the aperture shape is required (option ii) the Program asks for a further choice (option iii). When the width is chosen the program finds the individual with the widest and narrowest aperture in respect to its LA. It tests to see whether maximum or minimum is required, loads APER1 with the relevant values and makes a call to DRAW.

If where the aperture peaks is selected (option iii) the program finds the individual with the minimum and maximum distance of peak, from the top of the aperture in respect to the length of the aperture. A test checks whether maximum or minimum is required, APER1 is loaded and a call is made to DRAW.

Output: the number of the selected individual is printed on the VDU or lineprinter unless the average shell shape has been requested (option i). The rest of the output is on a graphical device (see 4.1.4). The aperture shape is drawn against scaled axes; the vertical axis representing the coiling axis and the horizontal axis recording the aperture width. The amount of translation is marked with a labelled line across the aperture shape. The amount of whorl expansion is written next to the shape, the sample size is printed and the plot headed with a three line title.

Size: when running the program is 31 Kwords long.

4.2.4 PREDAT.

The program was designed and written to produce accurate composite diagrams from samples of bored bivalves, to avoid the ambiguity of hand drawn diagrams (see 2.4.1 (c)). A shell shape representing an average shape for the sample is drawn and onto this the position of predatory boreholes made by gastropods. The distinction between muricid and naticid boreholes is made as is the difference between left and right-hand valves.

Input: once a data file has been chosen all the information is read from this. Firstly 10 lines of 3 real numbers are read into 3 one dimensional arrays X, Y and D. X and Y are the polar co-ordinates of the average shell shape and D is the vector distance from the umbo to these points. The integer value N is then read followed by N lines of data each representing the position of a single borehole on one valve (see 4.1.3). The title is input by the user in a response to a prompt from the program.

Structure: the co-ordinates of the variables X and Y are joined with a smooth curve giving the shape of the left-hand valve of a bivalve. These values are then reversed and positioned to the right of the left-hand valve shape and joined with a smooth curve. The data for each borehole is tested to see if it should be plotted on the left or right-hand valve. A call is then made to the subroutine HOLE which positions the borehole in the correct place using trigonometry. A symbol is selected depending on whether the borehole is a muricid or a naticid one and is then drawn. This procedure is iterative and continues until all of the boreholes have been plotted.

Output: the diagram is output on a graphical device (see 4.1.4) and is headed with a title, the sample size and a key to the symbols used is plotted.

Size: the program is 22.5 Kwords when running with a maximum array size of 300.

Using PREDAT gives an accurate visual display of the type and distribution of predatory boreholes. The predominant predatory family can be ascertained as can the clustering of borehole loci, if present. A qualitative appraisal of whether the left or right-hand valves are preferred or a particular site on the valves can be made.

4.2.5 BORING.

This is a modification of the program PREDAT (see above 4.2.4) but instead of plotting symbols at the site of a borehole it plots a circle which corresponds to the diameter of the borehole in respect to the size of the shell it was drilled into. That is the boreholes are drawn to scale.

Option: Muricid or naticid boreholes may be considered.

Input: the same data files used for PREDAT are also used for this program (see 4.2.4 and 4.1.3).

Structure: the main difference between BORING and PREDAT is that the inner diameter of the borehole is taken into consideration and this is scaled depending on the size of the shell it is taken from. Otherwise (see 4.2.4).

Output: (see 4.2.4).

Size: the program is 22.5 Kwords when running with a maximum array size of 300 subscripts.

From these diagrams the size relationship of borehole to prey can be assessed.

4.2.6 RANDO2.

Is a program which utilizes the method of testing for randomness outlined in section 3.4.4. Twenty sets of random numbers are generated, each set being the same size as the actual distribution. The random numbers and the actual distribution are plotted cumulatively next to each other so that they can be visually compared.

Options are:

i) Random numbers or not.
ii) Random numbers or the square root of random numbers; for angular distribution or linear distribution comparisons.

Input: data files are of the same format as with PREDAT and BORING (see 4.2.4 and 4.1.3). The arrays X, Y and D are read although they are not used, this is for the compatibility of different programs using the same raw data.

Structure: twenty sets of random numbers or their square roots are generated (option ii), each set being the same size as the actual sample (twenty sets was decided upon after experimenting with more and less). Each random set is sorted into ascending order and scaled to fit predetermined axes lengths. Finally the actual sample is sorted in the same manner.

Output: is on a graphical device (see 4.1.4) and consists of a graph with a confusion of random distributions plotted in black with the actual distribution plotted in red to stand out. The diagram is headed with a title and the sample size.

Size: when running is 25 Kwords with a maximum array size of 300 subscripts.

This method gives a practical alternative to standard statistical tests and significance levels. A visual inspection of these graphs gives a readily interpretable view of the distribution, its closeness to randomness and if it does vary from a random distribution where it varies.

RANDO2 was modified to test data taken from borehole loci on a sample of the gastropod genus _Turritella._ The angular distribution is considered in the same way but the program is altered to cover the possibility of boreholes falling between 0-360° rather than 20-160° used for the bivalves (see 3.4.2).

4.2.7 ORIGIN.

A program to draw scatter diagrams of two variables.

Options are:

i) The axes can be set from 0 to the maximum value or from the minimum to the maximum value.

Input: data is read from a file containing an integer value N and then N lines of two real numbers. These were then stored in two one dimensional arrays X and Y.

Structure: the variables are scaled to fit the predetermined axes Lengths. The two sets of values are scaled and a Spearman's rank correlation performed to test whether the two variables are related and if so how strongly.

Output: is on a graphical device (see 4.1.4) and is a scatter diagram. It has labelled axes, a title and the size of sample. The points on the diagram are plotted with asterix symbols. The value of R (Spearman's rank correlation) is output on a VDU.

Size: when running the program is 29.5 Kwords long with array sizes of up to 300 subscripts.

PART III

SHELL SHAPE.

CH. 5. The shell shape of *Nucella lapillus* as a palaeoenvironmental indicator.

CH. 6. Shell shape variation in *Neptunea contraria*.

CH. 7. Uncoiling gastropods.

CHAPTER 5.

The shell shape of *Nucella lapillus* as a palaeoenvironmental indicator.

5.1 The dog-whelk an introduction.

5.2 Results.

5.3 The significance of the shell shape of *Nucella* from the Red Crag.

5.4 Summary.

5.1 The dog-whelk an introduction.

Nucella lapillus Linne (synonyms: Thais lapillus (L.), Purpura lapillus (L.)) is an extant marine prosobranch gastropod belonging to the Superfamily Muricacea. N. lapillus, the dog-whelk, is a rocky shore dweller which ranges from mean high water neap tide down to ten fathoms being most abundant intertidally (Fretter and Graham 1962, p.511). Dog-whelks are common inhabitants of the North Atlantic ranging from the -1°C winter ocean isotherm in the north to the 19°C summer ocean isotherm in the south (Moore 1936). They can be found on nearly all of the rocky shores around the British Isles (Cooke 1915).

N. lapillus is a predator its prey being barnacles and bivalves, especially Mytilus edulis (L.) (Largen 1967a, Morgan 1972, Bayne and Scullard 1978). Bivalve shells are usually drilled (see ch. 8) to obtain the flesh whereas barnacles are generally taken by the forcing apart of their plates (Largen 1967a).

The Red Crag is rich in N. lapillus, Wood (1848-82), Harmer (1914-25), Dixon (1977) and the author (see tab. 5.1) all record them. They must have lived on either the rocky shorelines cut by the Red Crag sea in the Chalk or the Coralline Crag, since the Red Crag lies unconformably on both of these (see 1.1). The present shorelines based on the London Clay, on which the Red Crag also lies, do not support populations of N. lapillus or other "hard" substrate dwellers. For this reason it is unlikely that the London Clay provided suitable habitats for N. lapillus during Red Crag times. Morgan (1972) has reported a population of N. lapillus on a pebble bank in the Humber estuary. This is however a somewhat uncommon habitat for the dog-whelk.

The abundance of barnacles and *M. edulis* in the Red Crag is further evidence supporting the proposal that rocky substrates were available during the Lower Pleistocene.

5.2 Results.

Altogether 246 specimens of *N. lapillus* were collected from 14 localities and measured. There were four major sites which provided more than 20 specimens each. These were: Stratton Hall [6] with 72 specimens; Bawdsey [27] with 30; Valley Farm [42] with 35; and Buckenay Farm [29] with 23 shells. The other 10 localities produced a further 86 specimens (see tab. 5.1).

The results of the program NUCELA (see 4.2.2) using these data are given in table 5.1. The exposure values range from 6.4 to 7.91. Ballantine (1961) describes 6 as sheltered, 7 as very sheltered and 8 as extremely sheltered. The exposure values for the 4 main sites range from 6.87 at Valley Farm [42] to 7.7 at Buckenay Farm [29]. The overall exposure value for the Red Crag is 7.21.

Table 5.2 includes statistics on *N. lapillus* with lengths greater than and less than the median value 29.15 mm, for all specimens from all localities. The two values, derived using NUCELA, for the mean L/LA are 1.483 ± 0.008 (for the 123 small shells) and 1.523 ± 0.007 for the large ones. The two populations were ranked and the non-parametric Mann-Whitney U test was applied. At the 95% confidence

Table 5.1 Ballantine's Exposure Values for the Red Crag from the shell shape of Nucella lapillus after Crothers (1973).

Locality.	Mean L.	Mean LA.	Mean L/LA.	Standard Error of Mean.	BEV.	Sample size.
Stratton Hall [6]	29.47	19.45	1.505	0.011	7.26	72
Brakenbury Cliff [9]	26.27	17.55	1.503	0.025	7.21	13
Brightwell [14]	27.77	18.2	1.528	0.016	7.73	4
Newbourn [16]	25.5	18.14	1.486	0.019	6.48	16
Waldringfield Heath [18]	28.95	20.55	1.498	0.019	7.10	13
Vale Farm [21]	22.85	15.57	1.465	0.015	6.40	13
Ramsholt Farm [23]*	24.8	19.03	1.520	0.026	7.57	5
Ramsholt Quay [24]*						
Bawdsey [27]	32.17	21.28	1.522	0.018	7.61	30
Buckenay Farm [29]	29.38	19.31	1.527	0.012	7.70	23
Cauldwell Hall Farm [31]	30.05	20.05	1.504	0.033	7.23	2
Neutral Farm [34]	24.02	15.86	1.536	0.033	7.90	8
Valley Farm [42]	30.44	20.64	1.487	0.014	6.87	35
Felixstowe Cliffs [44]	31.35	20.93	1.495	0.025	7.04	9
Rockhall Wood [46]	32.65	21.25	1.536	0.000	7.91	2
RED CRAG	27.5	19.4	1.503	0.005	7.21	246

Identifable fragments of Nucella lapillus were also recognised at Alderton [26] and Virtue's Farm [28].
*Two localities in close proximity treated as one.

Table 5.2 Ballantine's Exposure Values for the Red Crag calculated from the shell shape of _N_. _lapillus_ after Crothers (1973), considering the variation caused by shell size.

Length.	L/ LA of _N_. _lapillus_.	Standard error of the mean.	BEV.	Sample size.
>29.15	1.523	0.007	7.63	123
<29.15	1.483	0.008	6.78	123

Mann Whitney U test.
Smallest U value for the two populations is 5,526.6.
Critical U value for the two populations is 6,470.7 (at the 95% confidence level).
Therefore there is no significant difference between the two populations.

level there was no significant difference between the two. The smallest U value was 5,526.5 and the critical U value 6,470.7.

The distribution of the length of N. lapillus can be seen on fig. 5.1 produced by HISTO (see 4.2.1). The goodness of fit test for a normal curve produced a chi square value of 17.13 ($p > 0.1$ and $p < 0.05$) and so the distribution is not significantly different from a normal curve at the 95% confidence level. The L/ LA distribution seen on fig. 5.2 was analysed in the same way. The chi square value was 12.78 ($p > 0.25$ and $p < 0.1$), so at the 95% confidence level this distribution is not significantly different from a normal curve. The two largest samples taken from Stratton Hall [6] and Valley Farm [42] were similarly scrutinised. They too show that the L and L/ LA distributions are not significantly different from a normal curve at the 95% level.

Length against length of aperture of N. lapillus has a straight line relationship which passes through the origin.

Few shells of the variety N. lapillus imbricata were identified. The presence of these is all that can be ascertained; a count would be misleading as the N. lapillus shells are often worn and any sculpturing can be degraded or obliterated. The ones that have been identified do not all come from the same locality.

FIG. 5.1

THE LENGTH DISTRIBUTION OF <u>NUCELLA LAPILLUS</u> FROM THE RED CRAG (LOWER PLEISTOCENE).

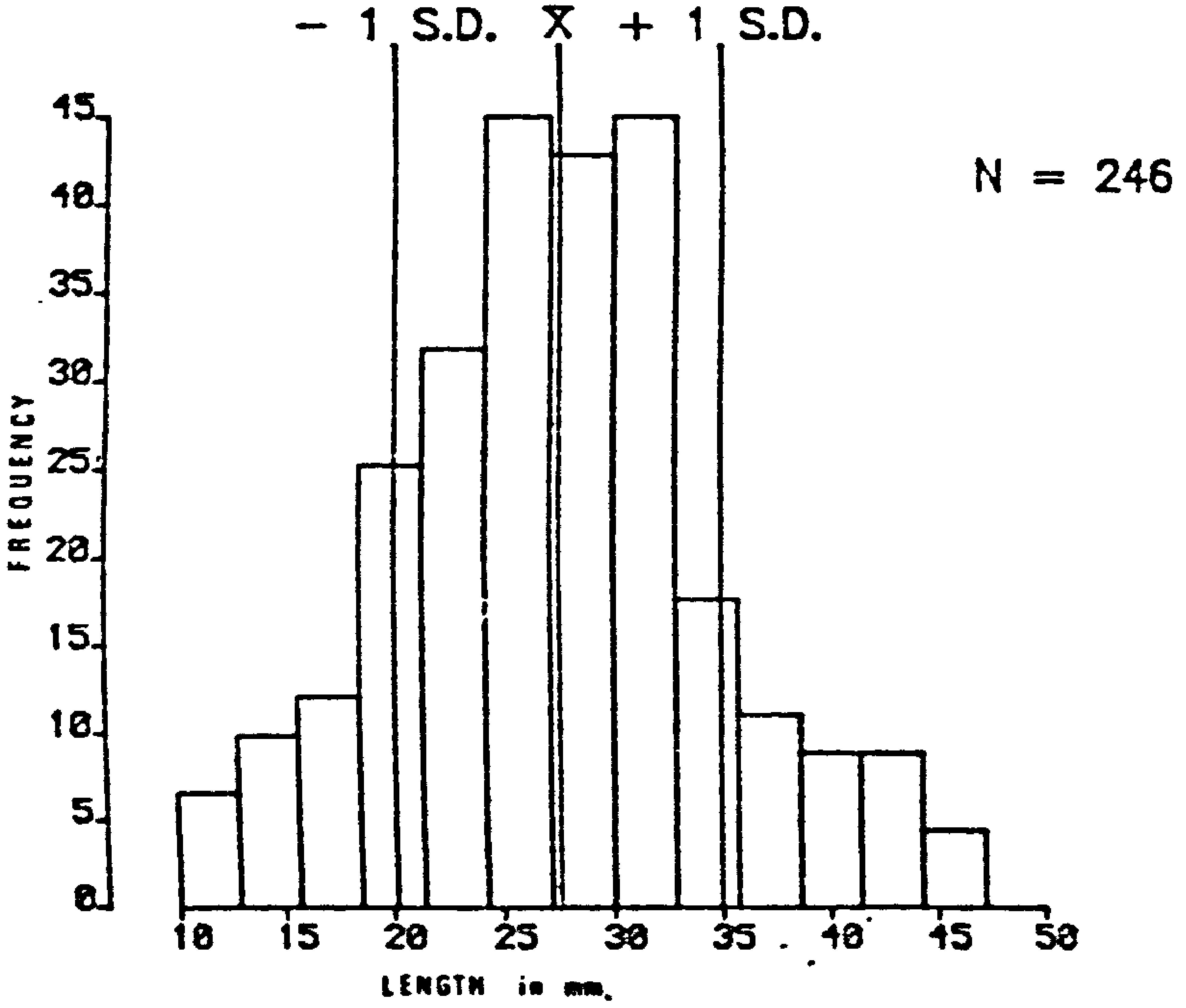
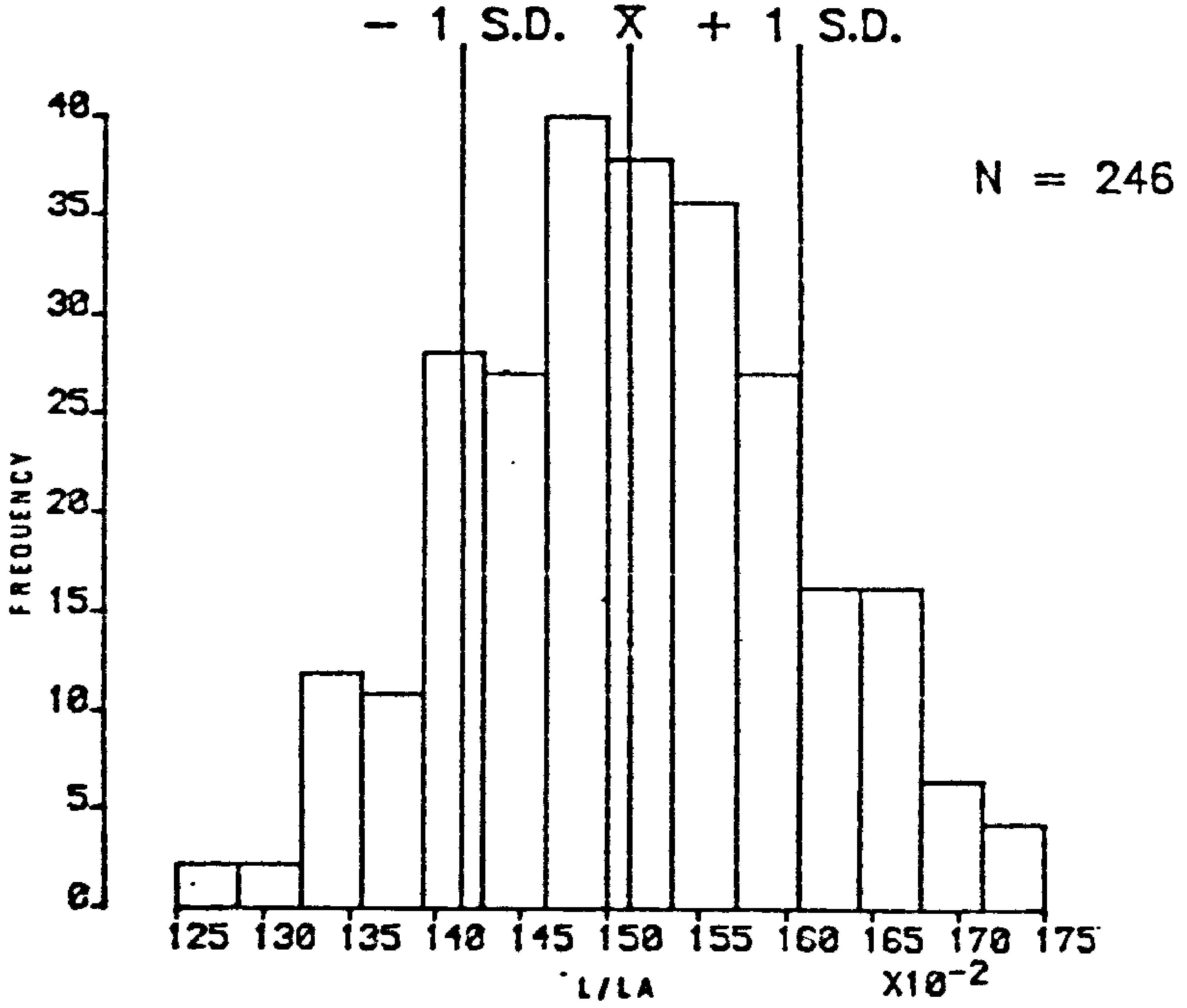


FIG. 5.2

THE LENGTH:LENGTH OF APERTURE DISTRIBUTION OF <u>NUCELLA</u> FROM THE RED CRAG.



5.3 The significance of the shell shape of Nucella from the Red Crag.

The data used by Crothers' (1973) to produce his regression equation, is spread about the regression line such that it is at best accurate to within plus or minus one BEV (see fig. 3.2). Assuming the results for the Red Crag N. lapillus have a similar accuracy then the BEVs are possibly one value out due to the inherent error of this method. As the mean values of Crothers (1973) are used then the spread of each sample must also be considered. The range of the L/ LA distribution from the Red Crag is 0.5 and this adds another increment of potential error to the results. Bearing this in mind the variation in the results is surprizingly small, from 6.5 to 7.9 indicating coastlines which were sheltered, very sheltered or extremely sheltered. There is little doubt that the rocky coastlines of the Red Crag were not exposed to severe wave action.

The small range inferred by the results, plus the wide confidence levels (which can be accounted for by the above degree of error) makes it impossible to detect any valid spatial pattern. A plot of the data on a map showed no apparent simple spatial trend over the area (even assuming the results are completely accurate). A similar plot for the mean lengths of N. lapillus was also lacking an obvious trend.

Modern N. lapillus populations do approximate a normal distribution (Crothers pers. com.) mainly due to the fact that they breed all year round (Fretter and Graham 1962, p. 410). These are however living populations and do not represent the shells that are available for fossilization (Craig and Oertel 1966). If the shells have been sorted and the distribution is a result of this, the fact that the BEVs are all similar and that size of shell does not significantly affect the results means that little information has been lost.

Ballantine (1961) states that rocky coasts of his value 7 and 8 are rare, as conditions are too calm for them to form. The rocks in East Anglia however, namely Chalk and Coralline Crag, are softer than those of South Wales (where the scale was erected). This would favour the formation of rocky coastlines under the placid conditions of BEV 7 and 8.

The problems relating to such an interpretation of wave exposure based on Crothers' (1973) regression are: i) can Ballantine's scale of exposure and the regression relationship be extended far from South Wales and ii) can they be extended into the past. Ballantine himself conceded the first problem, when he extended his scale to Norway and Spain. His method suggested that Norway had few exposed coastlines while nearly all of Spain's were exposed. This latitudinal variation is minimized as Suffolk is at a similar latitude to Pembrokeshire and Crothers (1975) successfully extended the scheme to north-west France. The second problem is one that affects all geological interpretation. There is however no evidence to suggest that *N. lapillus* was any different during the Red Crag than at present.

The Ebling *et al.* (1964) and Kitching *et al.* (1966) theory suggests that the shape of *N. lapillus* from the Red Crag denotes a high incidence of crab predation. The form with a high L/ LA being the better shell in resisting crab induced breakage. A few examples of probable breaks due to crabs have been observed in *N. lapillus* from the Red Crag (see ch. 9). This however does not contradict the wave exposure argument as crab predation is most prevalent in situations of low exposure to wave action (Ebling et al. 1964, Kitching et al. 1966). In fact crab predation is governed by the degree of exposure to wave action and one would expect crab predation to be high in the Red Crag if the coastal conditions were calm.

It is possible that the form of N. lapillus which inhabits exposed coasts had not evolved by Red Crag times. This may be tested by a collection of Coralline Crag dog-whelks and if they include the form which inhabits high exposure coasts then they had evolved by this time. If they show low exposure to wave action then there is still that possibility. It is also possible that the dog-whelks from highly exposed areas have not been preserved due to the very nature of the environment they lived in. This is however unlikely as one would expect a certain degree of mixing with other populations during sedimentary transport and this does not appear to be the case.

Having accepted that the coastlines were sheltered leads one to wonder why they were not exposed to the winter gales and severe storms that are common in the area today. Unfortunately no BEVs have been calculated for the east coast of England. There are, almost certainly, however more exposed coastlines than were inhabited by the dog-whelks of Red Crag times. Perhaps the low pressure systems which affect the British Isles at present were concentrated at different latitudes than today. The literature has revealed no information on wind patterns for this period except for Dixon's (1977a) inference that Red Crag submarine dunes were being driven westwards by easterly and north-easterly gales.

5.4 Summary.

The shells of *N. lapillus* collected from the Red Crag are elongate with a mean length to length of aperture ratio of 1.503. This suggests a low exposure to wave action 7.21 on Ballantine's (1961) scale (very sheltered). The results do not vary markedly from locality to locality suggesting that uniform conditions prevailed.

CHAPTER 6.

Shell shape variation in *Neptunea contraria*.

6.1 The ecology of *Neptunea*.

6.2 Results.

6.3 Discussion.

6.1 The ecology of *Neptunea*.

Neptunea contraria (Linne) is a extant marine prosobranch Neogastropoda, of the Buccinicea Superfamily (Fretter and Graham 1962, p. 643) which lives off the Mediterranean and Atlantic coasts of Spain (Harmer 1914-25, p. 157). Very little is known about this sinistrally coiled whelk and a search of the literature has drawn very little information concerning *N. contraria*. Work on other species of this genus however has revealed some useful facts.

The genus *Neptunea* originated in the Pacific and reached the North Atlantic during the Beringian transgression; late Miocene or Pliocene (Nelson 1973). *N. despecta* and *N. hero* being the two species to penetrate the Bering straits and span the Arctic. *N. despecta* is represented in the Red Crag along with *N. contraria*.

Neptunea is epifaunal (Nelson 1978), *N. humboldtiana* lives on mud and sand substrates between 100-150 fathoms; ~183-328 m (Smith 1971), *N. antiqua* prefers mud or sands but is found on most substrates between 15-110 m (Pearce and Thorson 1967) in the North Atlantic at present.

It is not clear which feeding strategy *Neptunea* uses. Pearce and Thorson (1967) suggest they are scavengers rather than predators whilst Smith (1971) says *N. humboldtiana* preys on bivalves and other gastropods. Fange (1958) found that extracts from the salivary glands of *N. antiqua* are toxic being ammonia based. This is used as a poison to kill or paralyse prey. So at least some of the feeding of *N. antiqua* is the result of active predation.

Both N. antiqua and N. humboldtiana are separately sexed (Pearce and Thorson 1967 and Smith 1971 respectively) and have a 50:50 male to female ratio. Neptunea do not have free swimming larvae (Nelson 1978).

6.2 Results.

Using the program ORIGIN (see 4.2.7) the relationship between the various parameters taken from N. contraria by the shadow casting method (see 3.2) were analysed. From the scatter diagram (fig. 6.1) it can be seen that there is a strong positive correlation between length and length of aperture. Using Spearmans rank correlation [It was decided to use a non-parametric test of correlation as the parameters of the sample do not approximate a normal curve (see below)] a highly significant value of $R=0.97$ was calculated for this distribution ($P < 0.001$). The other parameters were not so dependent for example there is a weak positive correlation of length against translation (see fig. 6.2) $R=0.3$ ($P > 0.001$). Whorl expansion rate shows a very weak negative correlation with both length and translation (see figs. 6.3 and 6.4) $R=-0.2$ ($P > 0.01 < 0.001$) and $R=-0.18$ ($P > 0.01 < 0.001$) respectively.

Switching to the distribution of these parameters it can be seen (figs. 6.5-6.8) that the whorl expansion rate (WER) is the closest approximation to a normal curve out of the four distributions. A chi square comparison was carried out and a value of $X^2=6.11$ was calculated for WER ($P > 0.5 < 0.75$). The values for the other distributions are: length $X^2=10.01$ ($P > 0.9 < 0.95$); length divided

FIG. 6.1

LENGTH AGAINST LENGTH OF APERTURE IN *NEPTUNEA CONTRARIA* FROM THE RED CRAG.

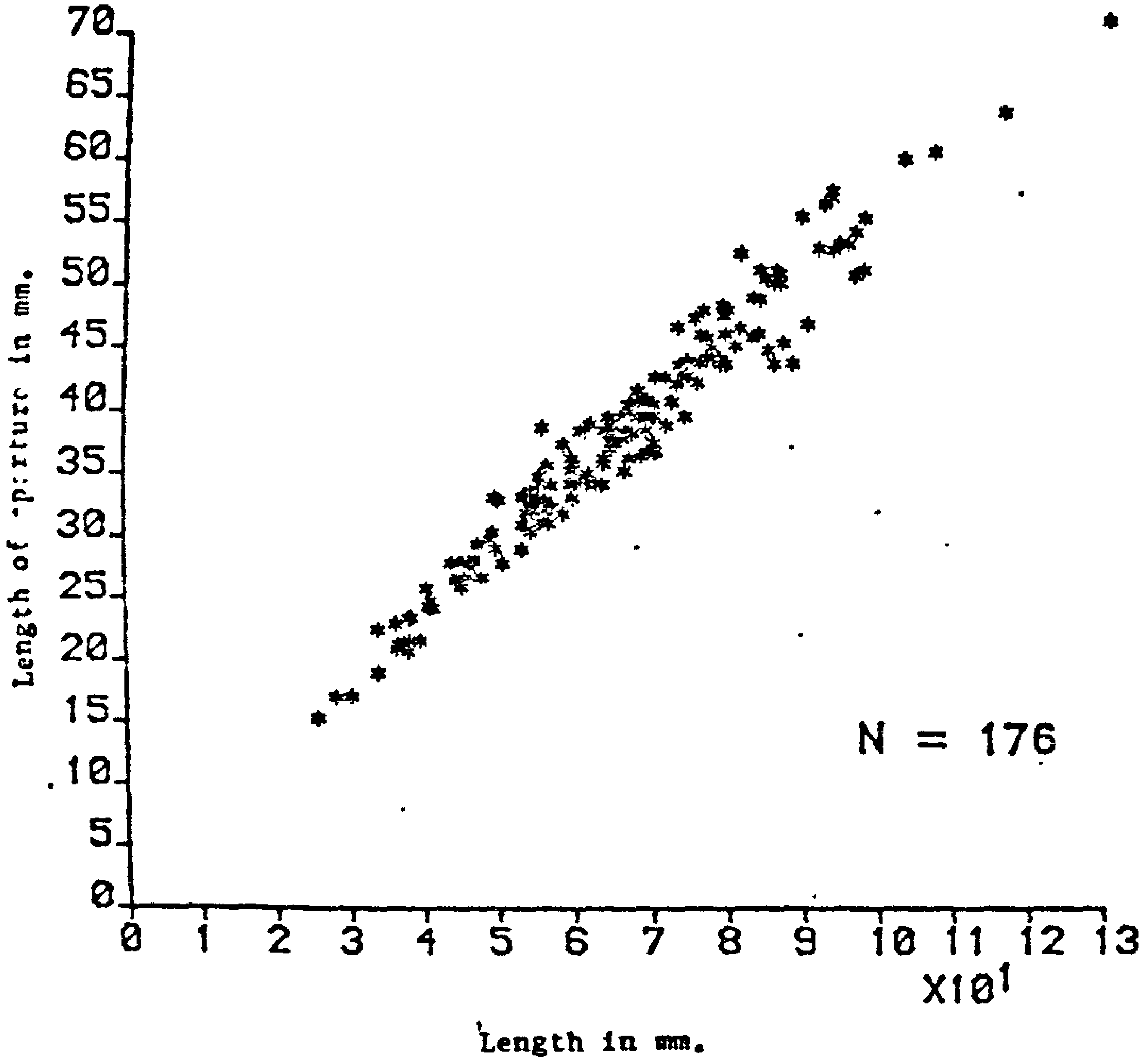


FIG. 6.2

TRANSLATION AGAINST LENGTH IN *N. CONTRARIA* FROM THE RED CRAG.

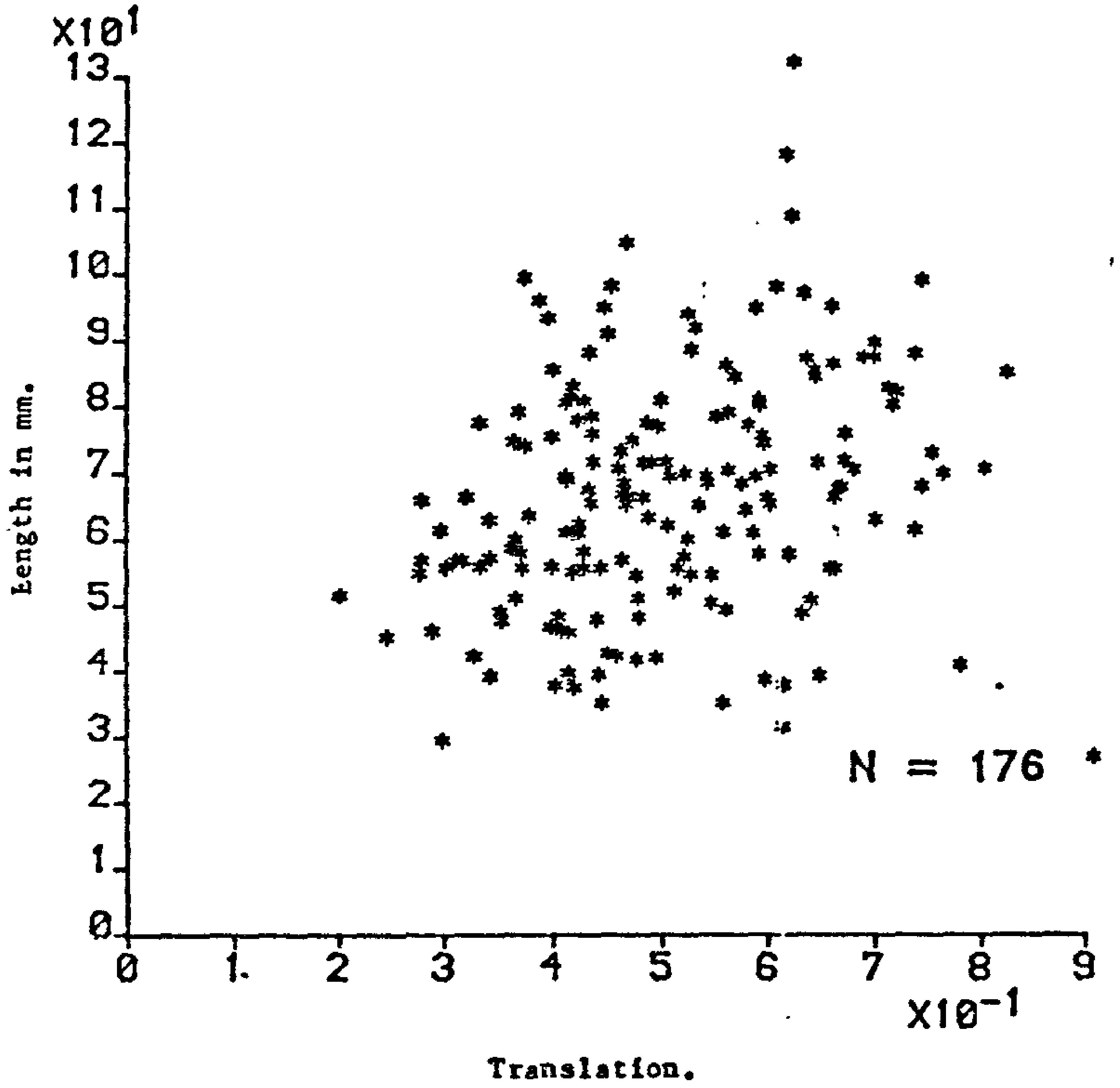


FIG. 6.3

WHORL EXPANSION RATE AGAINST LENGTH IN N. CONTRARIA FROM THE RED CRAG.

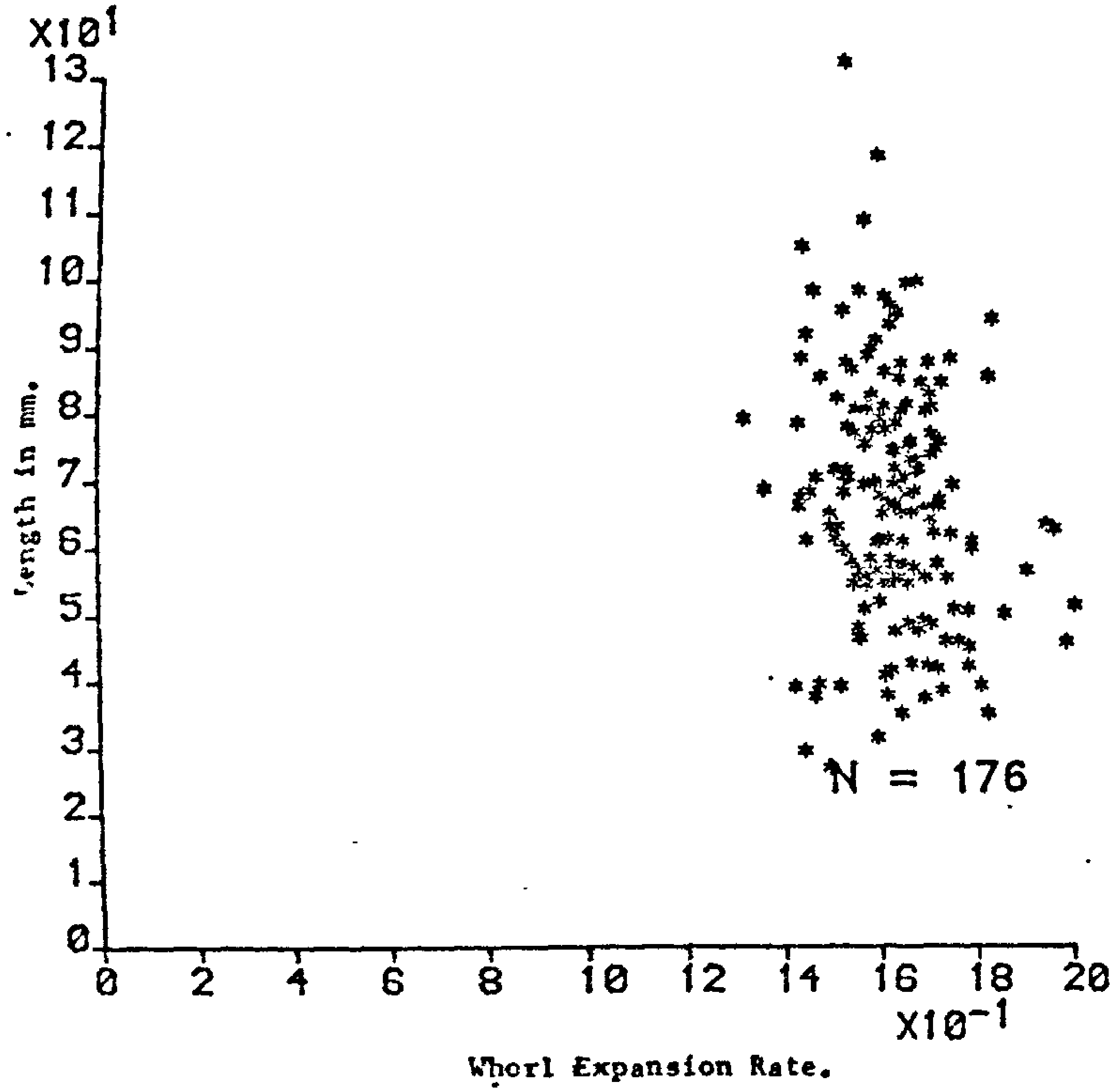


FIG. 6.4

TRANSLATION AGAINST WHORL EXPANSION RATE IN N. CONTRARIA FROM THE RED CRAG.

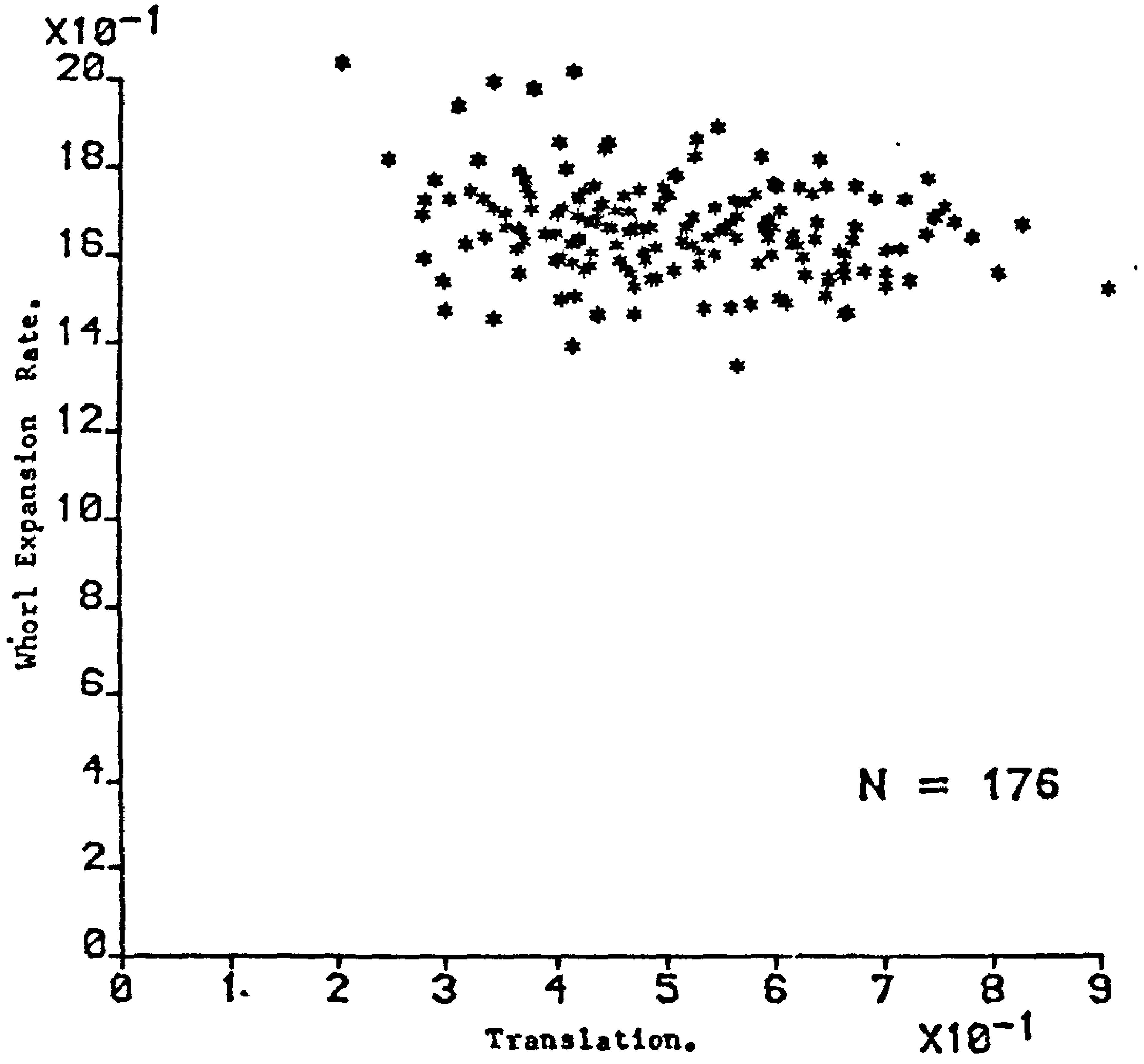


FIG. 6.5

THE LENGTH DISTRIBUTION OF NEPTUNEA CONTRARIA FROM THE RED CRAG.

N = 176

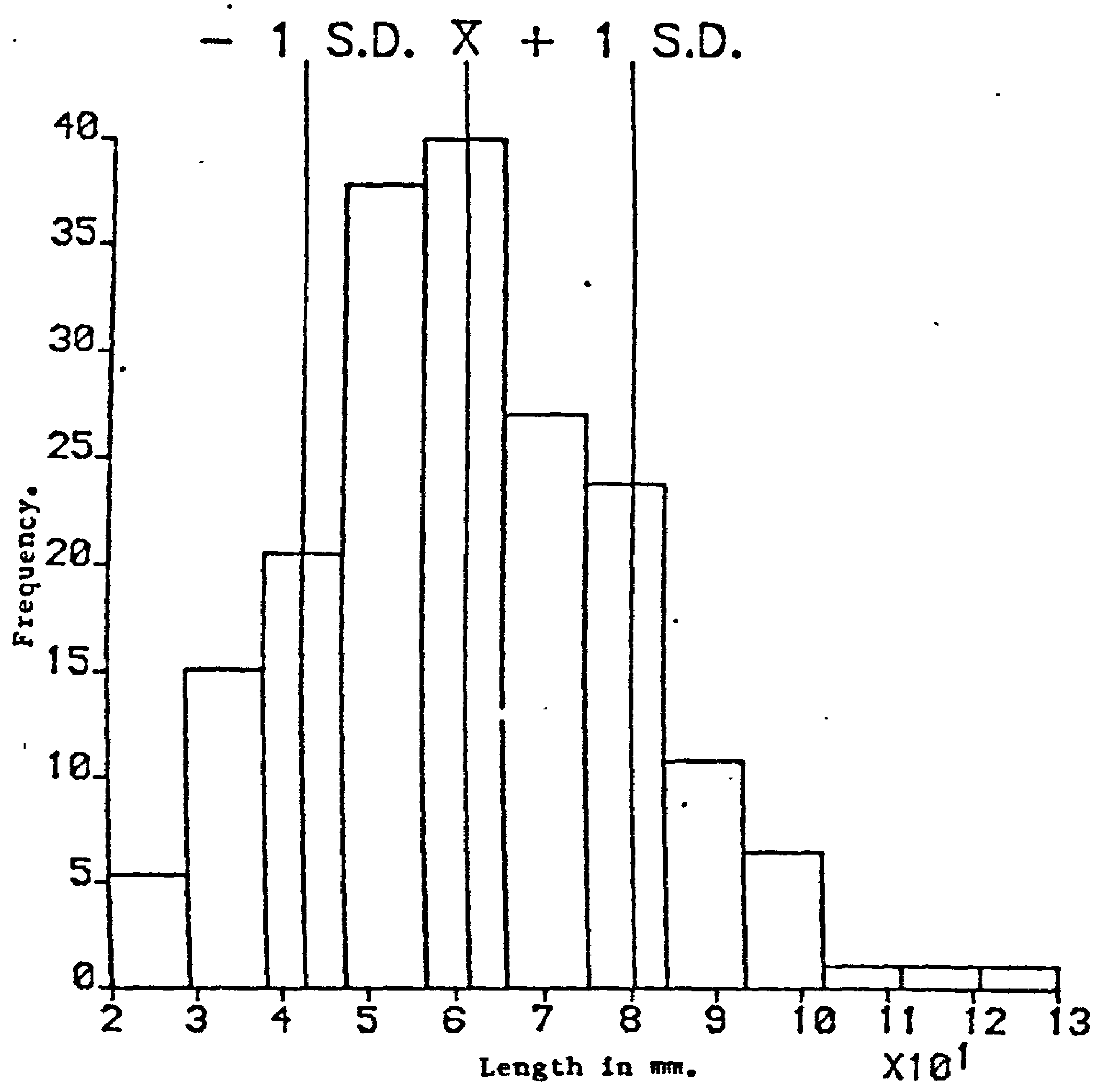


FIG. 6.6

THE LENGTH TO LENGTH OF APERTURE RATIO DISTRIBUTION OF N. CONTRARIA FROM THE RED CRAG.

N = 176

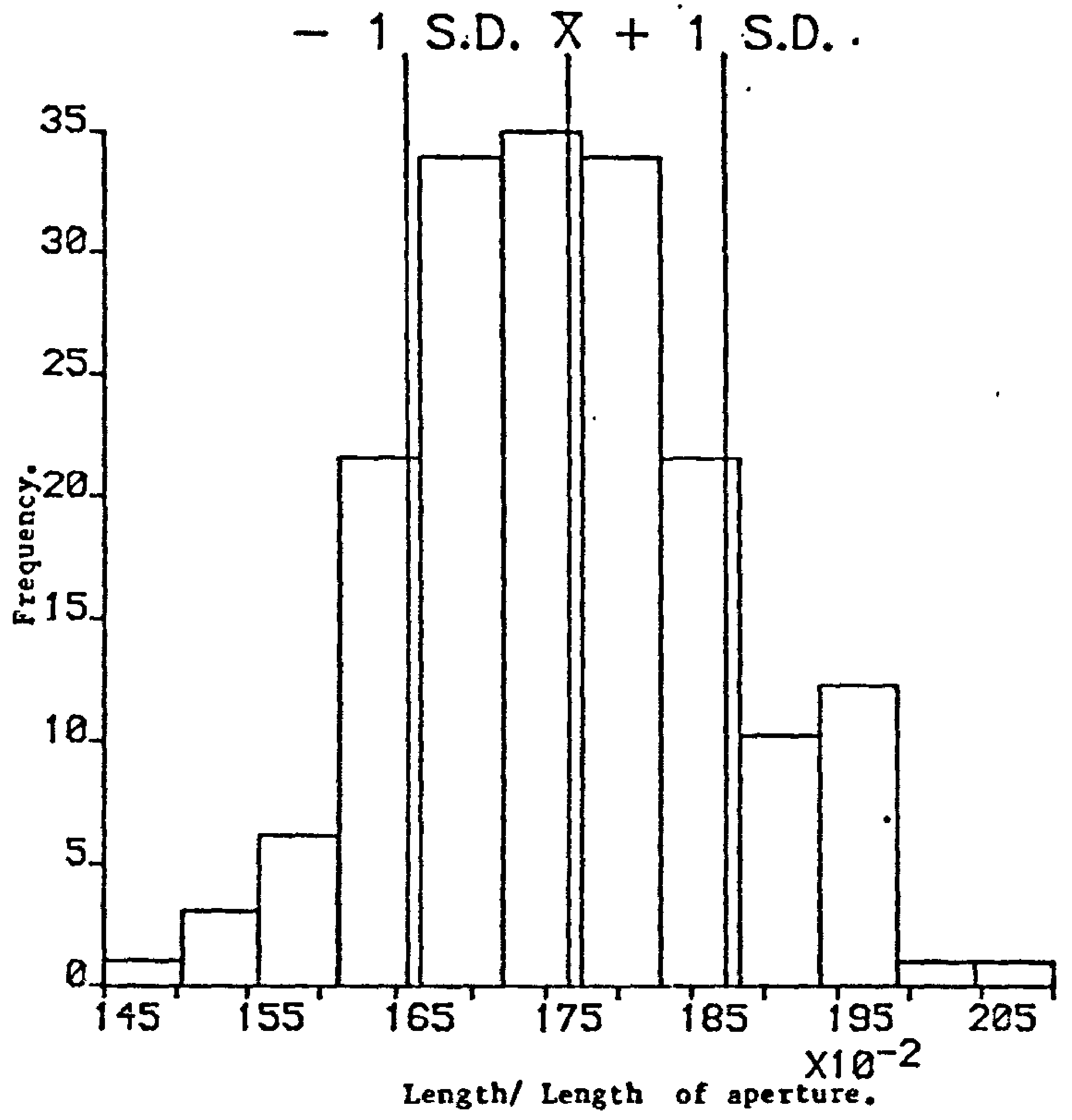


FIG. 6.7

THE TRANSLATION DISTRIBUTION OF *N. CONTRARIA* FROM THE RED CRAG.

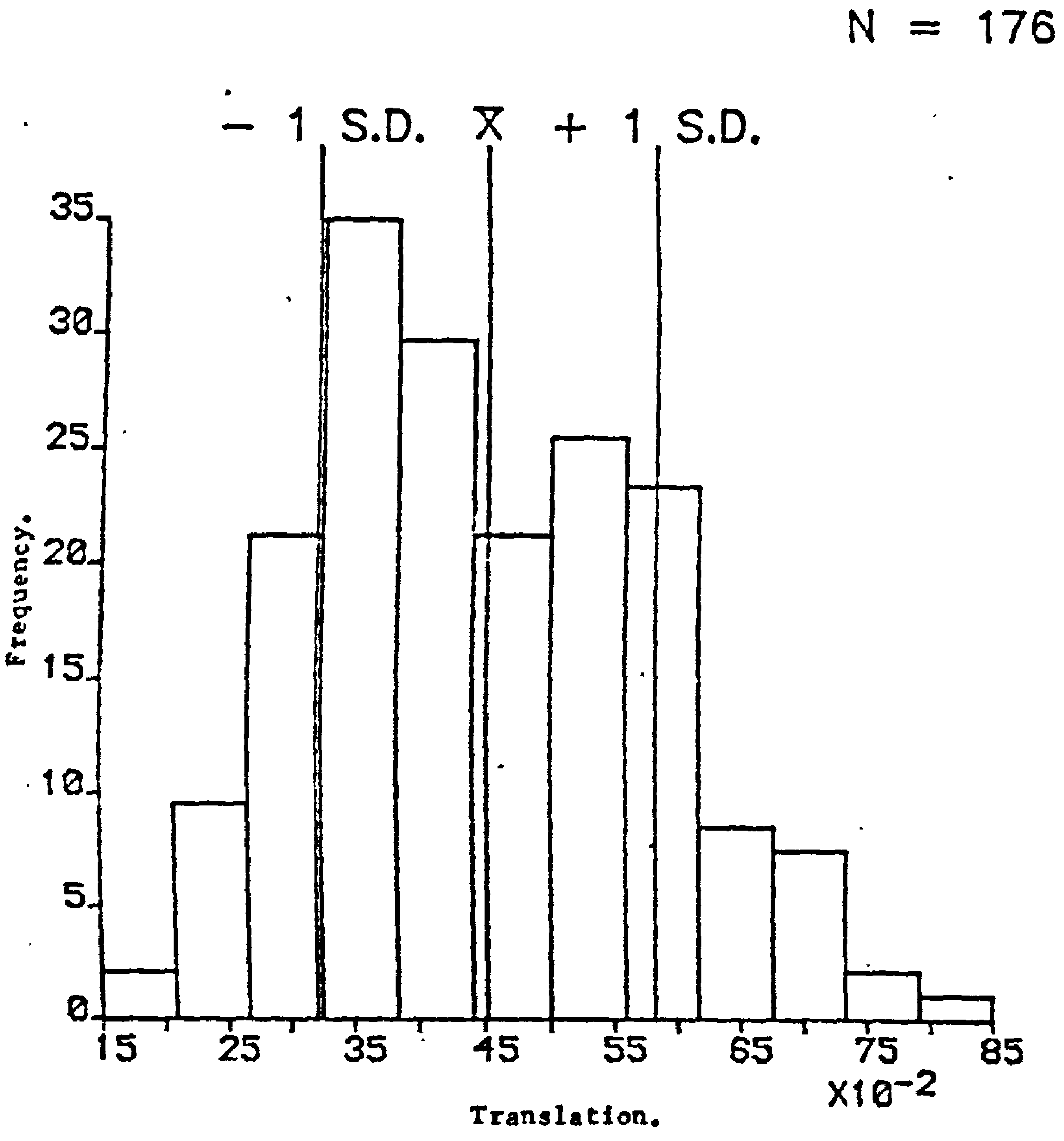
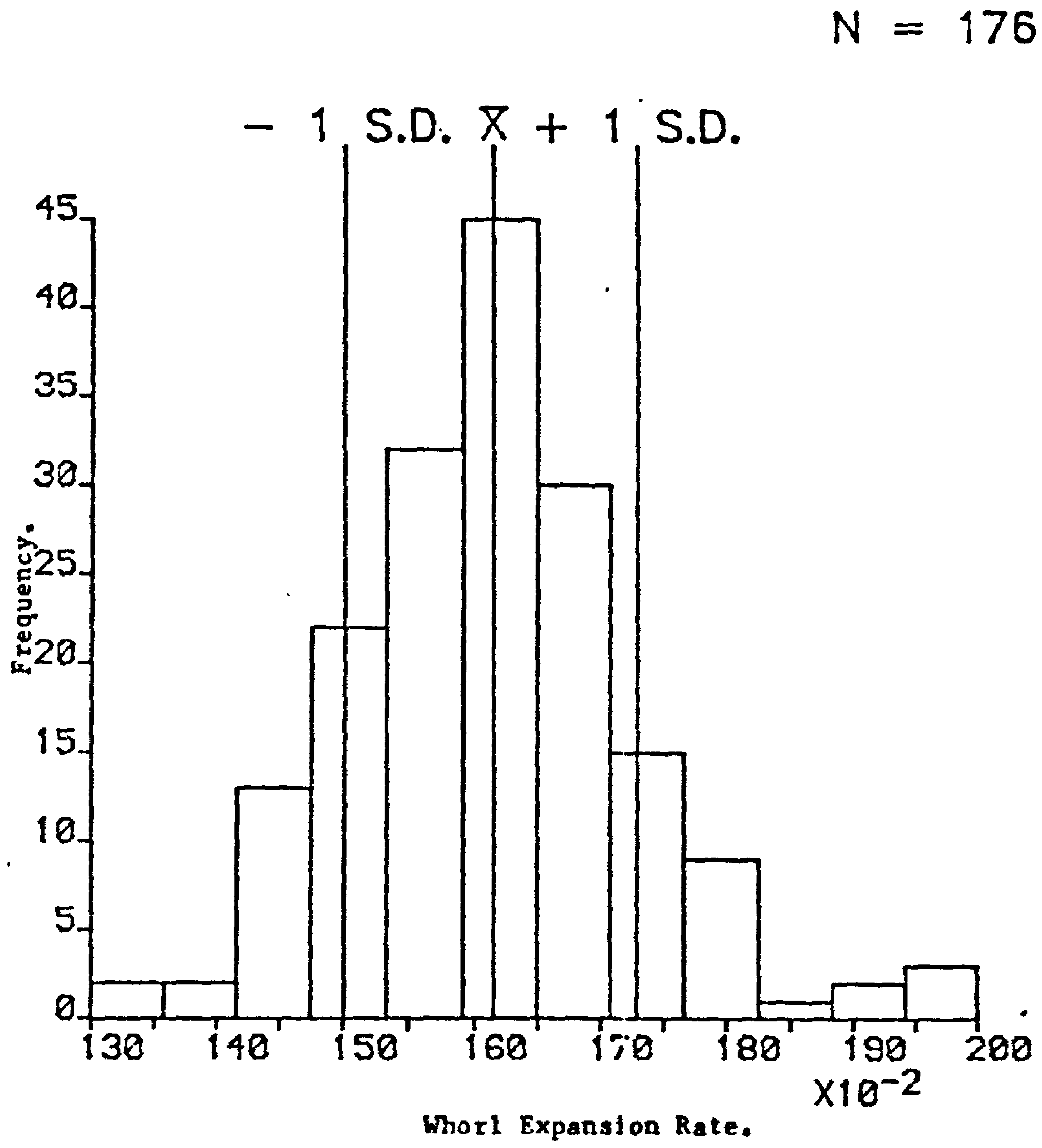


FIG. 6.8

THE WHORL EXPANSION RATE OF *N. CONTRARIA* FROM THE RED CRAG.



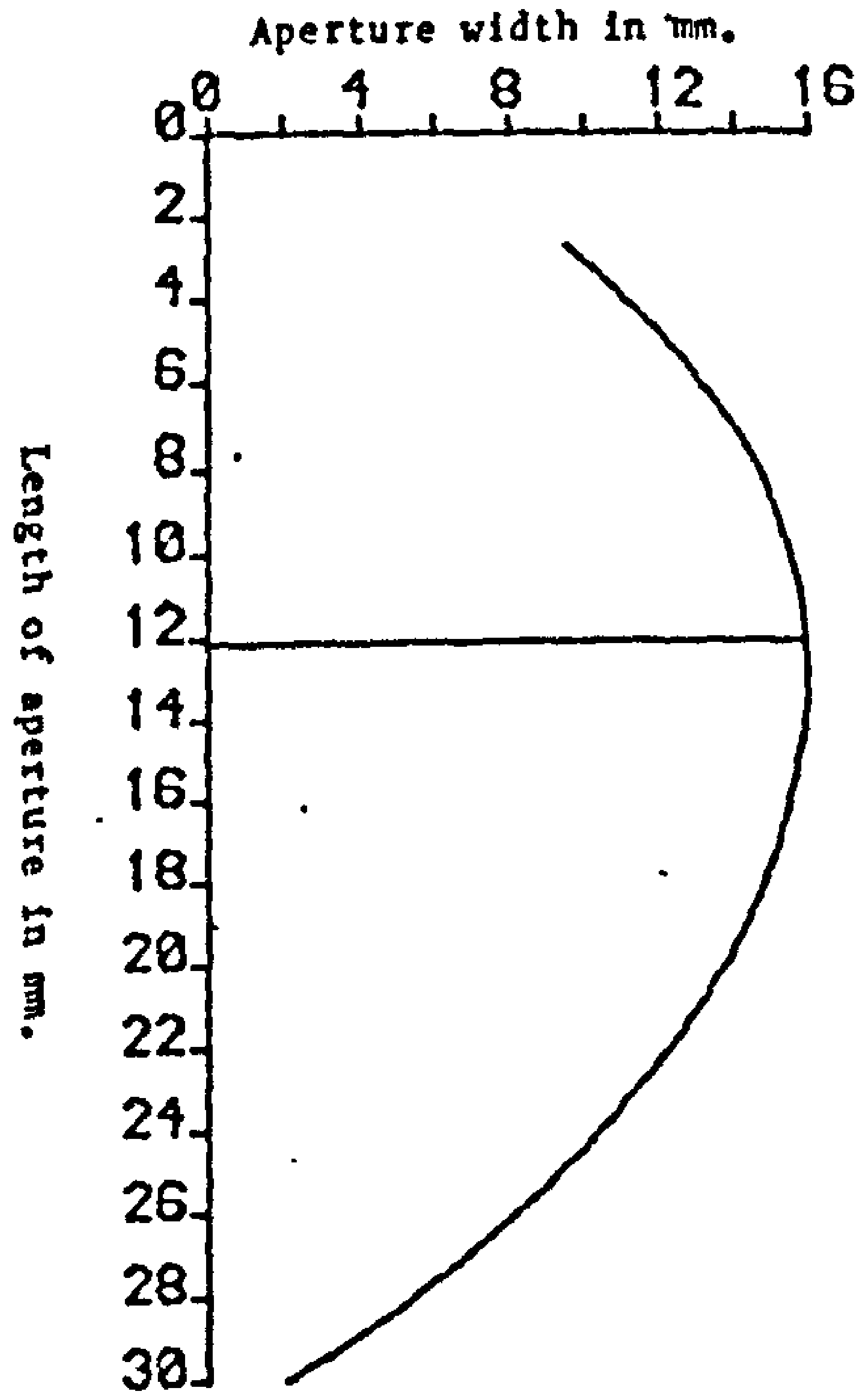
by length of aperture (L/ LA) $X^2=11.74$ ($P > 0.95 < 0.975$); and translation, $X^2=10.97$ ($P > 0.9 < 0.95$). Although none of these three distributions are particularly close to a normal curve only translation (see fig. 6.7) is markedly bimodal.

The output from the program GASTRO (see 4.2.3) can be seen in figs. 6.9-6.21. The first three diagrams (figs. 6.9-6.11) represent an average shell shape for two localities, Stratton Hall [6] and Waldringfield Heath [18], and for the entire Red Crag sample. Altogether 176 specimens were shadow casted, measured and included in the data file, NEPALL. The remaining diagrams represent individuals from that sample with the most extreme examples, both maximum and minimum, of the parameters measured. This gives an impression of the range of variation of these parameters. Some of the specimens demonstrated the most extreme examples of more than one parameter and in these cases only one diagram was plotted. A list was compiled (see below) of the specimen number with the maximum and minimum of each parameter and the corresponding diagram from GASTRO can be found between figs. 6.12 and 6.21.

A specimen number list of N. contraria with maximum and minimum parameters (see text for explanation).

	Maximum.	Minimum.
Length	22	13
LA	22	13
L/ LA	79	137
Translation	13	118
WER	118	151

Fig 6.9



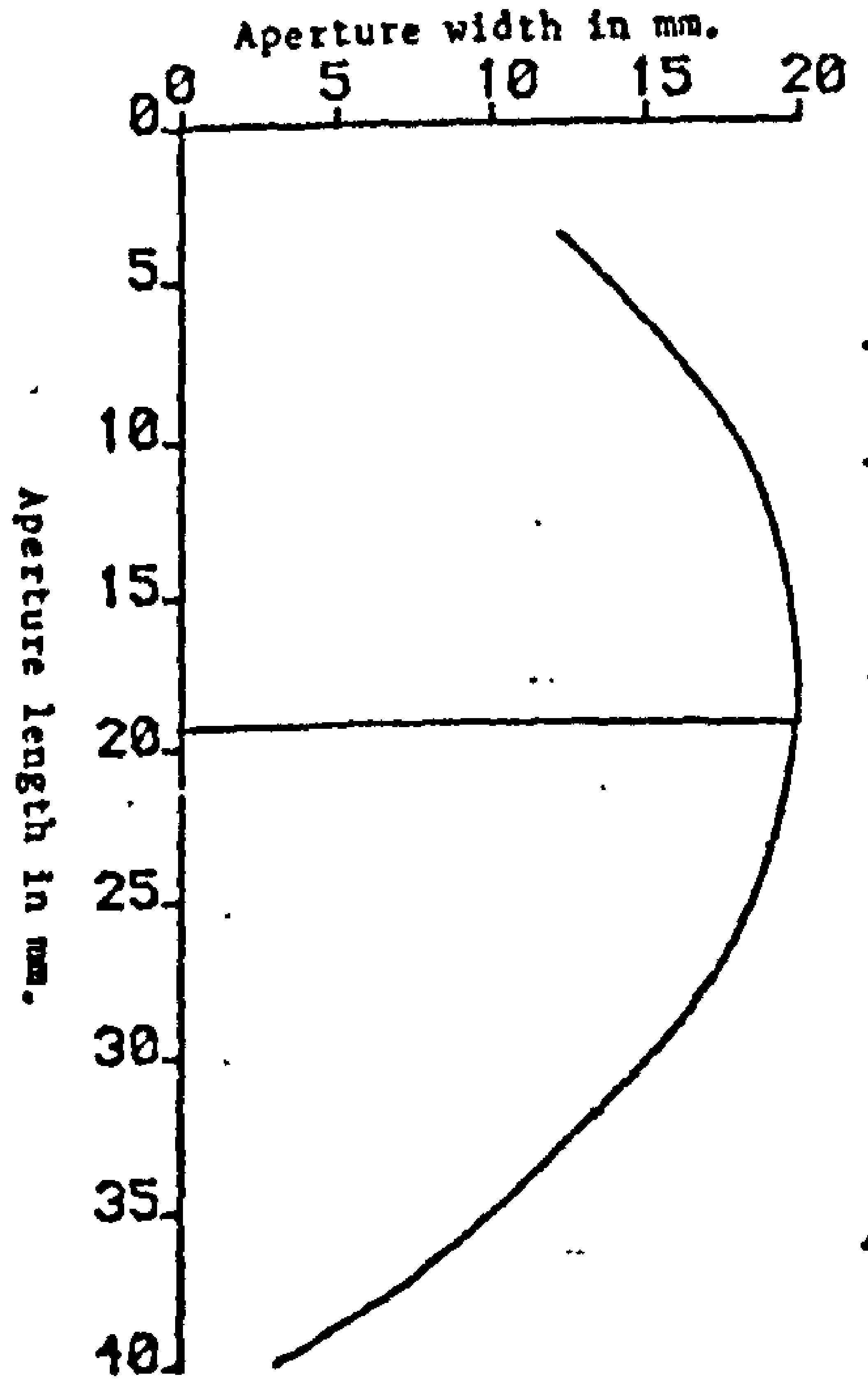
THE AVERAGE SHAPE OF NEPTUNEA CONTRARIA FROM STRATTON HALL.

TRANSLATION = 0.40

WHORL EXPANSION = 1.65

N = 54

Fig 6.10



THE AVERAGE SHAPE OF NEPTUNEA CONTRARIA FROM WALDRINGFIELD.

TRANSLATION = 0.48

WHORL EXPANSION = 1.60

N = 96

FIG. 6.11

THE AVERAGE SHELL SHAPE OF

NEPTUNEA CONTRARIA, RED CRAG

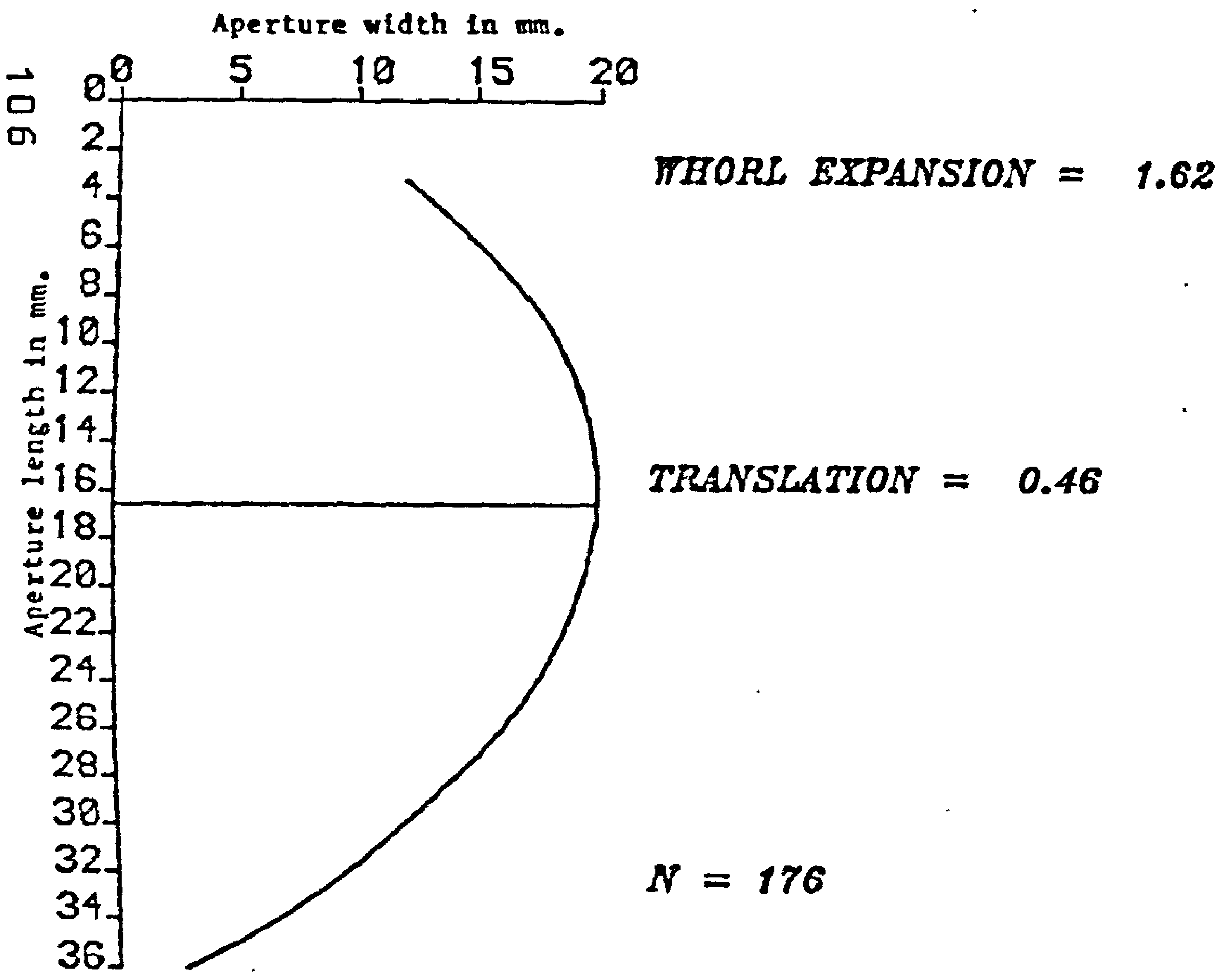


FIG. 6.12

THE SPECIMEN OF N. CONTRARIA

WITH THE GREATEST

TRANSLATION:13.

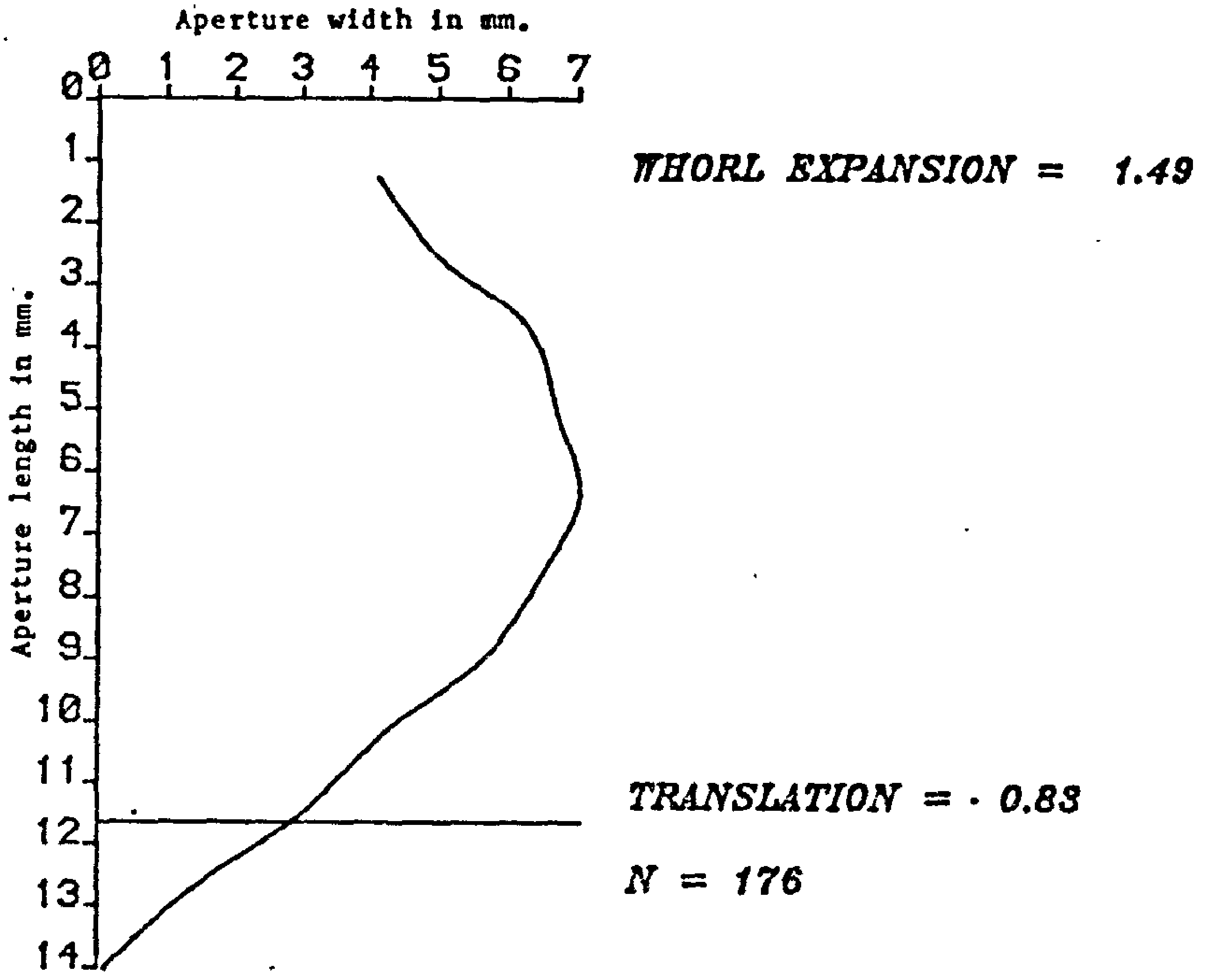
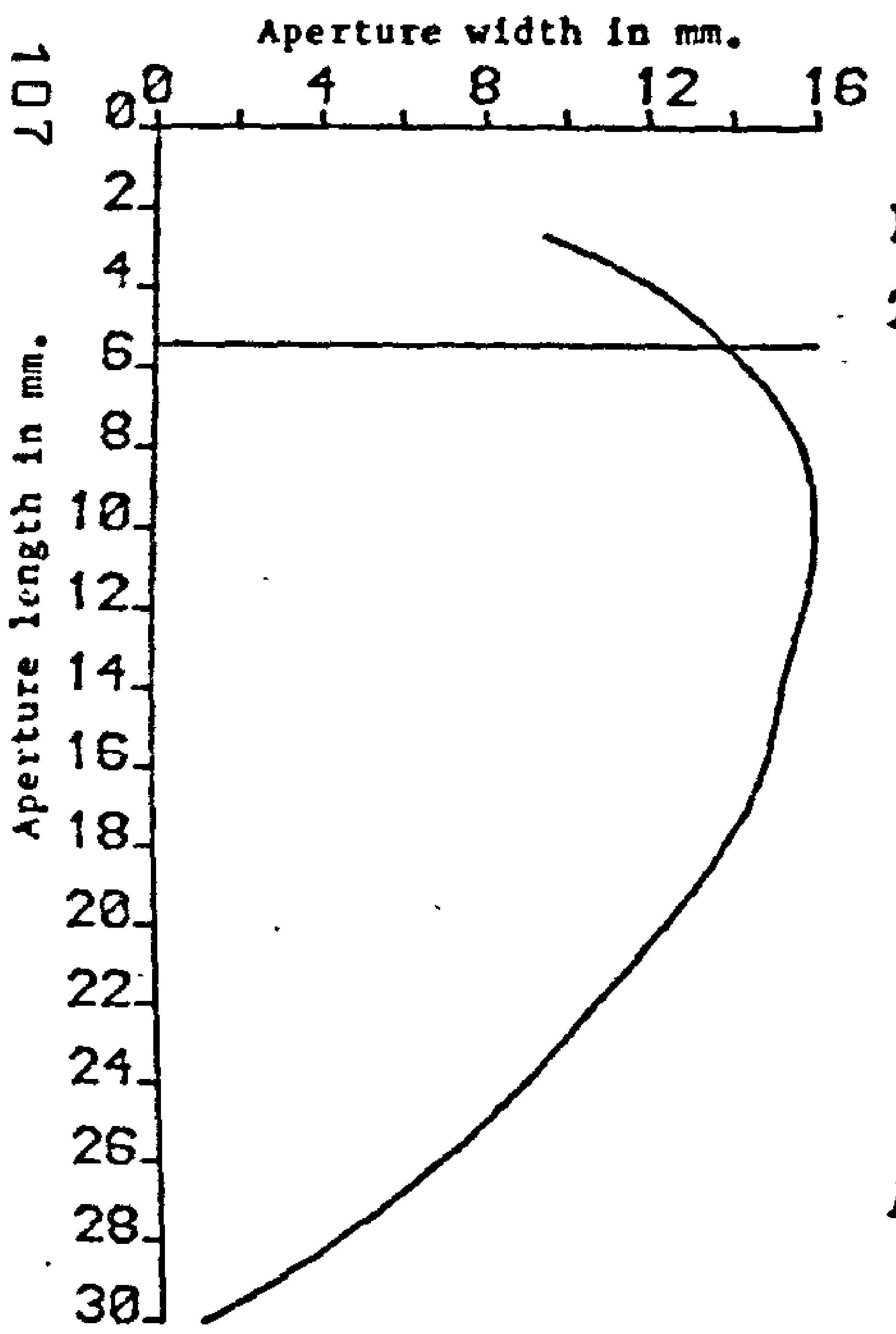


FIG. 6.13

THE SPECIMEN OF N. CONTRARIA WITH THE GREATEST WHORL EXPANSION, 118.



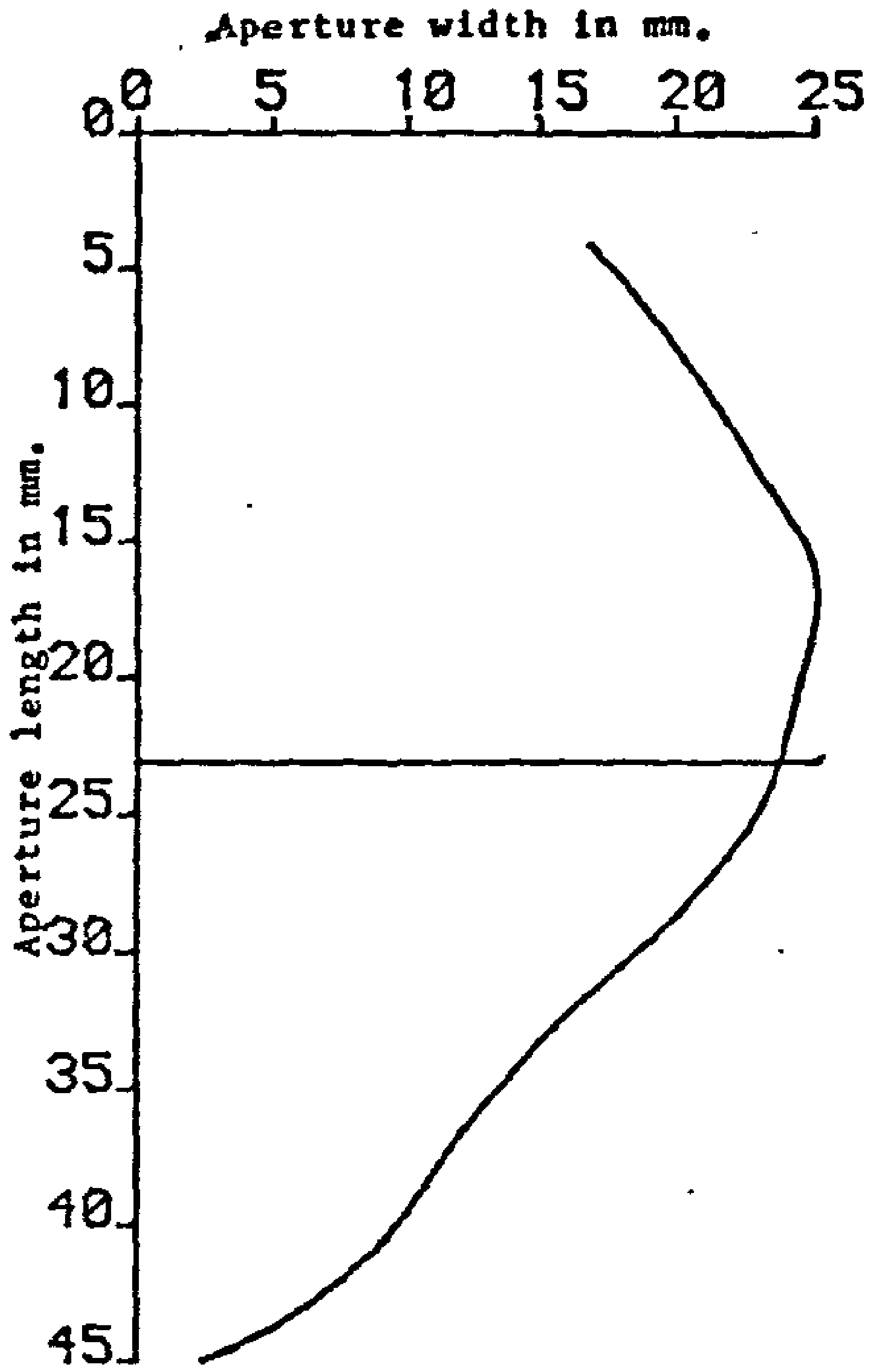
WHORL EXPANSION = 2.00

TRANSLATION = 0.18

N = 176

FIG. 6.14

THE SPECIMEN OF N. CONTRARIA WITH THE SMALLEST WHORL EXPANSION RATE:151.



WHORL EXPANSION = 1.31

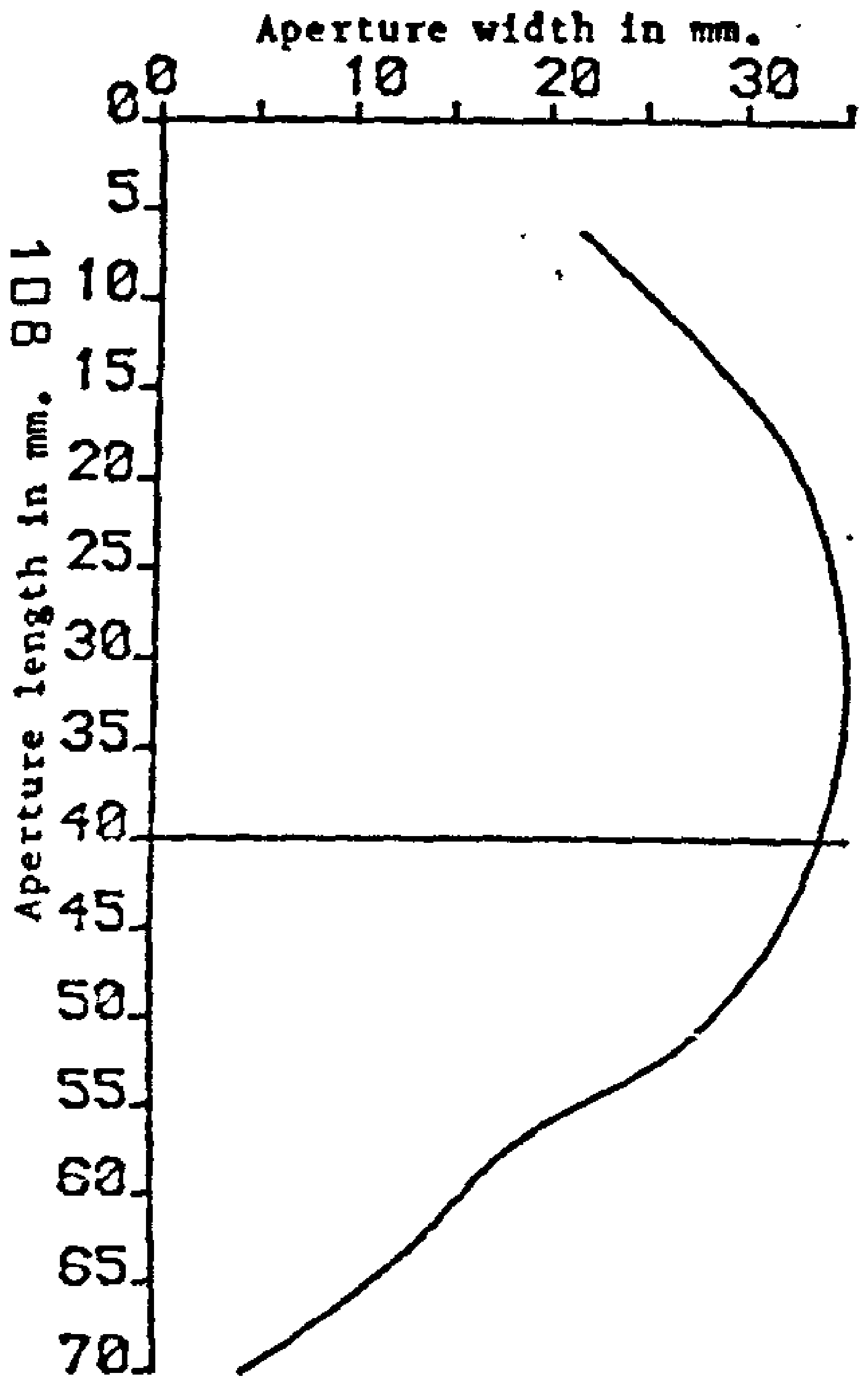
TRANSLATION = 0.51

N = 176

FIG 6.15

THE SPECIMEN OF N. CONTRARIA

WITH THE MAXIMUM LENGTH:22.



WHORL EXPANSION = 1.51

TRANSLATION = 0.57

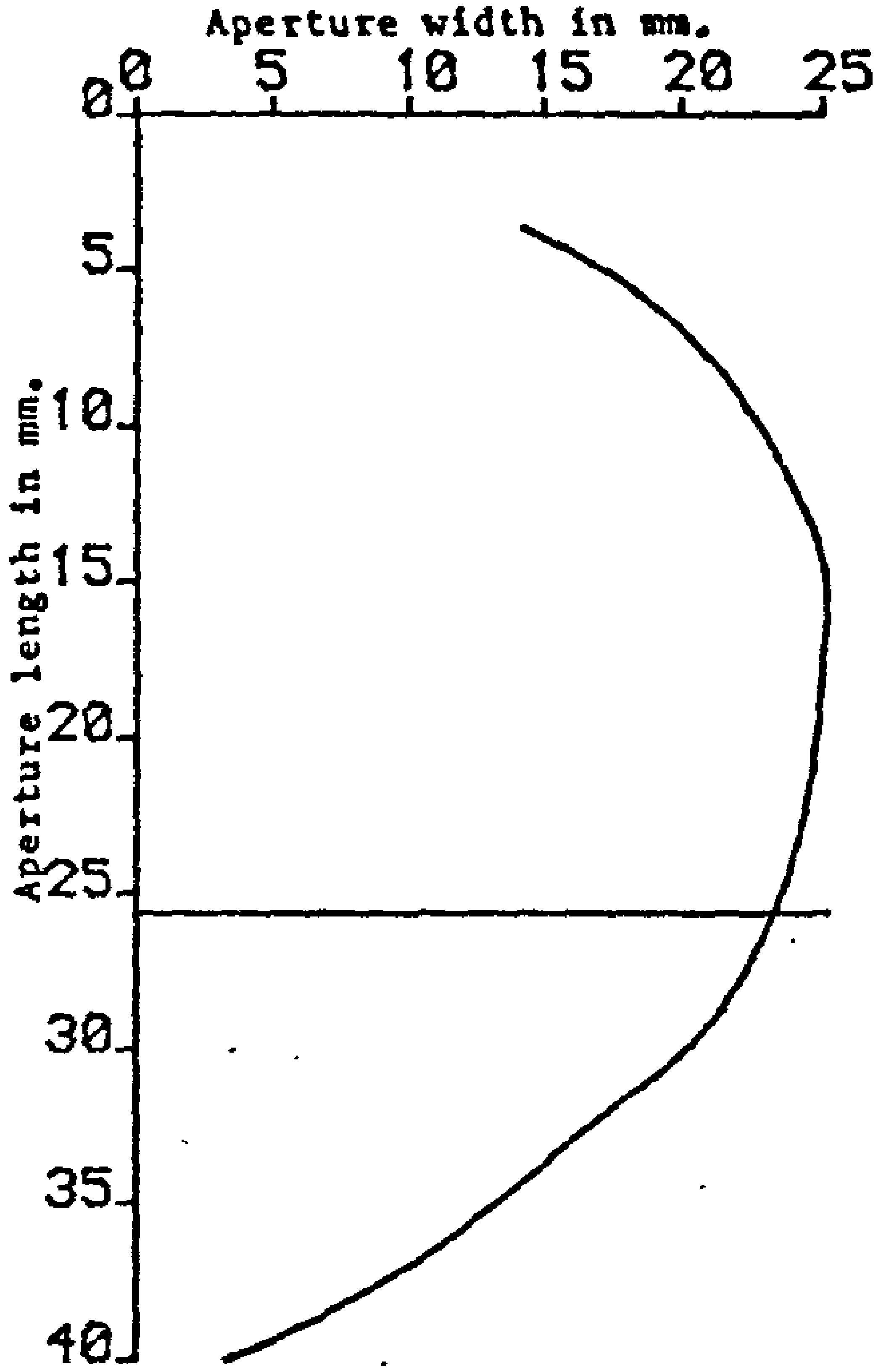
N = 176

FIG. 6.16

THE SPECIMEN OF N. CONTRARIA

WITH THE MAXIMUM LENGTH TO

LENGTH OF APERTURE RATIO:79.



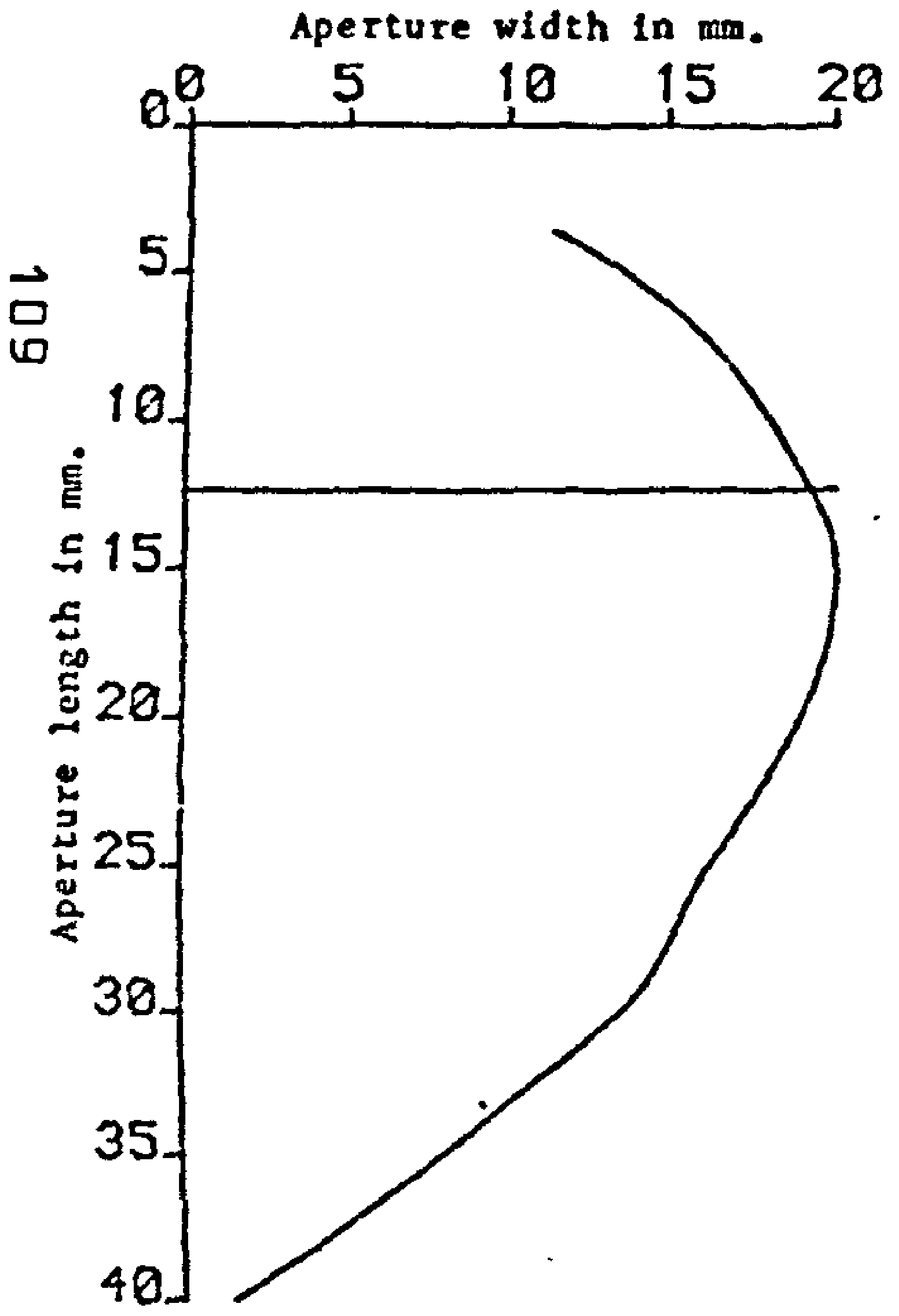
WHORL EXPANSION = 1.57

TRANSLATION = 0.64

N = 176

FIG. 6.17

THE SPECIMEN OF N. CONTRARIA
WITH THE MINIMUM LENGTH TO
LENGTH OF APERTURE RATIO:137



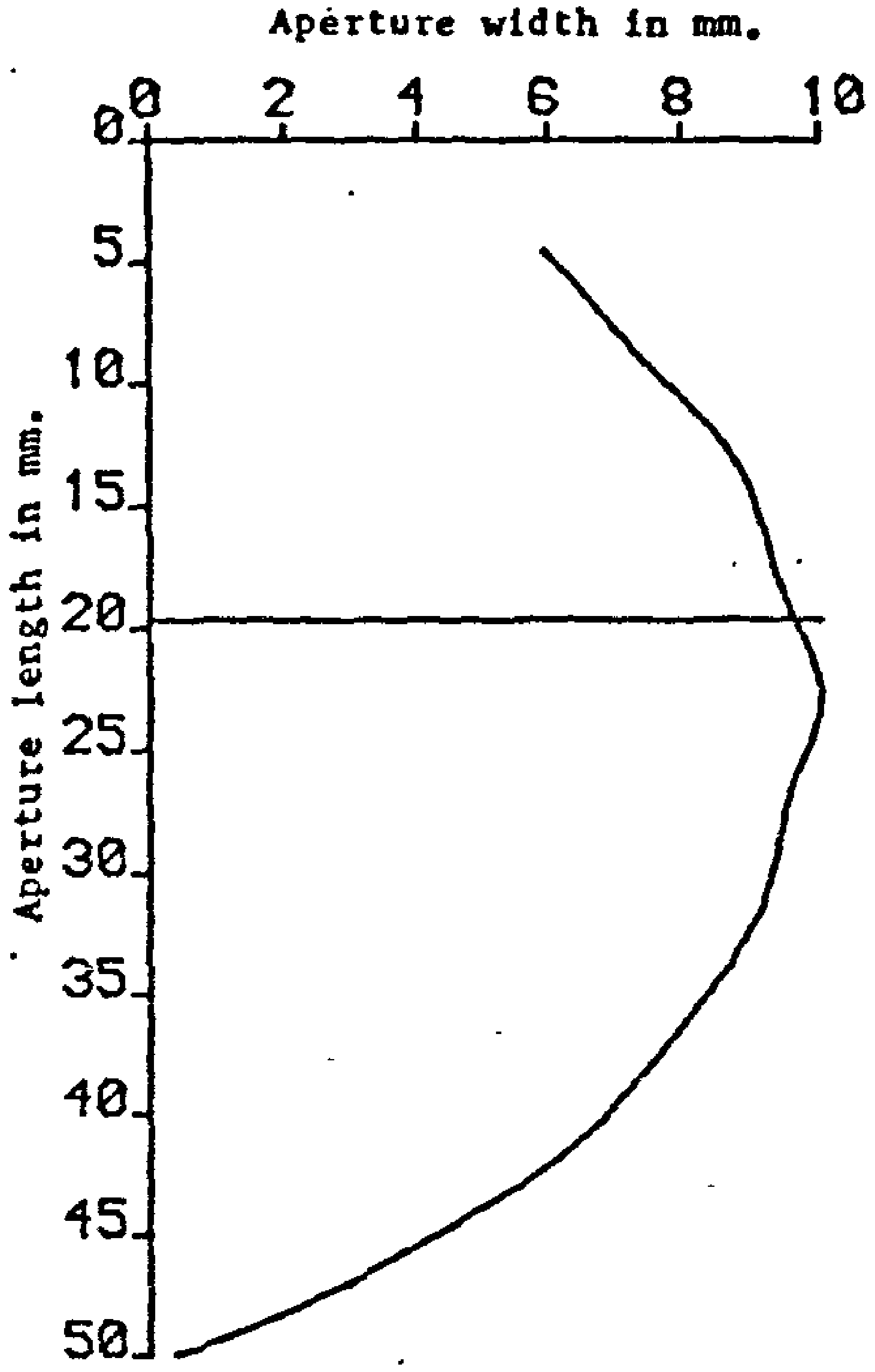
WHORL EXPANSION = 1.67

TRANSLATION = 0.31

N = 176

FIG. 6.18

THE SPECIMEN OF N. CONTRARIA
WITH THE NARROWEST APERTURE
IN RESPECT TO LENGTH:154.



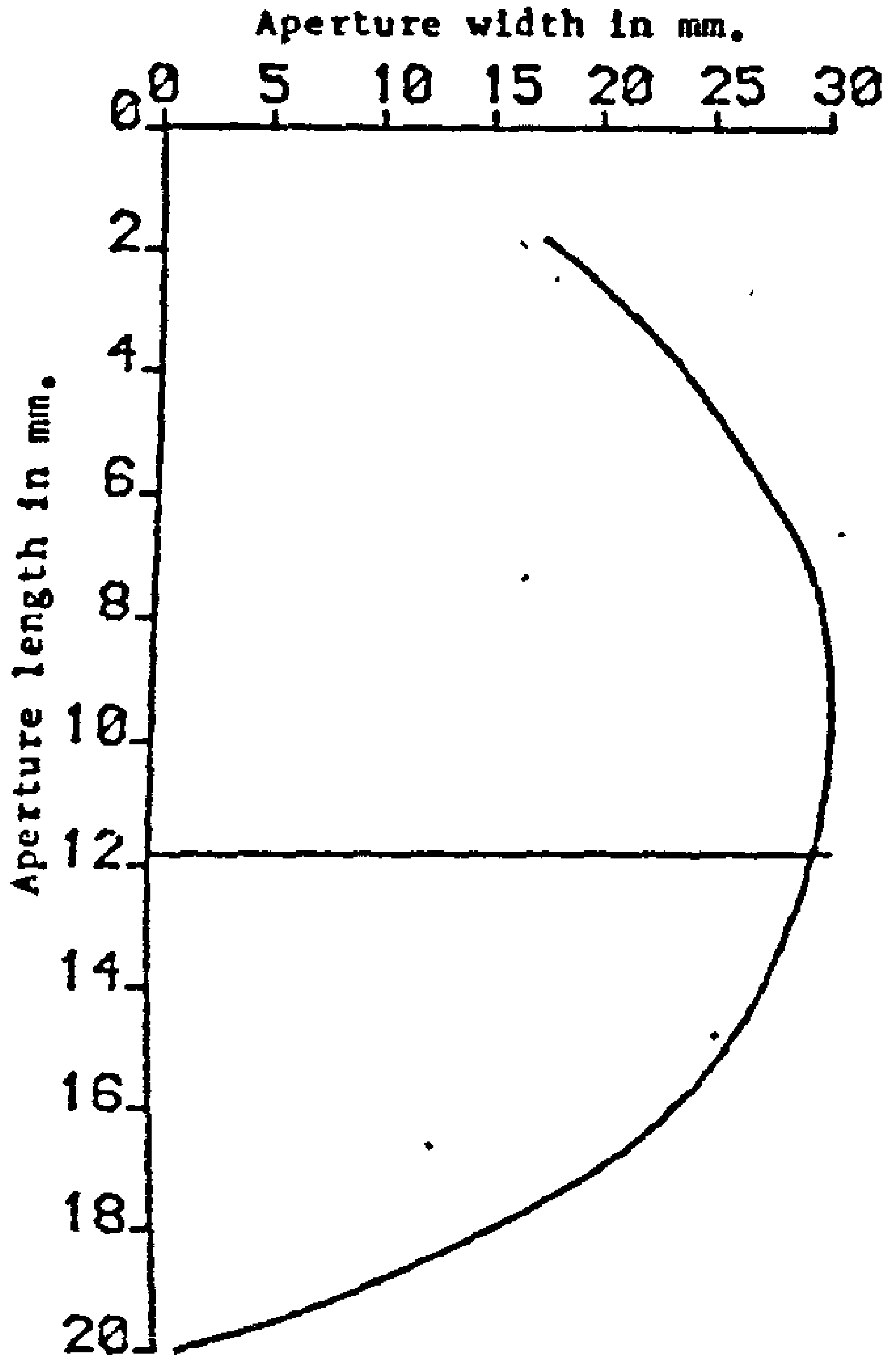
WHORL EXPANSION = 1.43

TRANSLATION = 0.39

N = 176

FIG. 6.19

THE SPECIMEN OF N. CONTRARIA WITH THE WIDEST APERTURE IN RESPECT TO LENGTH:153.



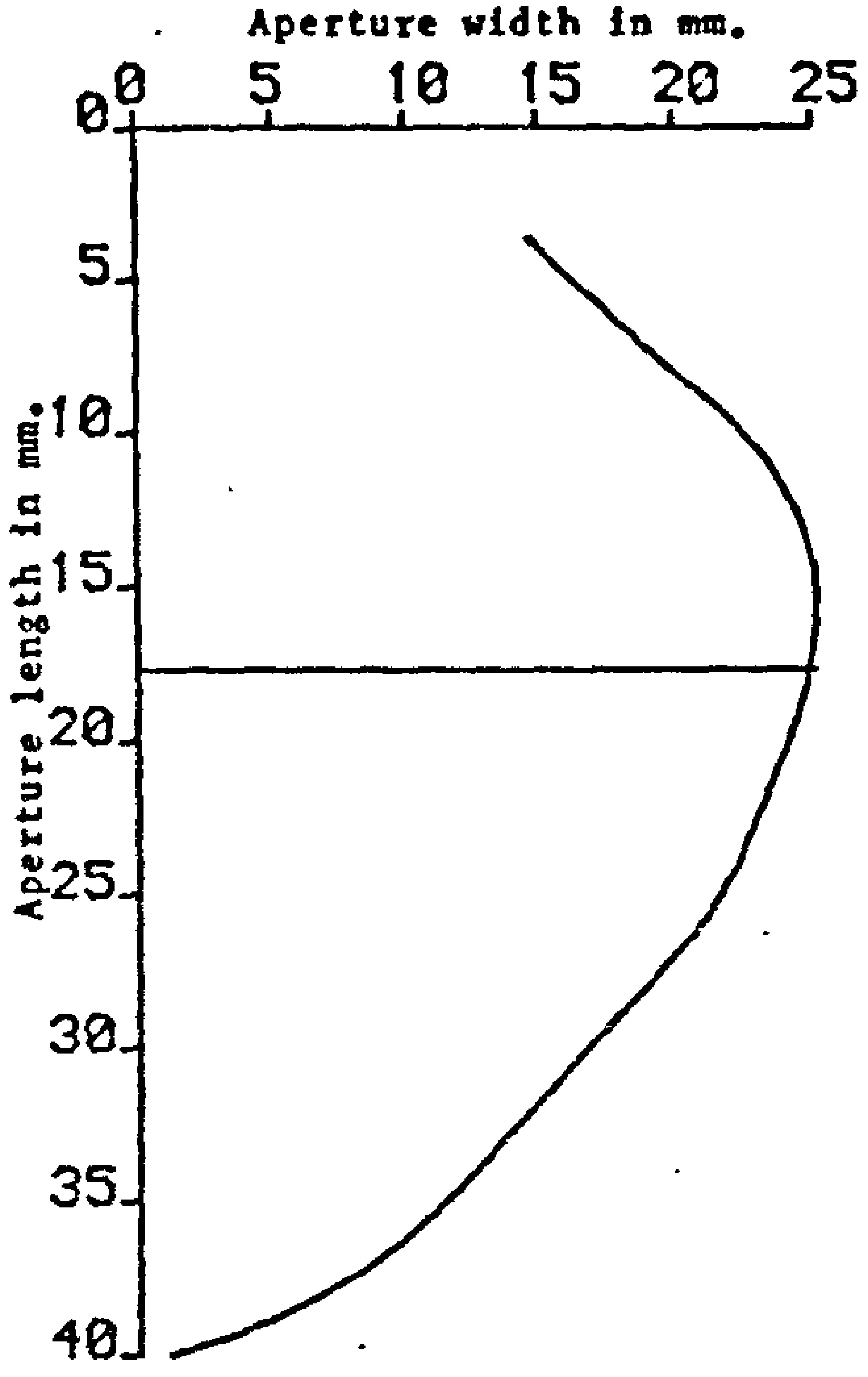
WHORL EXPANSION = 1.51

TRANSLATION = 0.59

N = 176

FIG. 6.20

THE SPECIMEN WITH THE WIDEST POINT OF THE APERTURE HIGHEST ON THE APERTURE:176.



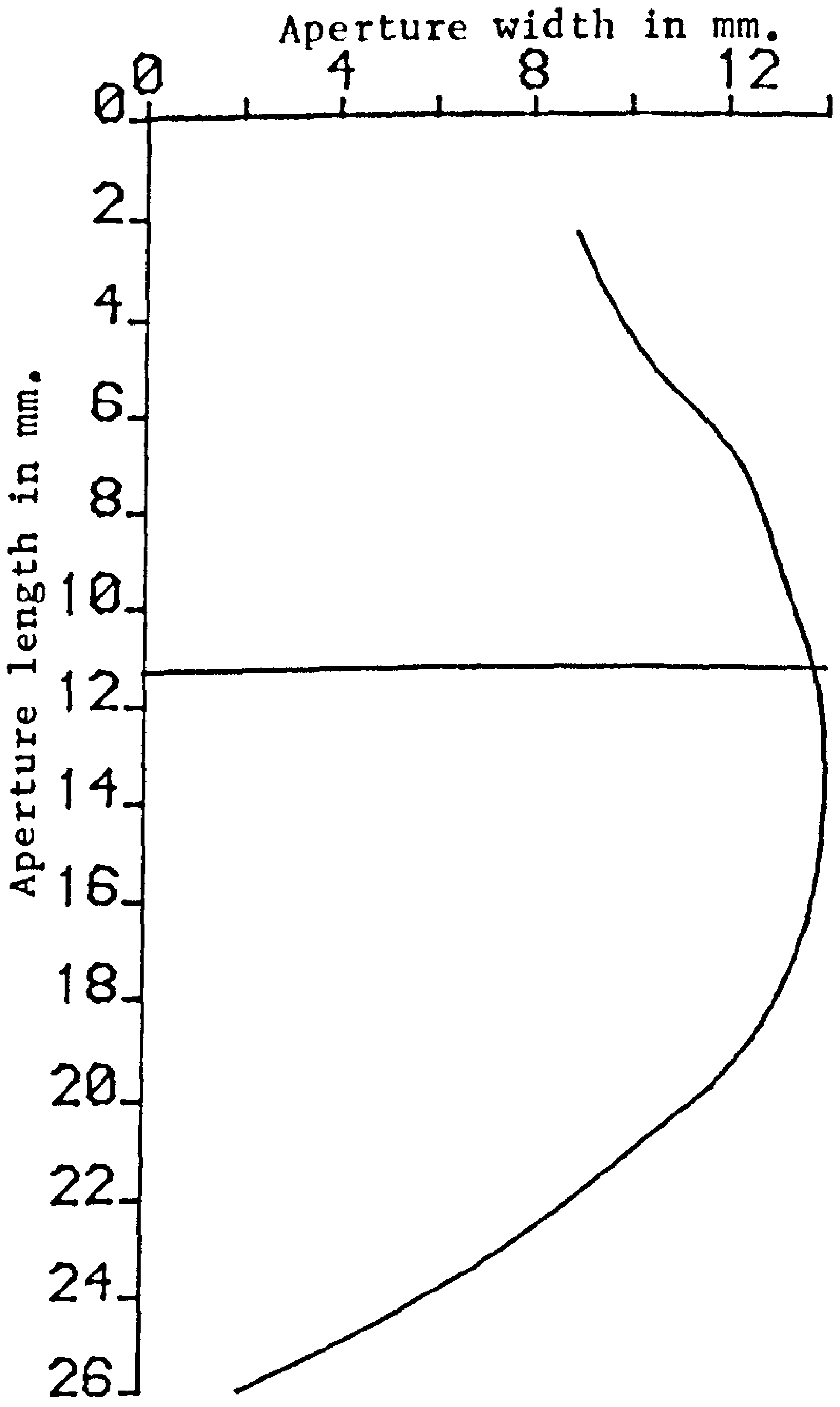
WHORL EXPANSION = 1.58

TRANSLATION = 0.44

N = 176

FIG. 6.21

THE SPECIMEN WITH THE WIDEST POINT OF THE APERTURE LOWEST DOWN THE APERTURE:131.



WHORL EXPANSION = 1.55

TRANSLATION = 0.43

N = 176

Aperture width 153 148

The two diagrams 6.21-6.22 show the range of variation in where the aperture "peaks", or where it is the widest in respect to the length of aperture. The range of variation is not large.

The amount of variation is dependant on the parameter being considered. L/ LA varies from 1.46 to 2.1; translation from 0.15 to 0.85, a very large range (see figs. 6.11 and 6.12); while WER only ranges from 1.32 to 2.0 (see figs. 6.12 and 6.13). The range of aperture widths is quite large also with the narrowest being 10.0 mm in respect to a shell length of 63.9 mm and the widest 30.0 mm to a shell length of 80.6 mm. These are unusual examples of aperture width as most have a very similar relationship to one another (see fig. 6.23) and there is strong positive correlation between length and width of aperture (see fig. 6.22). A significant Spearman's rank correlation of $R=0.82$ ($P > 0.001$) was calculated for these parameters from this sample. The highly anomalous points (see figs. 6.22 and 6.23) of length against aperture width show a wide deviation from the mean, the significance of these specimens is not clear, if indeed there is one, and they are considered to be very excentric forms of *N. contraria*.

FIG. 6.22

LENGTH AGAINST APERTURE WIDTH IN *N.* CONTRARIA.

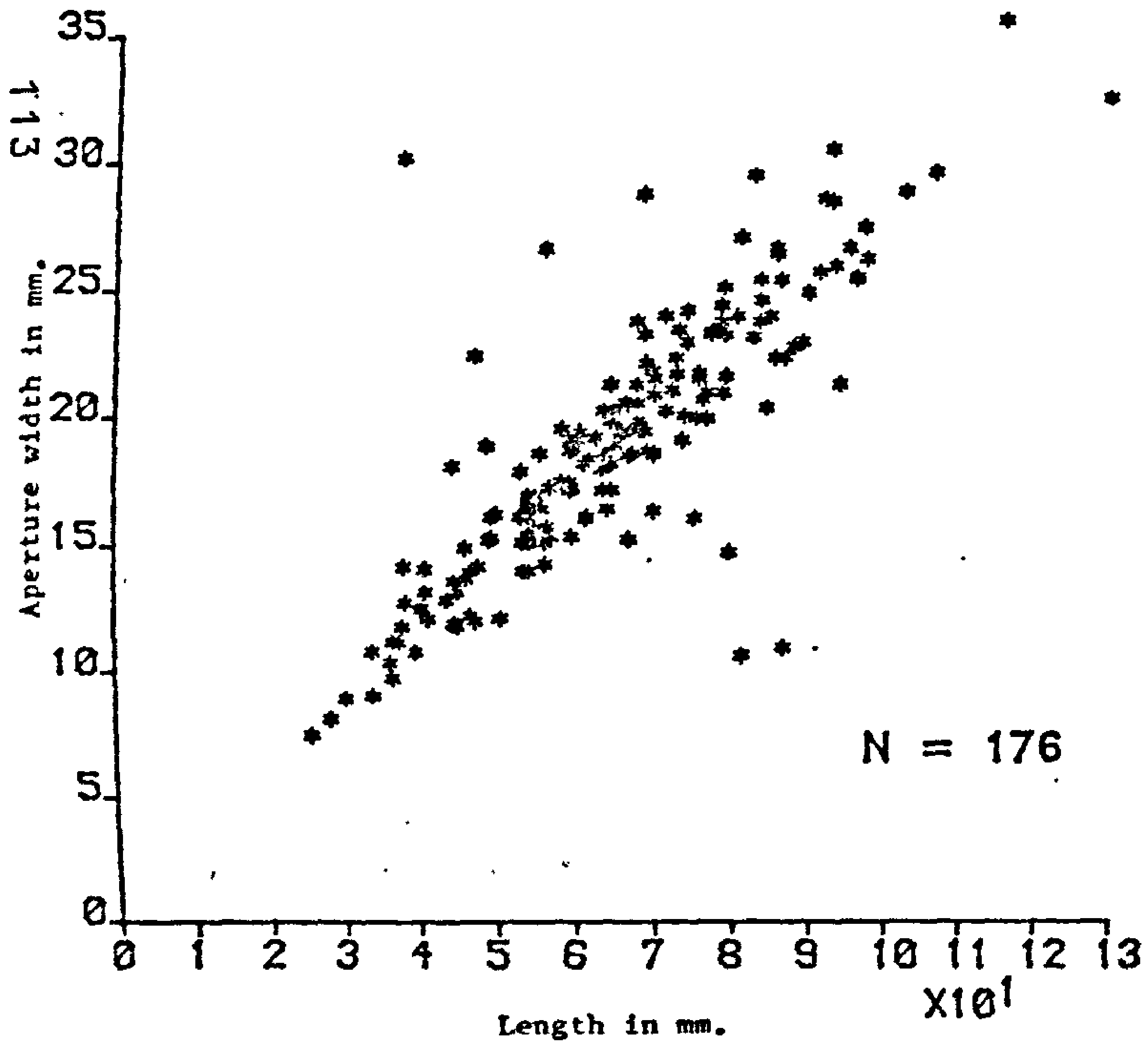
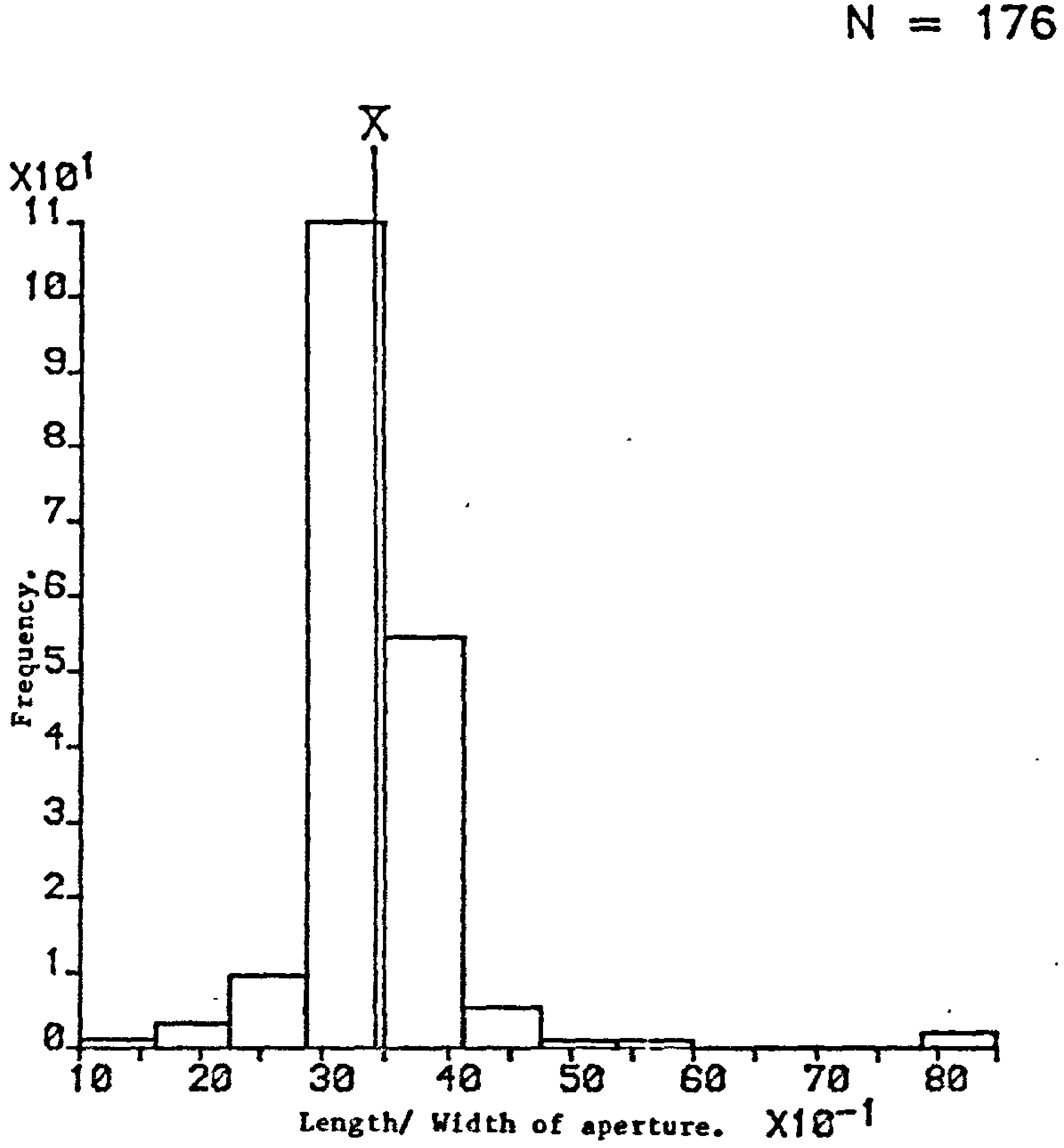


FIG. 6.23

THE DISTRIBUTION OF WIDTH OF APERTURE IN RESPECT TO LENGTH IN *N.* CONTRARIA.



6.3 Discussion.

Any dimorphism in the shape of the shell of N. contraria would be most apparent in those parameters showing the greatest amount of variation. So rather than look at WER which has a total variation of only 0.07 we must study length with a total variation of 110 mm, L/ LA total variation 0.6, translation 0.7 and L/ Width of aperture 7.5.

Hallers-Tjabbes (1979, p. 117) showed that sexual dimorphism exhibited in the shell of Buccinum undatum is shown mainly in the aperture shape, but no dimorphism is apparent in the aperture shape of N. contraria (see fig. 6.24). The greatest bimodality is shown in the distribution of translation (see fig. 6.7). This dimorphism may be related to sex but without a study of live specimens (which has not been possible as yet) it is difficult to be more definite.

Shell shape does vary due to other factors in gastropods, for example physical factors (see 2.3.3 and chap. 5). A variation of shell shape parameters is thus expected but where the size of the gastropod shell is unimodal (see fig. 6.5) one would expect the other parameters to vary likewise. The bimodality of the translation in N. contraria was not caused by sedimentary sorting or it would be evident in the distribution of the animal's shell size, and this is not the case.

CHAPTER 7.

Uncoiling gastropods.

7.1 Encrusters and overgrowths.

7.2 The significance of the encrusting organisms.

7.1 Encrusters and overgrowths.

Many specimens of common Red Crag gastropods are encrusted by various organisms; some of these encrusters have been overgrown by the gastropod shell. This phenomenon causes the shell shape to be distorted as the coiling path is diverted around the obstruction. In some examples of this kind the encrusting organism is not preserved giving the appearance that the shell has uncoiled. In extreme cases the growing edge of the whorl can become separated from the previous whorl (see pl. 1A-C).

The affected species are _Neptunea antiqua_, _Neptunea contraria_, _Neptunea despecta_, _Nucella lapillus_ and _Turritella_ spp. A total of 1,079 specimens of these species have been collected from various localities of the Red Crag (see table 7.1). These shells have been examined for signs of encrusting organisms and the overgrowth of the same. The encrusting organisms observed were Annelida, Cirripedia (Barnacles) and Bryozoa (see table 7.1).

Five specimens of _N. antiqua_ out of the 30 examined supported encrusting organisms, these were all barnacles: one in every six individuals. Three out of five of these encrusted shells exhibited overgrowth structures and there were also two other specimens with empty overgrowth cavities.

Out of the 488 specimens of _N. contraria_ only 13 exhibit encrusting organisms (1 in 37.54). Of these ten are bryozoan colonies, two are barnacles and one is an annelid. There are 49 examples of overgrowths in the collection of _N. contraria_ shells. One of these was caused by

Table 7.1 Encrusted and Uncoiled gastropods from the Red Crag.

	Collection.		Encrusters.				Uncoilers.				
Species.	Localities.	Total.	Worms.	Barnacles.	Bryozoa.	Total.	Worms.	Barnacles.	Bryozoa.	Empty.	Total.
B. undatum	1,28	3	0	0	0	0	0	0	0	0	0
N. antiqua	6,12,14, 16,18,26, 27,28,29, 34,45,47	30	0	5	0	5	0	3	0	2	5
N. contraria	1,4,6,9, 10,12,14, 16,18,21, 25,26,27, 28,29,42, 44,45,46, 47	488	1	2	10	13	1	0	2	46	49
N. despecta	6,9,18, 26,27	13	0	3	0	3	0	1	0	1	2
N. lapillus	1,6,7,9, 10,12,14, 16,17,18, 21,25,26, 27,28,29, 34,36,40, 42,44,45, 46	498	0	38	1	39	0	5	1	34	40
N. tetragona	1,6,7,29	22	0	0	0	0	0	0	0	0	0
Turritella sp.	3,6,7,14, 16,17,18, 21,25,26, 27,28,34, 44,47	50	0	0	0	0	0	0	0	2	2
Total.		1,104	1	49	11	60	1	9	3	85	98

an annelid and two by Bryozoa. The other 46 structures are empty. It is among these 46 specimens that the most spectacular examples of overgrowths are exhibited. In one individual the final whorl is completely separate from the rest of the shell (see pl. 1A-C). In another case an overgrowth half way down the spire has deflected the coiling axis bending the spire (see pl. 1D).

Of the 13 specimens of N. despecta examined three exhibited encrusters. These were all barnacles. In one of these cases a barnacle has been overgrown and in another there is an empty overgrowth structure.

There are 39 encrusted specimens of N. lapillus out of the 498 examined. Of these 38 are barnacle encrusted (1 in 13.11) and the other one is encrusted by Bryozoa and barnacles. Some of these shells are completely covered with barnacles, mostly Balanus sp. making them unrecognisable without the aperture in view (see pl. 1E-F).

Forty of the 498 dog-whelks exhibited overgrowth structures. Five of these were due to barnacles and one due to a bryozoan colony associated with a barnacle. The remaining 34 examples of overgrowth had no obvious encrusting organism to blame.

Finally the 50 Turritella specimens that were examined revealed no encrusting organisms. There were two which exhibited overgrowth structures, which were really deviations in whorl shape rather than true overgrowth structures (see pl. 2D).

The most striking statistic to arise from this study is the number of empty overgrowth cavities: 85 out of a total of 98. Why are so few encrusters preserved? Of the 85 examples of empty overgrowth cavities 34 are in specimens of *N. lapillus* and 46 in *N. contraria* (that is 1 in 10.6 of the total sample).

By far the most common encruster to infest the shell of *N. lapillus* is the barnacle. In many of the empty overgrowth cavities there is some evidence of barnacle attachment. When barnacle plates disaggregate they often leave a scar from their basal plates and these can be seen in many of the empty cavities of *N. lapillus*.

Unlike the dog-whelk *N. contraria* is rarely encrusted by barnacles; only two in the whole sample which is 1 in 244. There is also an absence of barnacle attachment scars on *N. contraria* shells. Boekschoten (1967) figures *N. contraria* overgrowing barnacles from the Belgium Pliocene. If the incidence of barnacle encrustation on *N. contraria* was as rare as in the Red Crag this is a very unusual specimen indeed. The empty overgrowth cavities in *N. contraria* from the Red Crag are not the same shape as the ones in *N. lapillus*, *N. antiqua* and *N. despecta*.

There are ten examples of bryozoan encrusted *N. contraria* shells in the collection. The bryozoan responsible has been identified as *Turbicellepora coronopus* (Wood 1844) (Taylor, P. D. pers. com.). Two of these bryozoan colonies have been overgrown forming narrow cavities along the sutures. Most of the empty cavities are much more bulbous in shape than the bryozoan formed ones. The fossilized bryozoan colonies preserved on the shells of *N. contraria* are robust and there seems to be no reason why such a colony would not be preserved in preference to a shell of N. contraria. Bryozoa are an unlikely suspect for the elusive encruster.

There is one specimen of an annelid encrusted N. contraria shell in the collection. This is a Serpulidae Pomatoceros triqueter (Linne) (George, J. D. pers. com.) and it secretes calcite tubes. These would stand the test of time as well as the shell itself. There is one tubular cavity on a N. contraria shell (see pl. 2E) and this was probably occupied by an annelid at the time of overgrowth. Most of the other empty overgrowth cavities are not tubular but bulbous.

Pearce and Thorson (1967) recorded sea anemones, octocorals and sponges exploiting the shells of N. antiqua as a substrate. Octocorals usually have some hard parts and if these were the mystery encruster we would expect to find some evidence. None has been found. Sea anenomes are mobile to a certain extent, (George and George 1979) and are therefore unlikely to be caught by the growing margin of a gastropod shell. Sponges however may have been a potential cause of uncoiling: they are soft bodied (apart from their spicules) and would not be preserved; they are sedentary not moving from their place of attachment.

The most convincing evidence has been provided by some modern specimens of N. antiqua and Buccinum undatum collected from the beach at Southend-on-Sea (Hewitt, R. A.) and from the beach at Bawdsey [27]. These specimens display overgrowths of the Spionidae Annelida Polydora ciliata (Johnson) (George, J. D. pers. com.). This annelid forms tubes of mud on the shells of these whelks and the tubes are arranged into mound-like structures. These are the most likely suspect for the vast majority of the empty overgrowth cavities in N. *contraria* from the Red Crag (see pl. 2A-C). They are soft and would not be preserved in the fossil as well as being the right shape.

Attempts to mould the shape of the overgrowth cavities with Vinamould were unsuccessful as the entrances to the cavities are often smaller than the maximum dimensions of the cavity. Further attempts with Araldite were also unsuccessful.

7.2 The significance of the encrusting organisms.

The frequent occurrence of *Balanus* sp. encrusting the shells of *N. lapillus*, *N. antiqua* and *N. despecta* suggests that these gastropods inhabited environments suited to these barnacles, that is shallow water with rocky substrates. Modern dog-whelks inhabit these environments (see chapter 5). Pearce and Thorson (1967) report N. *antiqua* living on a wide variety of substrates as does *N. despecta*.

The rarity of barnacles on the shells of *N. contraria* (also noted by Harmer 1914-24, p. 159) from the Red Crag suggests very strongly that this species had a strong preference for soft substrates, and or deeper water. Bryozoa are not uncommon encrusters on *N. contraria* shells from the Red Crag showing them to be epifaunal, as are the rest of this genus (Nelson 1978).

The absence of barnacles on the shells of the 22 specimens of *Nucella tetragona* (J. Sowerby) collected, is curious. *N. tetragona* now extinct is a close relative to the dog-whelk. The lack of barnacle encrustation may point to the species occuppying a different niche to *N. lapillus*, that is a soft sediment dweller. Barnacles are rugophilic (Crisp and Barnes 1954) that is they prefer grooved to smooth surfaces. This makes *N. lapillus* shells ideal sites of attachment. *N. tetragona* however has more ornamentation than the dog-whelk shell with prominent ridges running at right angles to one another in a crossed hatch pattern. This surface could have proved too rough for barnacle attachment.

A most intriguing aspect of this phenomenon is the behaviour of these gastropods to soft bodied encrusters. *N. antiqua* a predator come scavenger (Fange 1958) and *N. contraria* probably of a similar ilk overgrow these organisms rather than removing them. Perhaps the annelids such as *Polydora ciliata* have some defence mechanism which prevents the gastropod from removing it. Funnell *et al.* (1979) suggest that low salinity or ice persisting into the late spring could have enfeebled the gastropods when dealing with barnacle larvae (see 2.3.4), but they were dealing with *Nucella* and *Littorina* in the Norwich Crag.

PART IV

PREDATION.

CH. 8. The feeding habits of predatory shell-boring gastropods.

CH. 9. Predation on gastropods.

CHAPTER 8.

The feeding habits of predatory shell-boring gastropods.

8.1 Introduction.

8.2 Prey selection and predation rates.
    8.2.1 In bivalves.
    8.2.2 In gastropods.

8.3 Distribution of boreholes.
    8.3.1 On bivalves.
        a) Lack of valve preference.
        b) *Astarte*.
        c) *Glycymeris glycymeris*.
        d) *Macoma* and *Spisula*.
    8.3.2 On *Turritella*.

8.4 Predator:prey size relationships.
    8.4.1 Muricids.
    8.4.2 Naticids.

8.5 Multiple bores.

8.1 Introduction.

Numerous specimens of many mollusc species of the Red Crag bear the mark of predatory boring gastropods; both muricid and naticid boreholes are common. In this chapter an analysis of these predation traces is undertaken. The variety of prey species is studied along with the potential predator species. The ratios of bored to non-bored individuals are calculated for selected genera and predator preferences are discussed. The distribution of loci in particular genera are studied and stereotypy by the naticids is noted.

The population structure of selected prey genera is compared: bored to non-bored. Borehole diameter is used as a measure of the predator's size and this is compared to the size and type of prey. The phenomenon of multiple boring is recorded and discussed.

8.2 Prey selection and predation rates.

8.2.1 In bivalves.

Table 8.1 gives a list of bivalve prey, collected in this study, along with the numbers of the localities they were found at and the types of boreholes detected. The species of both families of predator that have been found by the author are listed in table 8.2, a longer list can be compiled if the monograph of Harmer (1914-25) is consulted but those listed are the more commonly preserved species. The nine named are thought to be the principal predators of Red Crag bivalves simply due to their abundance.

Table 8.1 Bivalve prey (drilled).

Species.	Localities.	Type.
Astarte basterotii La Jonkaire.	18	Muricid.
Astarte crenbrilirata S. Wood.	18	Muricid.
Astarte gracilis Munster.	18	Muricid.
Astarte obliquata J. Sowerby.	1,6,14,18	Muricid and naticid.
Astarte omali La Jonkaire.	6,14,18	Muricid.
Glycymeris glycymeris (Linne).	1,6,14,17,18,21,29,42,46,47,49	Muricid and naticid.
Macoma calcarea (Gmelin).	41	Naticid.
Macoma obliquata (J. Sowerby).	26	Naticid.
Macoma praetenuis (Woodward).	18,21,29,40,41	Naticid and muricid.
Tellina crassa Pennant	1,26,28,29	Naticid.
Spisula ovalis (J. Sowerby)	6,14,18,21,24,26,28,29,32,34,40,41,46,47	Naticid and muricid.
Spisula arcuata (J. Sowerby)	26	Naticid.

Table 8.2 List of potential predators (drills).

Species.	Localities.
NATICIDS.	
Lunatia catenoides (S. V. Wood).	1,6,7,14,18,27,28,29,44,47
Natica clausa Broderip and Sowerby.	1,6,28
Natica multipunctata S. V. Wood.	1,6,27,29,45
Natica (Lunatia) pallida Broderip and Sowerby.	1
Polinices hemiclausus (J. Sowerby).	1,6,27,45
MURICIDS.	
Nucella lapillus (Linne).	6,9,14,16,18,21,23,24,26,27, 28,29,31,34,42,44,46
Nucella tetragona (J. Sowerby).	1,6,7,18,29
Searlesia costifera (S. V. Wood).	6,18
Trophonopsis clathratus (Linne).	6,27,29

The four most commonly preserved genera of bivalve prey are *Astarte*, *Glycymeris*, *Macoma* and *Spisula* (see table 8.3), 1 in 2.04 individuals of *Astarte* having been bored, 1 in every 2.66 *Spisula*, 1 in 4.38 *Glycymeris* and 1 in 5.73 *Macoma*. The number of naticid and muricid boreholes on each of the four genera are also recorded on table 8.3. The chi square test provided significant results at the 99% level showing that all of the above genera were bored preferentially by one of the two families of predator. *Astarte* and *Glycymeris* by muricids and *Macoma* and *Spisula* by naticids.

The ratios of bored to non-bored individuals from the Red Crag are comparable to modern predation rates by drills. Davis (1923) found that, on the Dogger Bank, only 1 in 4 *Spisula subtruncata* (Da Costa) were not bored by *Natica alderi* Forbes. Smith (1932) found lower rates of predation for *Astarte triangularis* and *Glycymeris glycymeris* of 1 in 2.07 and 1 in 4.65 respectively. The predator in this case, off the Eddystone Grounds, was *N. alderi*. Reyment (1967) reported rates of 1 in 2.4 for *Ostrea stentina* Payr and 1 in 3.8 for *Cardium papillosum* Poli from the Niger Delta. Vermeij (1980) suggested that predation by naticids on bivalves may be underestimated in the fossil; as many bivalves are killed without drilling.

The data compiled by Davis (1923) show higher rates of drilling by a naticid on *Spisula* than was realised during the Red Crag. The modern species *N. alderi* may be a more successful than the Red Crag species although without more surveys of modern populations this can not be confirmed. Alternative circumstances could have resulted in this higher rate, such as a high concentration of *N. alderi* on the Dogger Bank at the time of collection. Predation rates may often fluctuate

Table 8.3 Ratios of bored to non-bored bivalves and naticid to muricid boreholes.

Genus.	Number of valves.			Bored valves.			Ratio.	Naticid.			Muricid.	Ratio.
		L.	R.		L.	R.			L.	R.		
<u>Spisula</u> [41].	222	110	112	42	22	20	1:2.65	40	19	21	2	20:1
<u>Spisula</u> (Total).	467	235	232	88	46	42	1:2.66	82	39	43	6	13.67:1
<u>Macoma</u>	126	61	65	11	5	6	1:5.73	24	12	12	2	12:1
<u>Astarte</u>	114	57	57	28	15	13	1:2.04	4	16	18	34	1:8.5
<u>Glycymeris</u>	447	219	228	51	23	28	1:4.38	9	24	18	42	1:4.67

The last "L." and "R." column refer to the boreholes made by the dominant predator. Final "Ratio" column refers to naticid to muricid borehole ratio.

as the numbers of prey and predator species in any one area vary. A burst in population growth by a prey species may result in low predation rates, a corresponding burst of population growth in the predator species will then result in a very high predation rate. Alternatively the Red Crag ratio of bored to non-bored valves could have been reduced by taphonomic processes although this is thought to be unlikely (see 1.4.2 and Appendix 3).

Astarte undata Gould and *Astarte castanea* (Say) are extant species and are shallow burrowers in coarse often gravelly substrates: they sit just beneath the sediment surface (Stanley 1970, p. 145). Similarly *Glycymeris pectinata* (Gmelin) and *Glycymeris glycymeris* (Linne) are extant shallow burrowing bivalves with a preference for coarse gravelly sands (Hunt 1925), though *G. pectinata* can often be found lying on the sediment surface (Stanley 1970, p. 127). Muricids are all surface dwellers and prefer stony or rocky substrates (Fretter and Graham 1962, pp. 675-693). This preference for coarse substrates and near surface positions makes *Astarte* and *Glycymeris* vulnerable to muricid attack. This was certainly the case during the Red Crag as only 13 out of the 89 predatory boreholes in the valves of these genera of bivalves collected were made by naticids.

Smith (1932) however reported that the predation on modern *Astarte triangularis* and *G. glycymeris* was by *N. alderi*. More recently Thomas (1976) comments that the predation of *G. americana* and G. *subovata* from the Neogene of eastern U.S.A. was mainly by naticids. The Red Crag is markedly different from this showing that these genera of bivalve were involved in a different food chain or web than in the modern and the Neogene of the U.S.A. Taylor *et al*. (1983) show that

Glycymerita umbonata and G. sublaevis from the Cretaceous (Albian) were bored equally by naticids and muricids. Perhaps the habitats of these bivalves have changed or the modern naticids now hunt in a wider variety of substrates. If so the muricids must have retreated from or diminished in importance in these same environments.

The extant bivalves Macoma tenta (Say), Macoma balthica (Linne) and Spisula solidissima (Dillwyn) all burrow in finer grained sediments, either sand or mud and they burrow deeper than Astarte and Glycymeris (Stanley 1970, Brafield and Newell 1961). This protects them from muricid predation but leaves them open to naticid attack. Naticids are infaunal and prefer sand, silt or mud to very coarse sediment (Fretter and Graham 1962, pp. 674-675). The evidence in the Red Crag inforces this with 106 out of a total of 114 boreholes being made by naticids, in the genera Macoma and Spisula.

A factor which could have influenced the choice of prey by predatory drills in the Red Crag is the shell thickness of their prey. Astarte and Glycymeris have much thicker shells than Macoma and Spisula. Muricids however were not averse to drilling thin-shelled prey as boreholes have been detected in Colus curtus (Jeffreys) and Scaphella lamberti (J. Sowerby) (see tab. 8.4) which are both thin shelled extinct gastropods. A naticid borehole has also been noted in Tellina crassa Pennant (see pl. 3A) as well as Glycymeris glycymeris and Astarte obliquata J. Sowerby, all thick-shelled bivalves relative to Macoma and Spisula. It is evident that muricids and naticids would bore the available prey and were not deterred by bivalves of different shell thicknesses.

Table 8.4 Gastropod prey (drilled).

Species.	Localities and type.
Colus curtus (Jeffreys).	6 Muricid.
Nassa incrassata (Strom).	18 Muricid.
Natica clausa Broderip and Sowerby.	1 Naticid.
Natica multipunctata S. V. Wood.	21 Naticid.
Natica (Lunatia) pallida Broderip and Sowerby.	1 Naticid.
Polinices hemiclausus (J. Sowerby).	1,6 Naticid.
Neptunea contraria (Linne).	6,18 Muricid.
Neptunea despecta (Say).	28 Muricid.
Nucella lapillus (Linne).	21,27 Muricid.
Nucella tetragona (J. Sowerby).	29 Muricid.
Scaphella lamberti (J. Sowerby).	14 Muricid.
Searlesia costifera (S. V. Wood).	18 Muricid.
Trivia coccinelloides (J. Sowerby).	18,47 Muricid.
Trochus (Calliostoma) zizyphinus (Linne).	18 Muricid.
Trophonopsis clathratus (Linne).	6 Muricid.
Turritella (Haustator) incrassata (J. Sowerby).	1,6,14,17,25 Muricid and naticid.
Turritella (Zaria) subangulata (Brocchi).	18 Muricid.
Turritella (Haustator) triplicata (Brocchi).	6,18,27,44 Muricid and naticid.
Ptychopotamides tricinctus (Brocchi).	6 Muricid.

Astarte, Glycymeris, Macoma and Spisula are the four most abundant genera of bivalves preserved in the Red Crag (Dixon 1977, pers. obs.). The division of prey between the muricids and naticids is a function of substrate preference and depth of burrowing of the prey. Astarte and Glycymeris prefer coarse sediments and shallow burrowing while Macoma and Spisula inhabit medium and fine grained sediments in deeper burrows. So muricids were more likely to come across Astarte and Glycymeris and naticids were more likely to encounter Macoma and Spisula.

8.2.2 In gastropods.

Amongst the gastropod prey of the predatory drills Turritella was the most popular genus preserved in the Red Crag (see tab. 8.4). There are 32 examples of gastropod borholes in the specimens of Turritella collected. The number of bored to non-bored individuals can not be calculated (see 3.4.3). The majority of the boreholes were made by muricids with only six being naticid holes. Turritella communis Risso an extant gastropod is an infaunal filter feeder living in muddy or sandy gravels (Fretter and Graham 1962, p. 567). Turritella having a similar habitat to Astarte and Glycymeris also shared the same predators during the Lower Pleistocene: the muricids.

Another notable phenomenon of gastropod predation is the incidence of canabalism. Four of the five naticids listed as potential predators have been found with naticid boreholes in their shells (see tables 8.2 and 8.4). Similarly two of the four potential muricid predators have been found with muricid boreholes in their shells. This phenomenon is not uncommon (Hoffman et al. 1974, Kojumdjieva 1974) and is apparent in the Red Crag.

8.3 Distribution of boreholes.

8.3.1 On bivalves.

a)Lack of valve preference.

None of the four common bivalve genera of gastropod prey showed any significant (95% level) variation from the expected distribution of half the boreholes on the left-hand valves and half on the right-hand valves. This is not surprizing in Macoma and Spisula, which are predominantly naticid prey as naticids manipulate their prey prior to boring. So even though Macoma lies preferentially on one valve (Stanley 1970 p. 185) the naticid will not drill the first valve it meets but will capture the shell in its foot and reorientate it (Taylor, J. D. pers. com.).

The lack of variation between the bored valves of Astarte and Glycymeris which are predominantly muricid prey shows that neither one of them sat preferentially on one valve or the other. If they had they would have been bored more often on the upward facing valve as muricids being epifaunal would attack from above (Reyment 1967) and they do not manipulate their prey.

Thomas (1976) found little preference for left or right-hand valves of Glycymeris but he was dealing with mainly naticid boreholes. Glycymeris does not lie consistently on one valve or the other (Stanley 1970, p. 128) and neither does Astarte.

b) Astarte.

The distribution of borehole loci on the valves of Astarte from the Red Crag can be seen on fig. 8.1. From fig. 8.2 and 8.3 it can be seen that the distribution of muricid boreholes, the main predator of Astarte, is very close to a random distribution. If Astarte were always orientated in the same attitude in the sediment one would expect the muricid boreholes to be concentrated on the part of the valves closest to the sediment surface. Stanley (1970, pp. 145-149) showed that modern Astarte have a variety of life positions, A. undata Gould has a tendency to lie with its posterior margin uppermost while A. castanea (Say) usually sits with its anterior margin up. Boekschoten (1967) showed that certain specimens of Astarte from the Pliocene of Belgium could be orientated into life position using Polydora blisters. Two of the species he studied are very common in the Red Crag namely Astarte obliquata Sowerby and A. basteroti De La Jonkaire and these were found to lie with their posterior margin closest to the sediment surface. The position of boring by muricids on the valves of these species does not suggest they adhered strictly to this stereotyped life position. The boreholes on the Red Crag specimens are randomly distributed and not concentrated at the posterior margin, suggesting a variety of life positions or a certain amount of excavation by their predators, or that the bivalves were attacked after they had been washed out of the sediment.

c) Glycymeris glycymeris.

From fig. 8.4 it can be seen that muricid boreholes are clustered in the dorsal half of both left and right-hand valves of G. glycymeris from the Red Crag. From fig. 8.5 it can be seen that this is outside the range of variation caused by randomness. The angular distribution

FIG. 8.1

THE DISTRIBUTION OF PREDATORY GASTROPOD BORINGS ON THE VALVES OF <u>ASTARTE</u> FROM THE RED CRAG.

NUMBER OF BOREHOLES = 38

NATICID = o
MURICID = ◻

THE LEFT VALVE

THE RIGHT VALVE

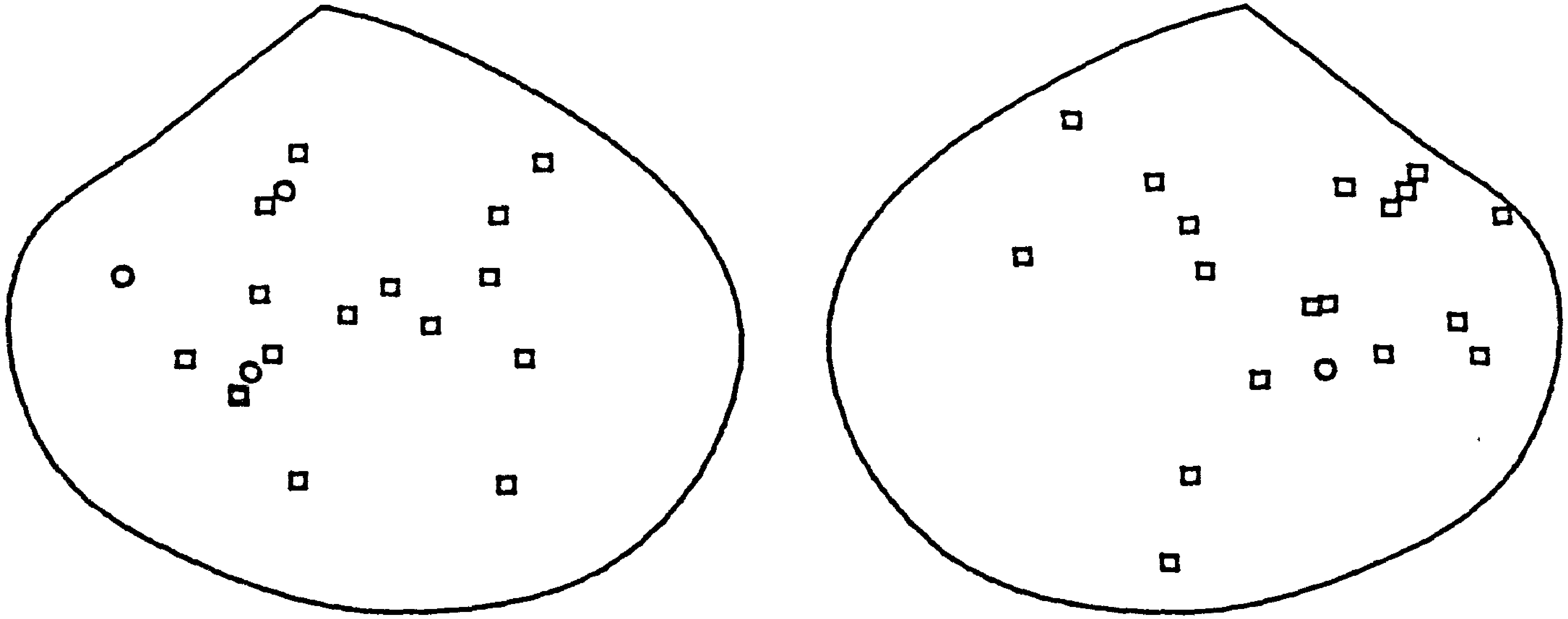


FIG. 8.2

THE DISTRIBUTION OF MURICID BORES ON ASTARTE COMPARED TO 20 RANDOM DISTRIBUTIONS (DISTANCE TO UMBO).

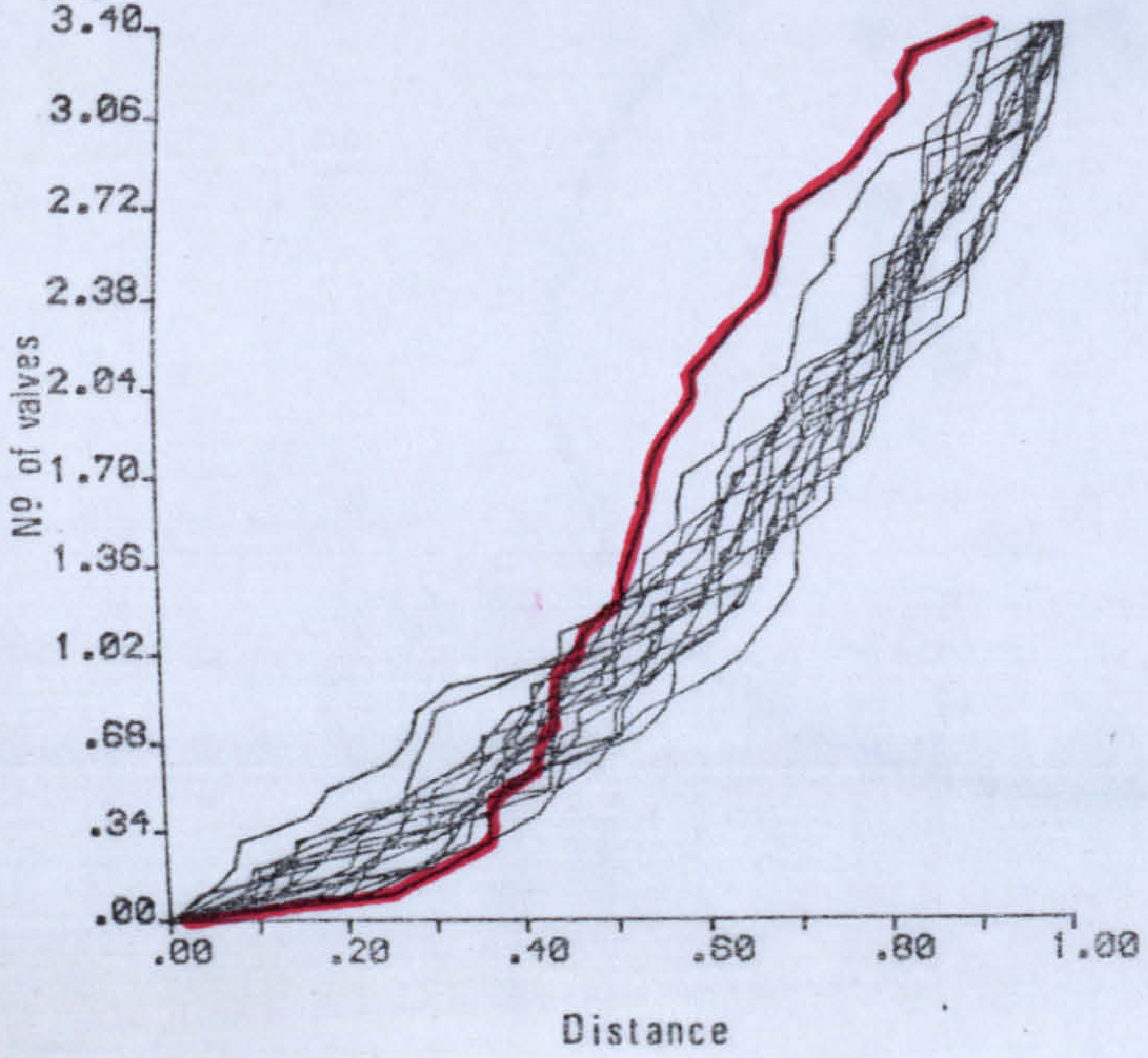


FIG. 8.3

THE ANGULAR DISTRIBUTION OF MURICID BORES ON ASTARTE COMPARED TO 20 RANDOM DISTRIBUTIONS.

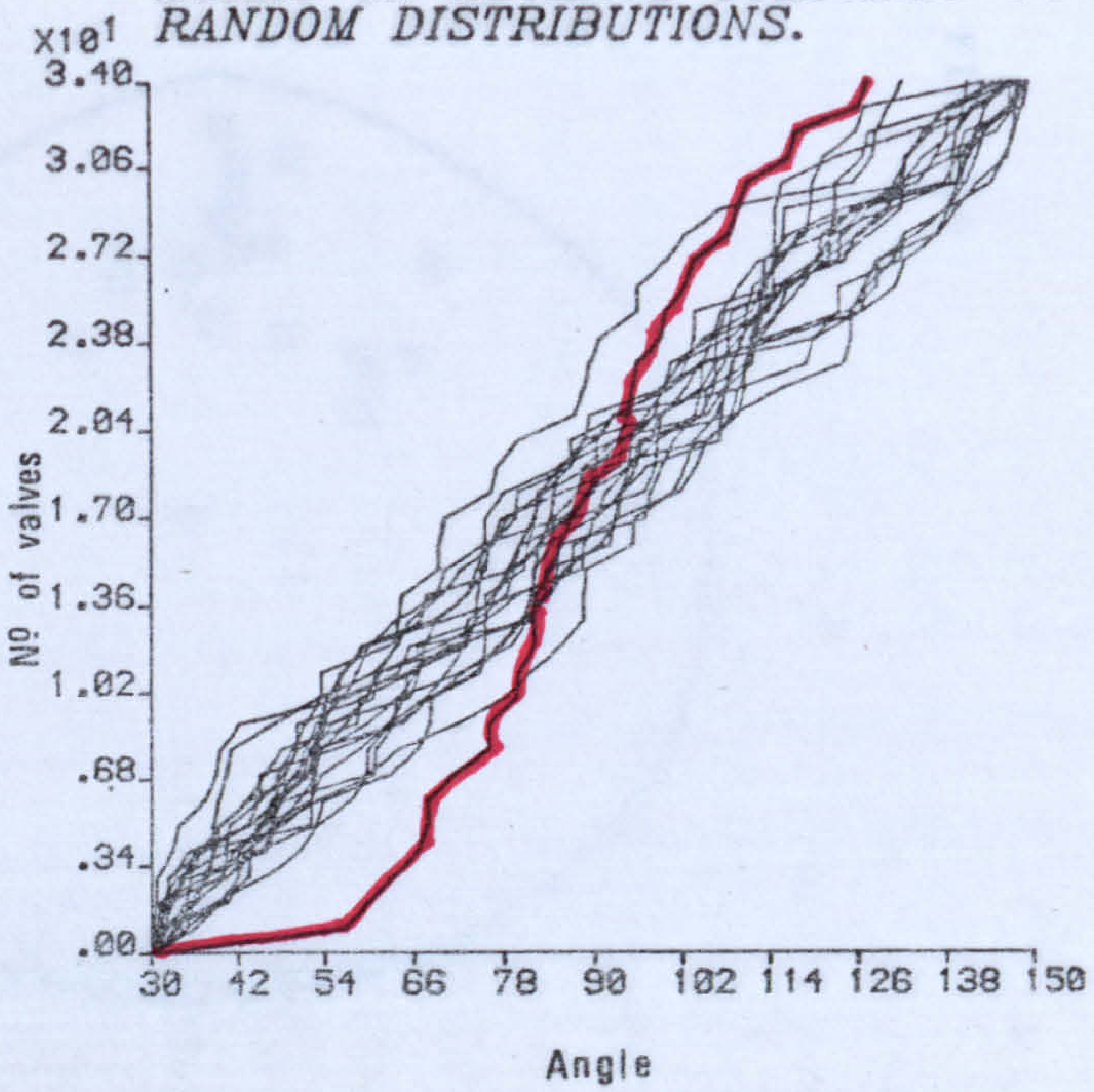
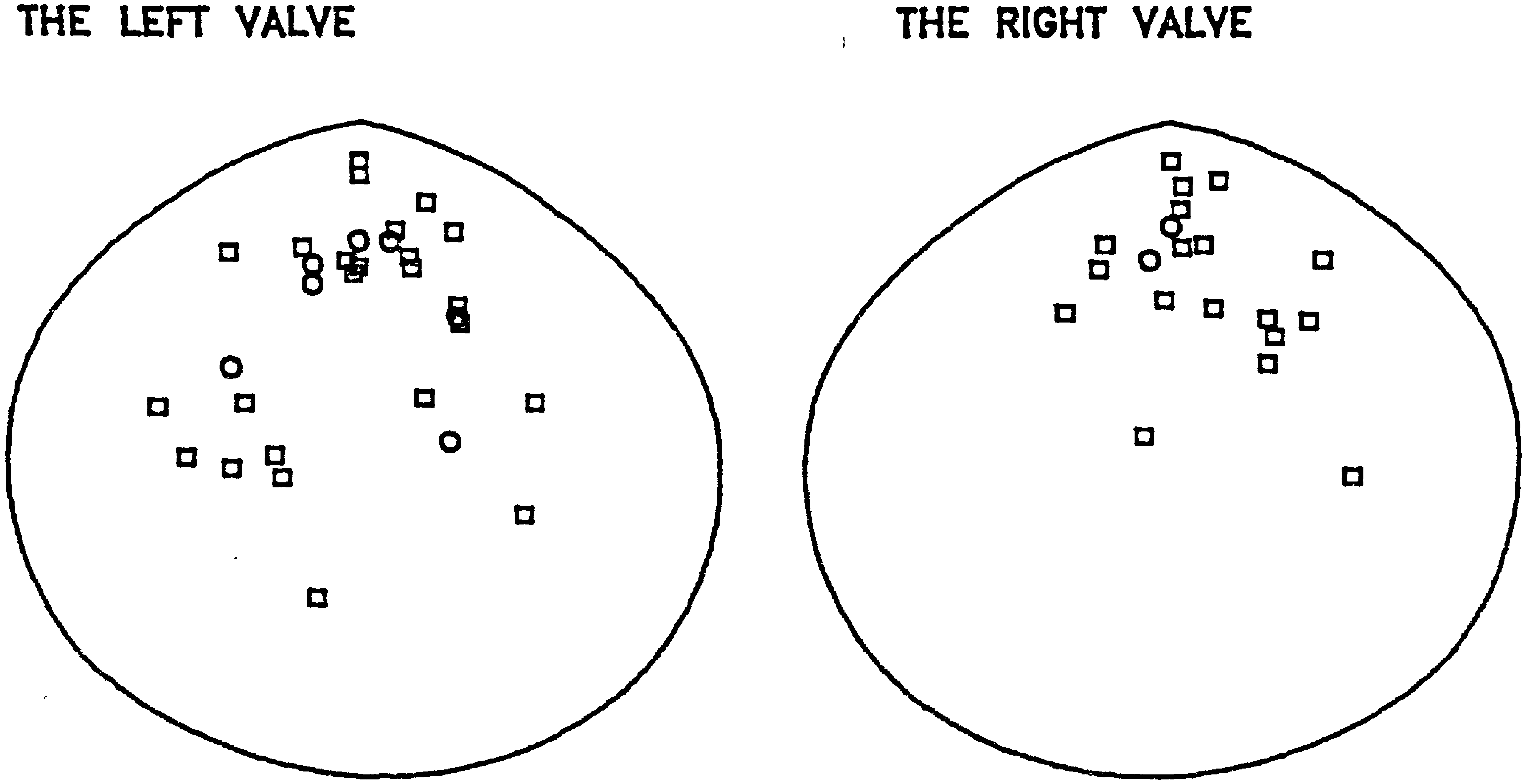


FIG. 8.4

THE DISTRIBUTION OF PREDATORY GASTROPOD BORINGS ON THE VALVES OF <u>GLYCYMERIS</u> FROM THE RED CRAG.

NUMBER OF BOREHOLES = 51

NATICID = ○
MURICID = □



of muricid boreholes (see fig. 8.6) is very close to a random distribution. This points to a life position for *G. glycymeris* of sitting upright in the sediment bringing its dorsal surface closest to the sediment surface. Any muricid attack from the surface would therefore be on the dorsal half of the shell.

This was not the case in the Neogene of the U.S.A. where Thomas (1976) reported muricid boreholes on *G. americana* and *G. subovata* to be scattered broadly over the shell or around the shell margins. These species had different life positions from *G. glycymeris* from the Red Crag. Stanley (1970, p. 128) shows modern *G. pectinata* and *G. glycymeris* lying buried in the sediment with their anterior margins uppermost. The evidence from the muricid boreholes in *G. glycymeris* suggests a different life position during the Red Crag than for modern *G. glycymeris*.

Taylor *et al.* (1983) show that the shells of *Glycymerita umbonata* from the Blackdown Greensand (Albian) are bored by naticids over the whole area of the shell but by muricids in the dorsal half of their valves. The muricid boreholes show a similar pattern to the ones on *Glycymeris glycymeris* from the Red Crag, suggesting a similar life position.

d) *Macoma* and *Spisula*.

From fig. 8.7 it can be seen that there is a cluster of predatory borehole loci close to the central part of both valves of *Macoma* from the Red Crag. This cluster is focused on a point slightly posterior and dorsal of the mid point. Fig. 8.8 and fig. 8.9 demonstrate that this cluster is very unlikely to be the result of a random

FIG. 8.5

THE LINEAR DISTRIBUTION OF MURICID BORES ON THE VALVES OF GLYCYMERIS COMPARED WITH 20 RANDOM PLOTS.

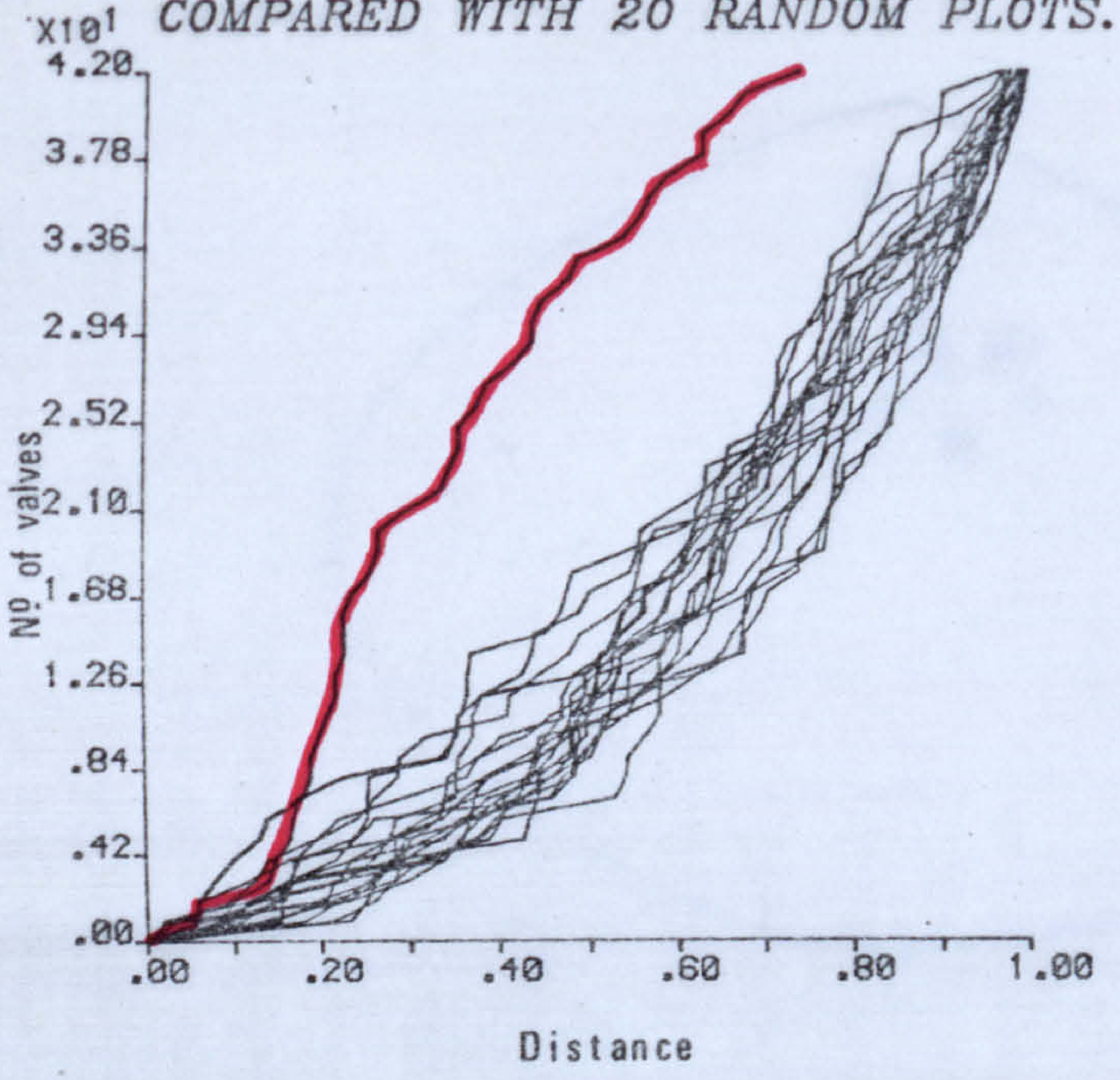


FIG. 8.6

THE ANGULAR DISTRIBUTION OF MURICID BORES ON GLYCYMERIS COMPARED WITH 20 RANDOM DISTRIBUTIONS.

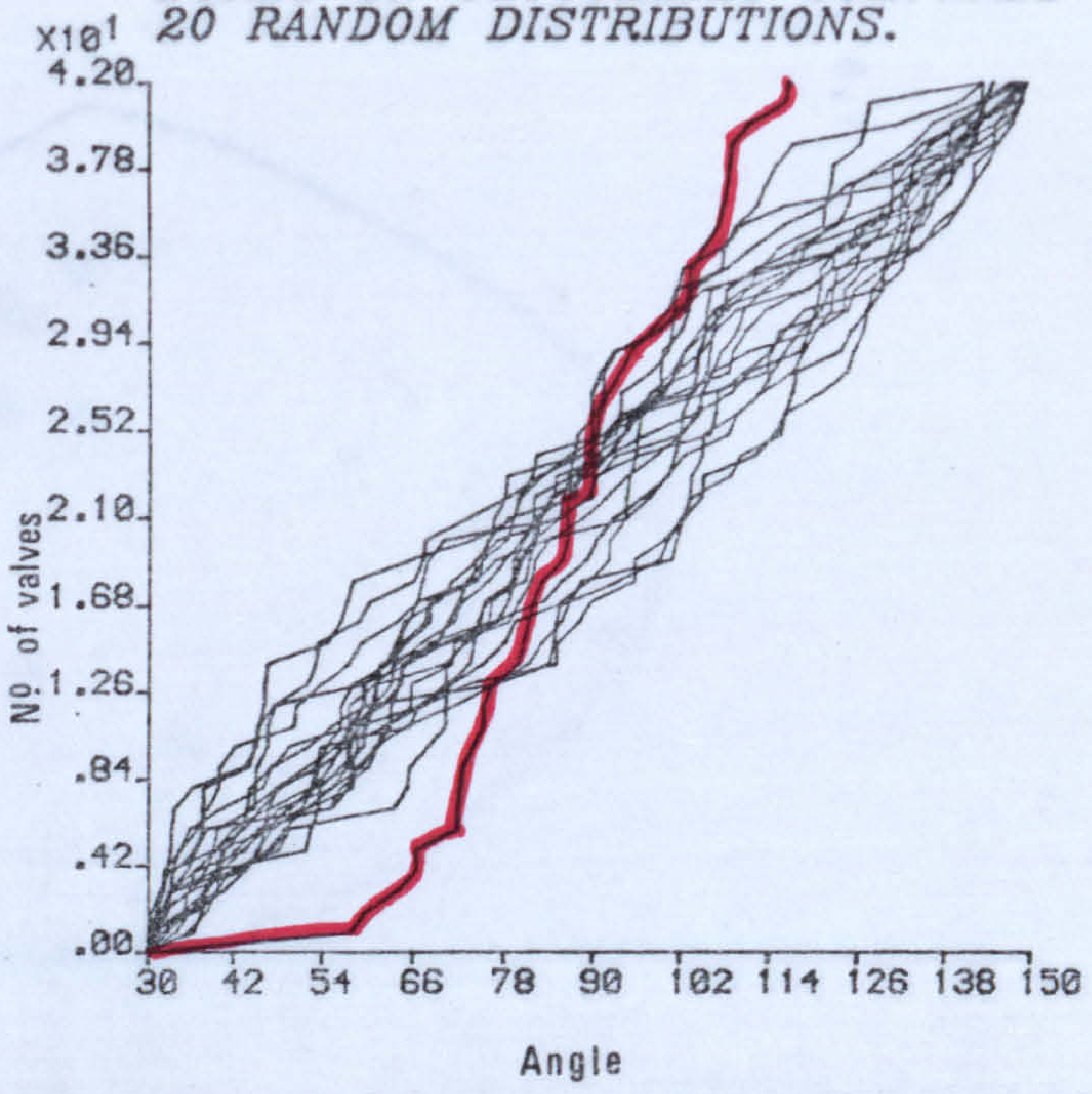
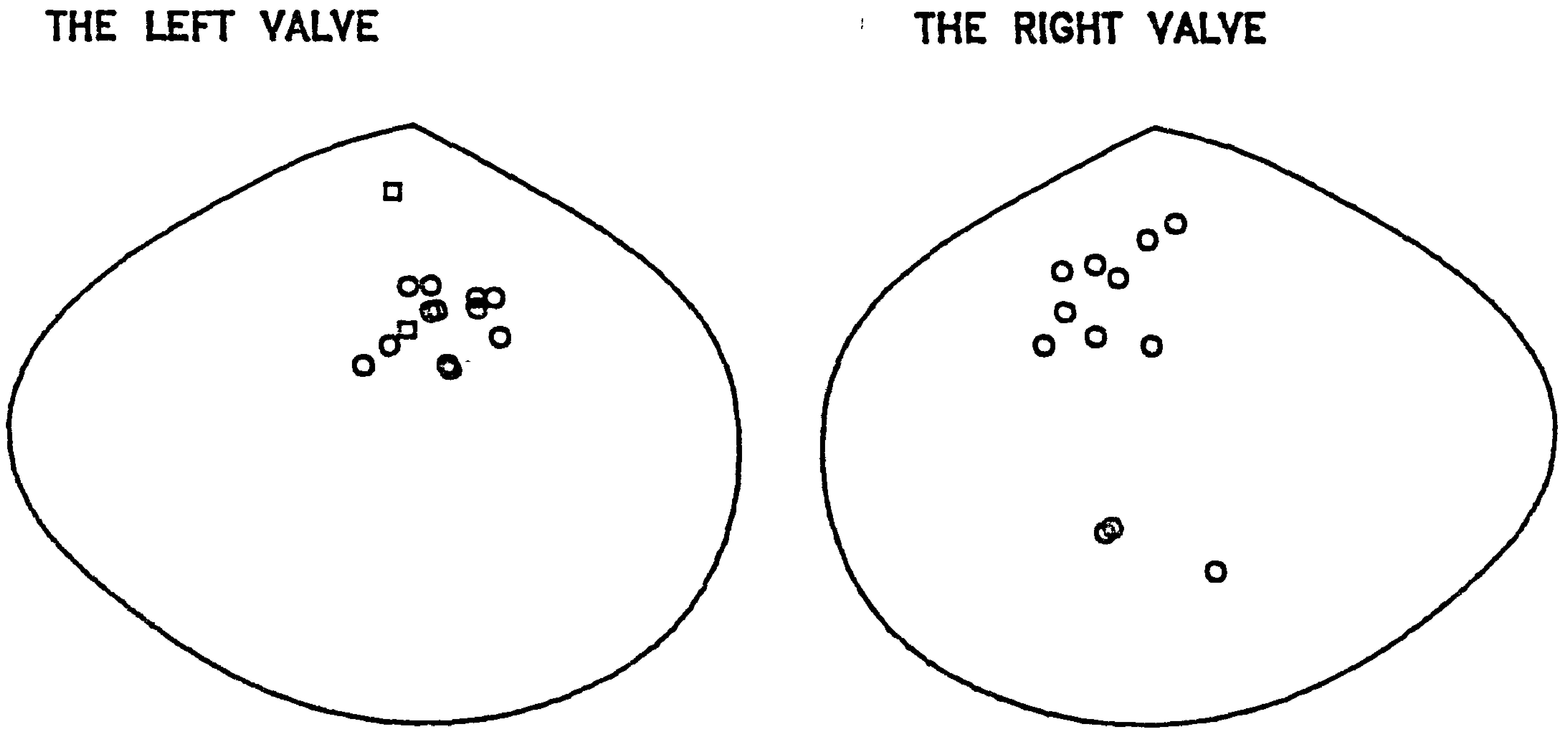


FIG. 8.7



THE DISTRIBUTION OF PREDATORY GASTROPOD BORES ON THE VALVES OF <u>MACOMA</u> FROM THE LOWER PLEISTOCENE.

NUMBER OF BOREHOLES = 26

NATICID = ○
MURICID = ☐

FIG. 8.8

THE LINEAR DISTRIBUTION OF NATICID BORES ON THE VALVES OF MACOMA COMPARED TO 20 RANDOM PLOTS

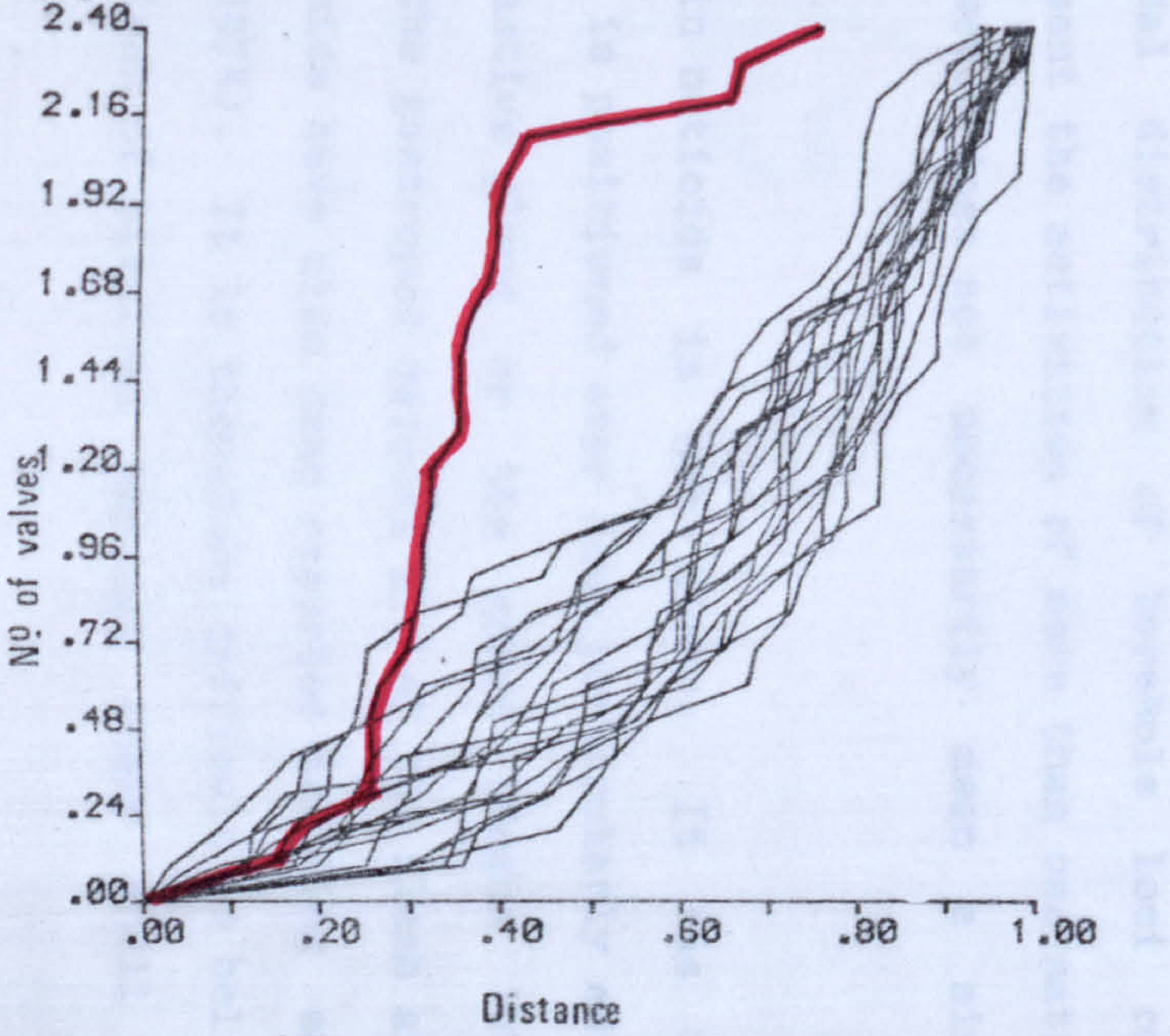
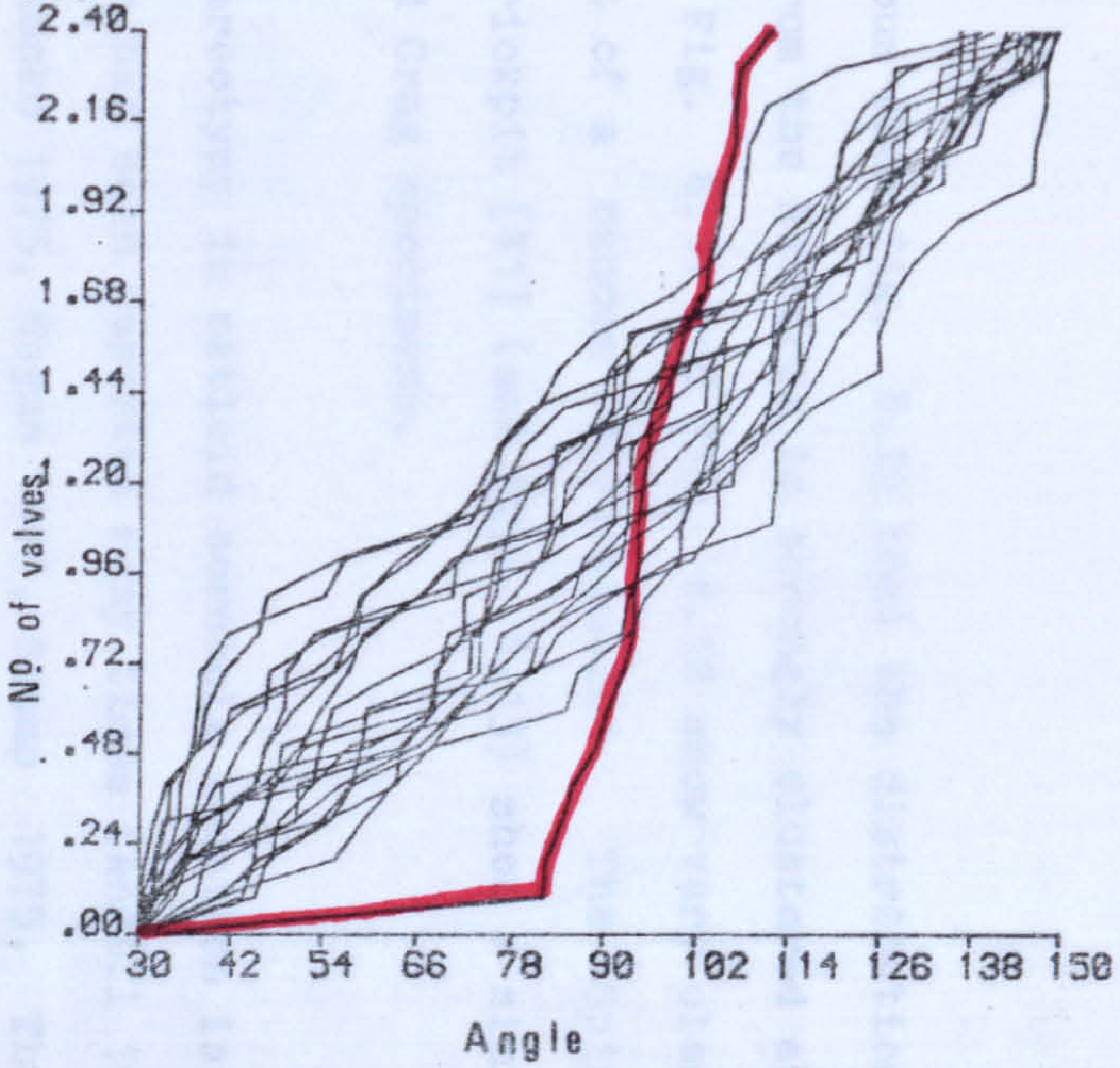


FIG. 8.9

THE ANGULAR DISTRIBUTION OF NATICID BORES ON THE VALVES OF MACOMA COMPARED TO 20 RANDOM PLOTS.



distribution. It is obvious from fig. 8.10 that the distribution of borehole loci on Spisula from the Red Crag is strongly clustered about the umbo of both valves. Fig. 8.11 and fig. 8.12 show very clearly that this is not the result of a random distribution. The Spisula collected from Aldeburgh Brickpit [41] (see fig. 8.13) show a similar clustering to the other Red Crag specimens.

This clustering showing stereotypy in naticid borehole location is not unusual and this phenomenon has been reported many times (Ansell 1960, Reyment 1966, Berg and Nishenko 1975, Negus 1975, Stump 1975, Thomas 1976, Mace 1979). Mace (1979) demonstrated that the modern species Polinices alderi (a naticid) bores Tellina (Macoma) tenuis in the central part of the valve. Spisula subtruncata was bored by the same predator around the ventral margin of the shell. She also showed that different predatory gastropods drilled the same prey at different loci. Polinices alderi bored Venus gallina close to the ventral margin but Natica maculata and Polinices catena bored the same prey close to its umbo. A bimodal distribution of borehole loci on a single prey could represent the activities of more than one naticid predator, a single mode however does not necessarily mean a single predator.

The reason for stereotypy in naticids is not clear. It has been argued that the borehole is positioned over some particularly edible organ, for example the digestive gland or the gonad (Negus 1975). This is very unlikely as the gastropod devours all of the flesh after drilling its prey and naticids have also been reported drilling empty shells (Hoffman et al. 1974). It is therefore difficult to believe that they can detect the flesh of bivalves through their shell and

FIG. 8.10

THE DISTRIBUTION OF PREDATORY GASTROPOD BORES ON THE VALVES OF <u>SPISULA</u> FROM THE RED CRAG.

NUMBER OF BOREHOLES = 46

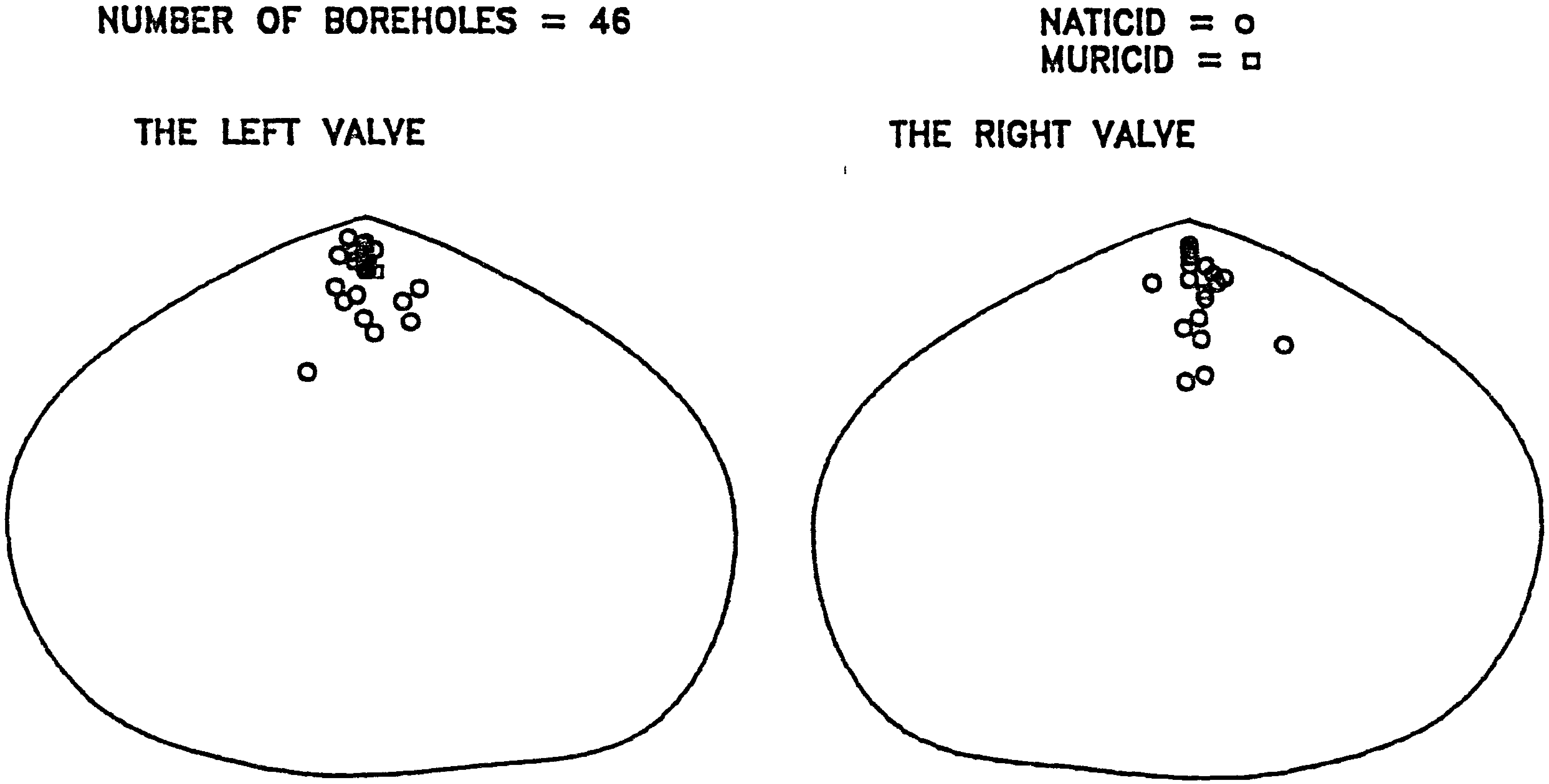


FIG. 8.11

THE LINEAR DISTRIBUTION OF NATICID BORES ON THE VALVES OF SPISULA COMPARED TO 20 RANDOM PLOTS.

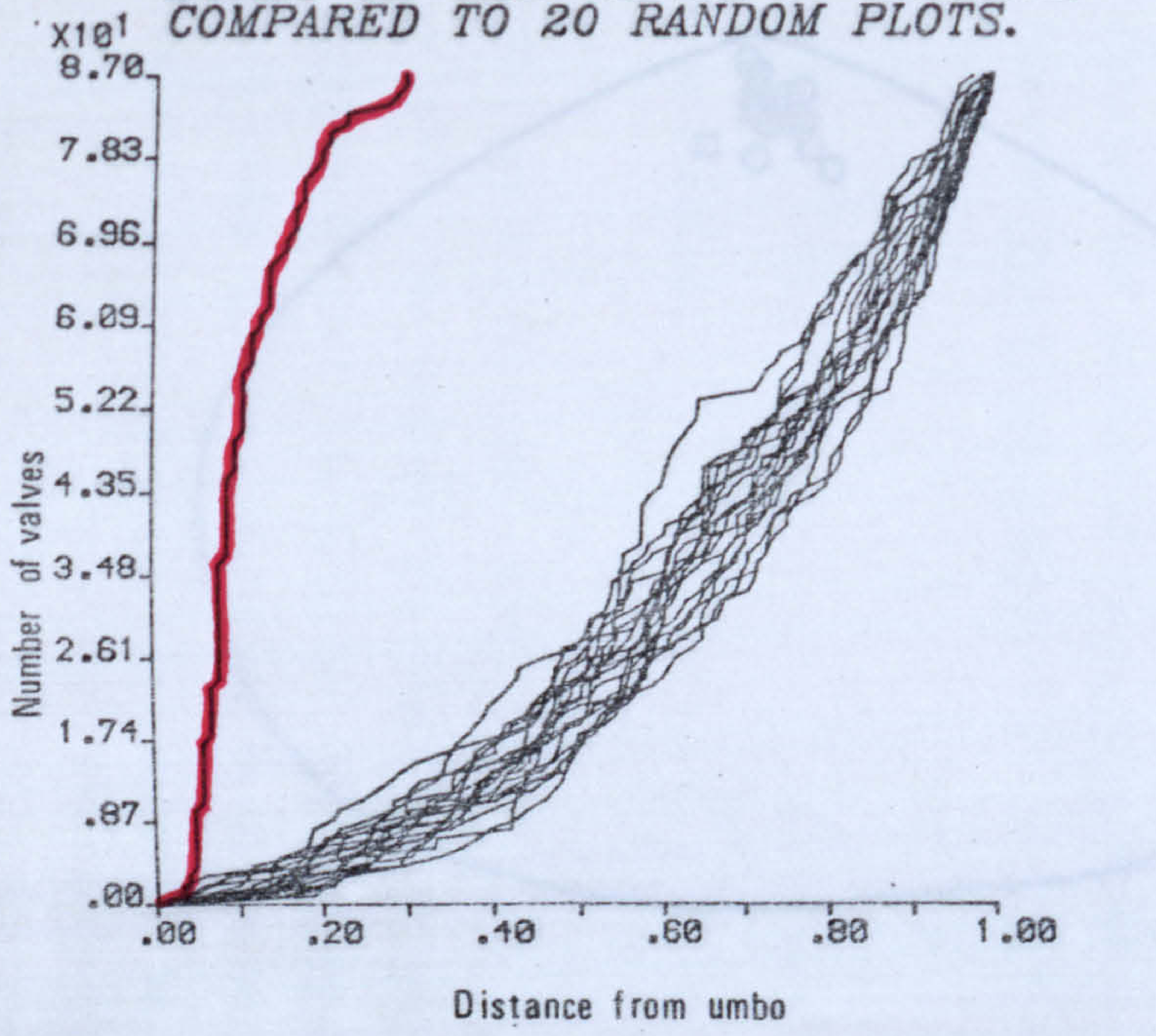


FIG. 8.12

THE ANGULAR DISTRIBUTION OF NATICID BORES ON THE VALVES OF SPISULA COMPARED TO 20 RANDOM DISTRIBUTIONS

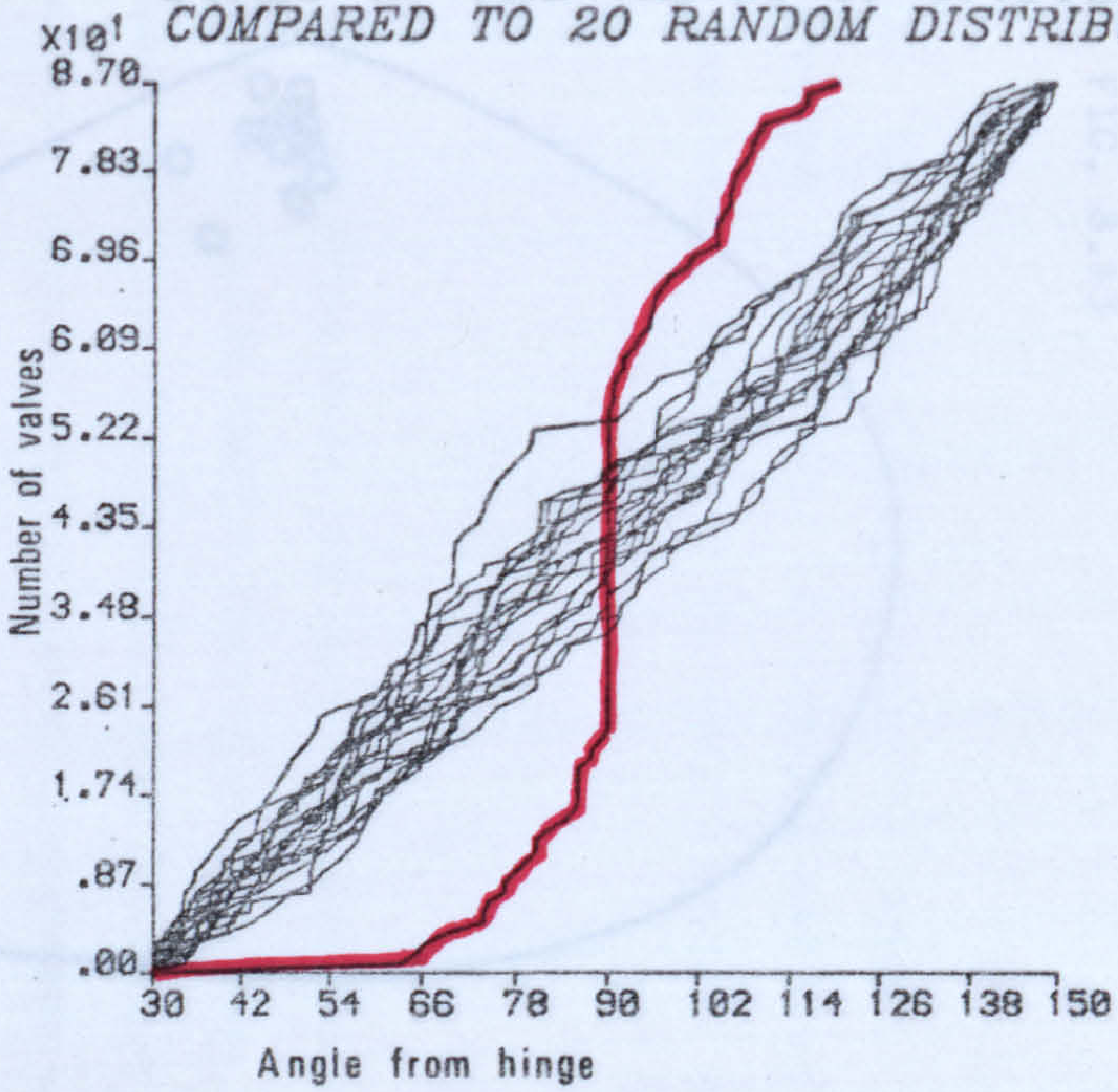
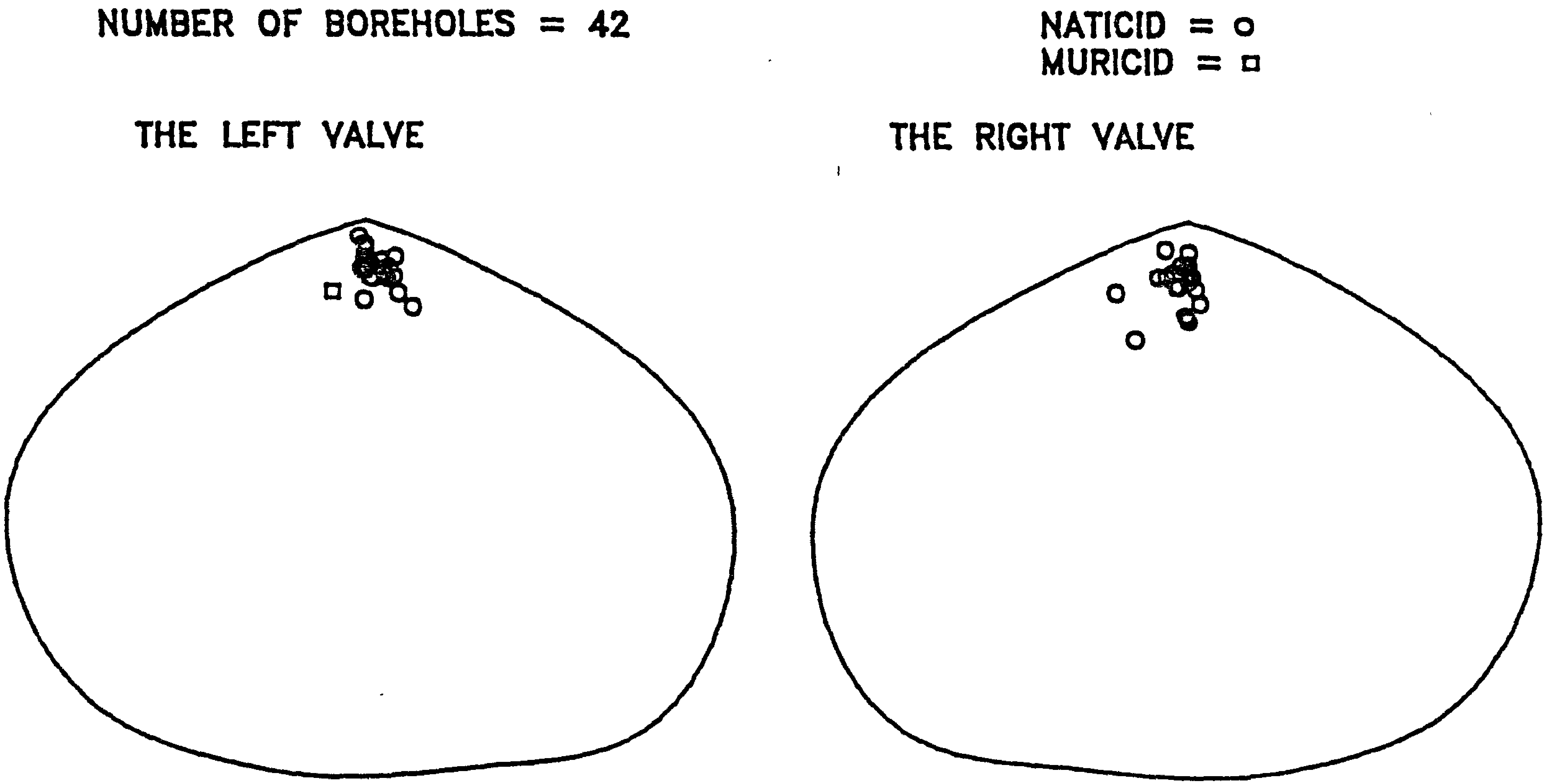


FIG. 8.13

THE DISTRIBUTION OF PREDATORY GASTROPOD BORES ON THE VALVES OF SPISULA FROM ALDEBURGH BRICK-PIT.



even more difficult that they could detect specific organs. Berg (1976) has shown that stereotypy in naticids is inherent and that they do not learn the more favourable sites for borehole location during ontogeny.

8.3.2 On *Turritella*.

The distribution of muricid boreholes over the shell of the gastropod genus *Turritella* was analysed using RANDO2 (see 4.2.6). From figs. 8.14 and 8.15 it can be seen that the distribution both in respect to distance from the apex and angular distribution in respect to the aperture can be explained as a random distribution. This lack of preference for a site of boring by the muricids suggests they had access to the whole shell, but modern *Turritella* is infaunal. Perhaps the *Turritella* which fell victims to the muricids were washed from the sediment when they were attacked or the predator pulled them from the sediment before drilling commenced. Another possibility is that the muricids were attacking the Sipuculid annelid *Phascolion strombi* (Montagu) which often inhabit the shells of *Turritella* after death. Campbell (1976, p. 137) figures *Phascolion strombi* in a *Turritella* shell.

8.4 Predator:prey size relationships.

The computer program BORING (see 4.2.5) was used to produce figs. 8.16 to 8.19 and these show the size of the boreholes drilled by muricids in *Astarte* and *Glycymeris* and by naticids in *Macoma* and *Spisula*. The boreholes in these diagrams are drawn to scale so that they represent the relative size of the borehole in respect to the

FIG. 8.14

THE LINEAR DISTRIBUTION OF MURICID BORES ON TURRITELLA COMPARED WITH 20 RANDOM PLOTS.

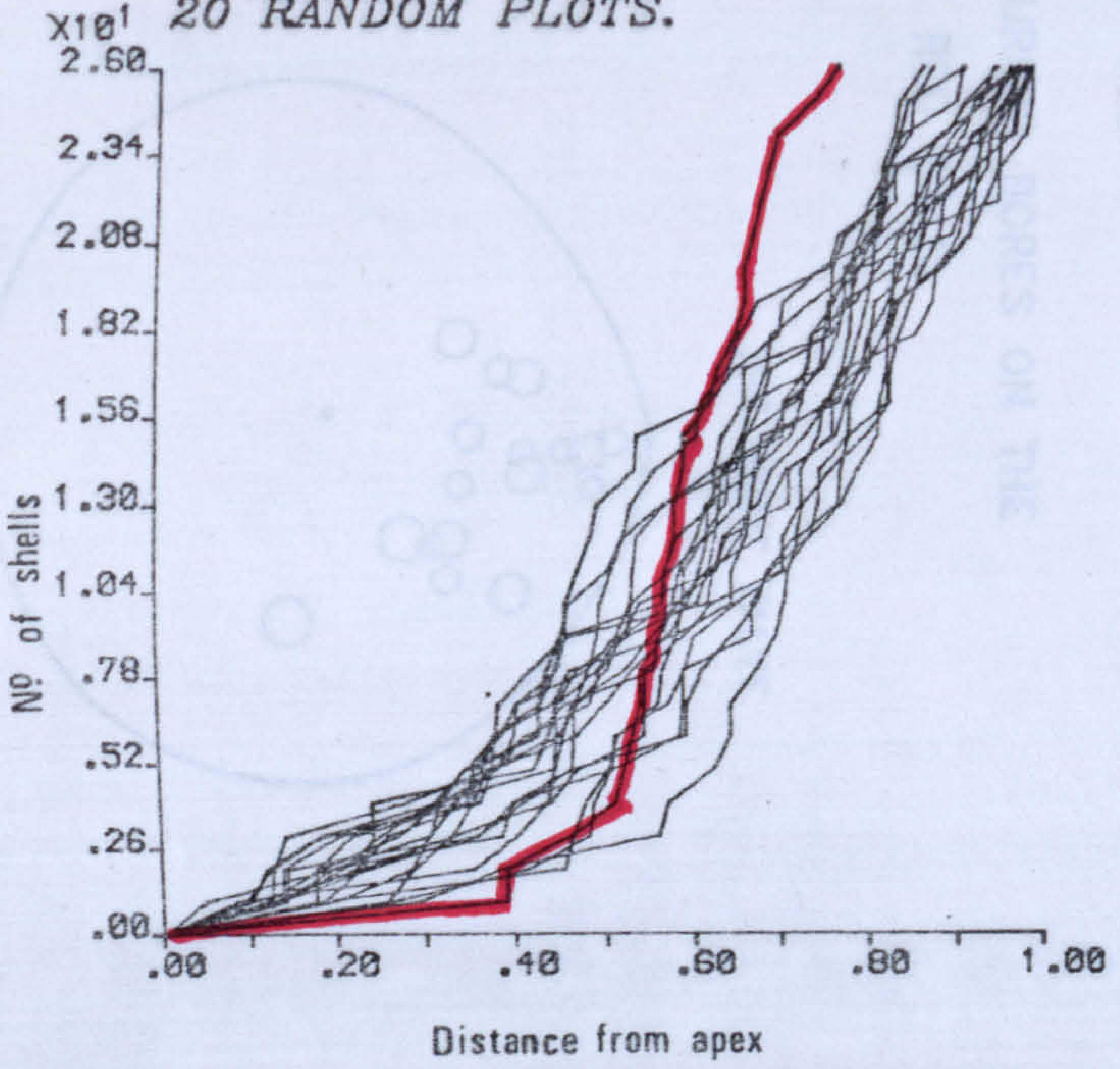


FIG. 8.15

THE ANGULAR DISTRIBUTION OF MURICID BORES ON TURRITELLA COMPARED WITH 20 RANDOM PLOTS.

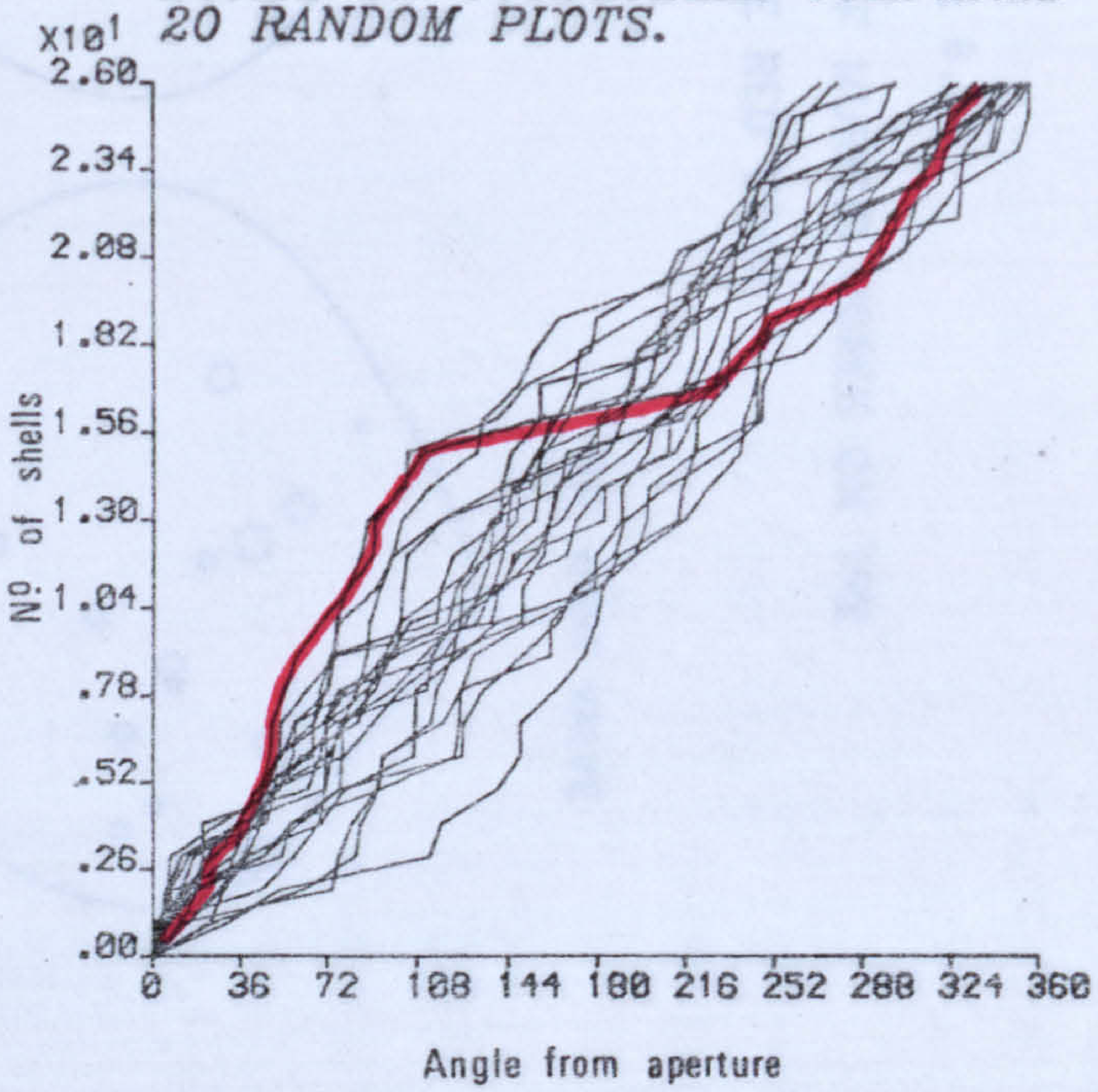


Fig 8.16

THE SIZE AND DISTRIBUTION OF MURICID BORES ON THE VALVES OF ASTARTE FROM THE RED CRAG.

NUMBER OF BOREHOLES = 34

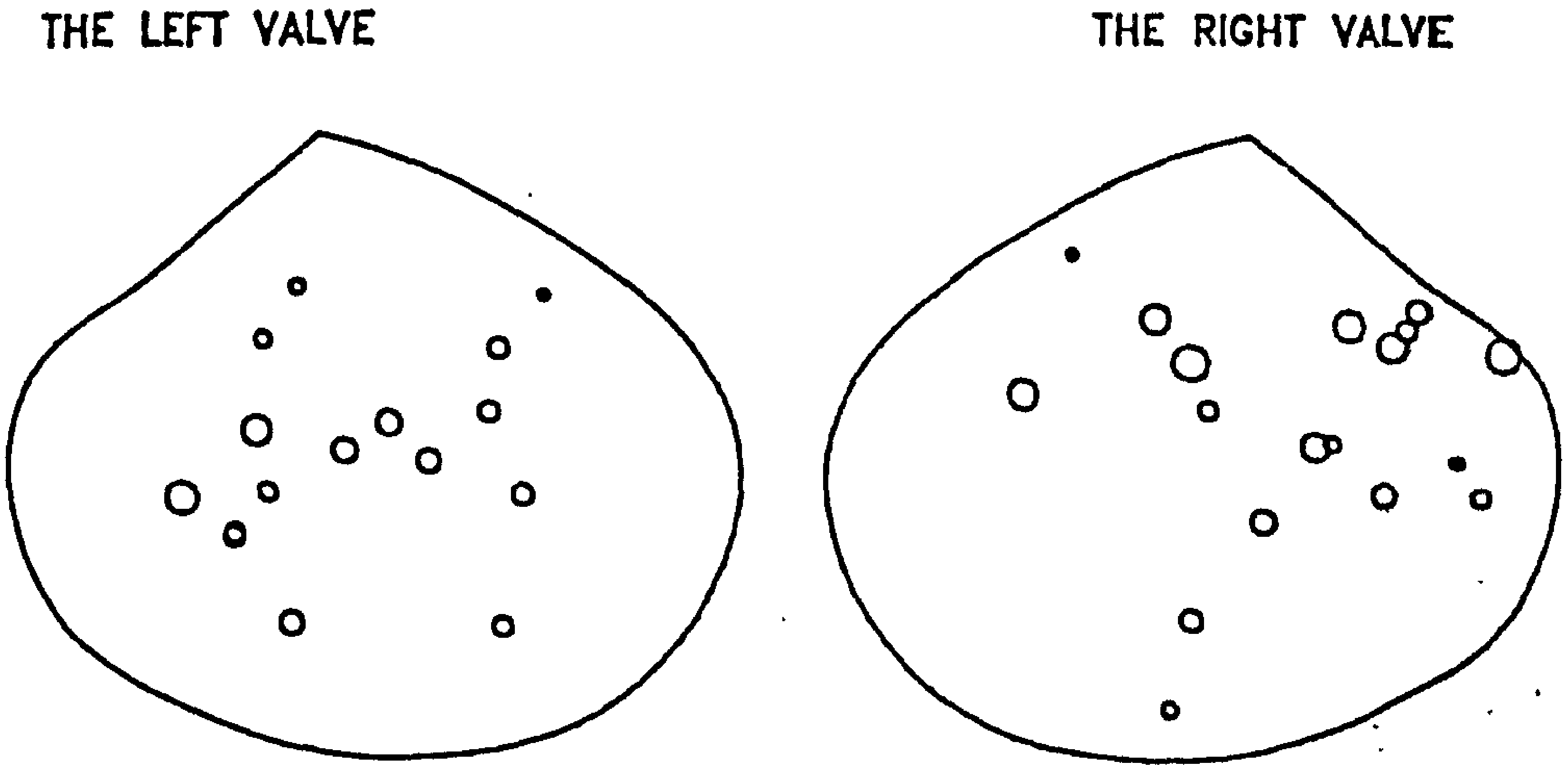


Fig 6.17

THE SIZE AND DISTRIBUTION OF MURICID BORES ON THE VALVES OF GLYCYMERIS FROM THE RED CRAG.

NUMBER OF BOREHOLES = 42

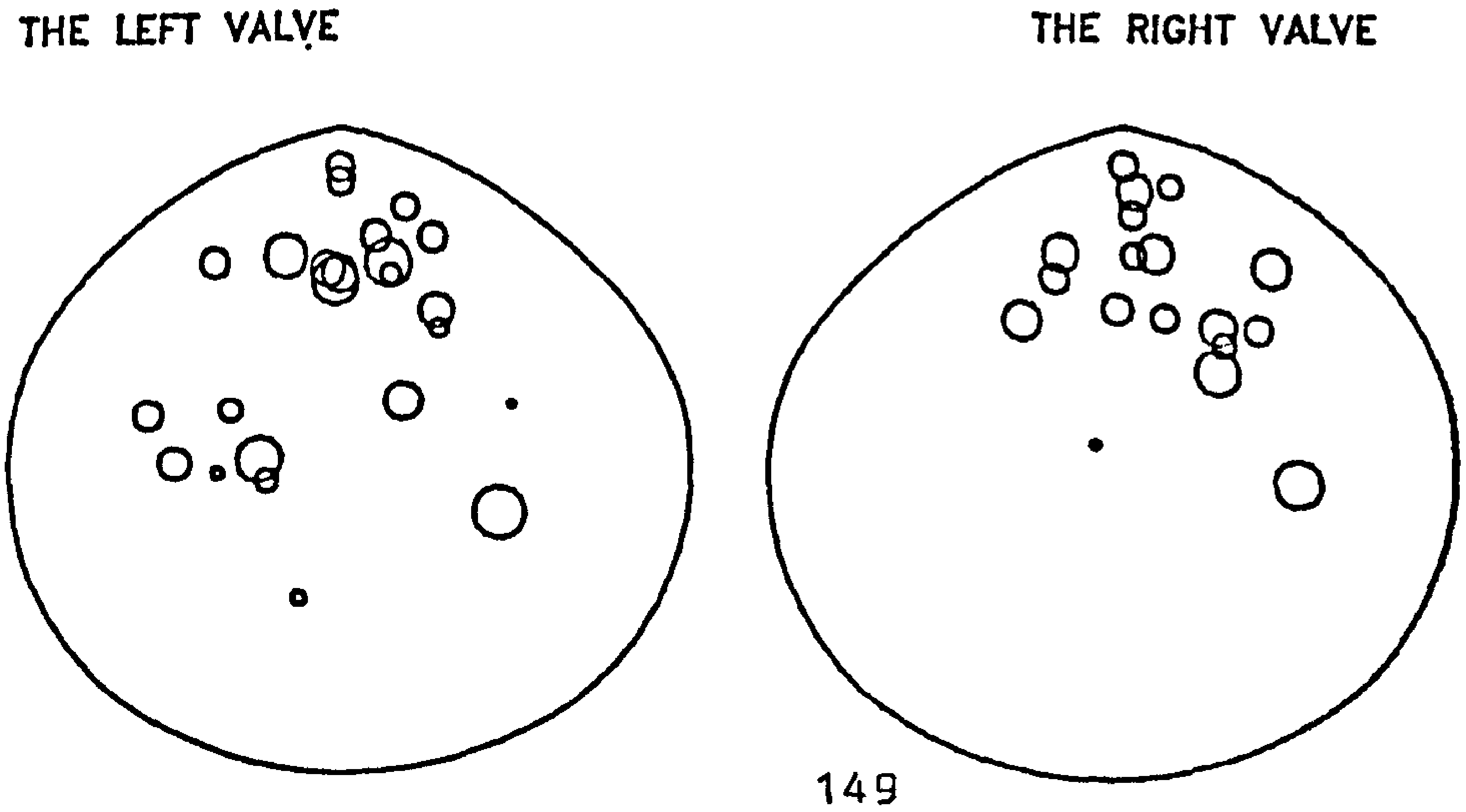


Fig 6.18

THE SIZE AND DISTRIBUTION OF NATICID BORES ON THE VALVES OF MACOMA FROM THE RED CRAG.

NUMBER OF BOREHOLES = 24

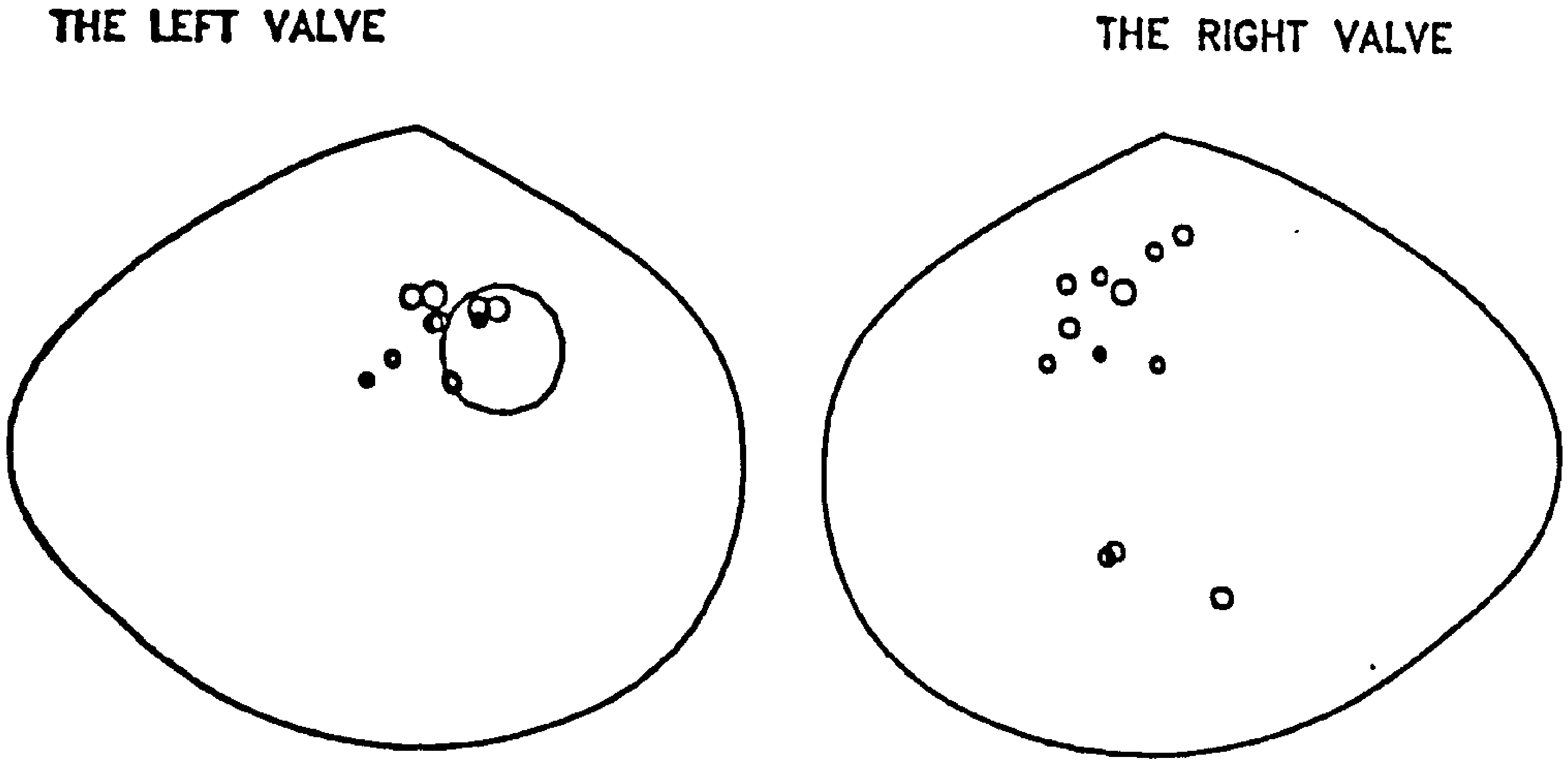
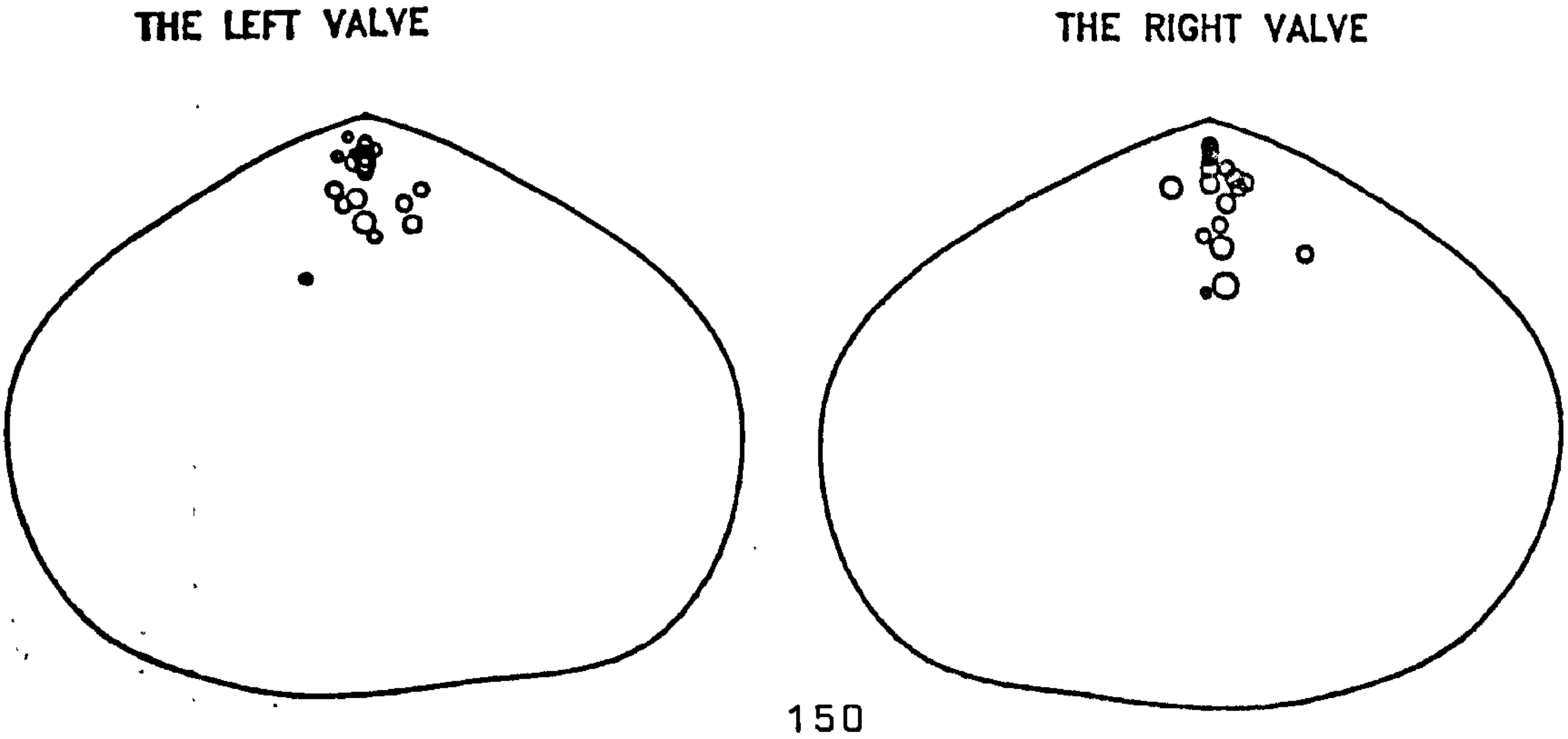


Fig 6.19

THE SIZE AND DISTRIBUTION OF NATICID BORES ON THE VALVES OF SPISULA FROM THE RED CRAG.

NUMBER OF BOREHOLES = 42



size of the bivalve it was drilled in, thus giving a qualitative impression of the borehole size to size of prey relationship.

8.4.1 Muricids.

From figs. 8.20 and 8.21 it can be seen that the Astarte bored by muricids are smaller than the non-bored sample, the bored specimens having a mean length of 18.5mm while the non-bored specimens have a mean length of 20.8mm. This is significantly different at the 95% level but not the 99% level. There was some preference for the smaller individuals from the Astarte population by muricids from the Red Crag. The larger Astarte may have been more effective when using escape responses when attacked by muricids.

Similarly Glycymeris reached a partial size refuge from muricid attack through ontogeny during the Red Crag. The mean length of bored individuals being 24.6mm and the mean length of the non-bored individuals is 38.4mm (see figs. 8.22 and 8.23) and these are significant at the 99% level. Thus the predation rates by muricids on these genera may be underestimated as the smaller valves of bivalves are less likely to be preserved and collected (see 1.4.3).

Glycymeris prey has a significantly (99% level) larger shell than Astarte prey (see figs. 8.21 and 8.23) with a mean length of 24.6mm compared to 18.5mm. Consequently the mean muricid borehole diameter is larger in Glycymeris than Astarte (see figs. 8.24 and 8.25), 2.48mm compared to 1.91mm and this is significant at the 99% level. The scatter diagrams (figs. 8.26 and 8.27) show a positive correlation between borehole size and size of shell. The Spearman rank coefficient is R=0.42 for Astarte and R=0.35 for Glycymeris both

FIG. 8.20

THE SIZE DISTRIBUTION OF <u>ASTARTE</u> FROM THE RED CRAG.

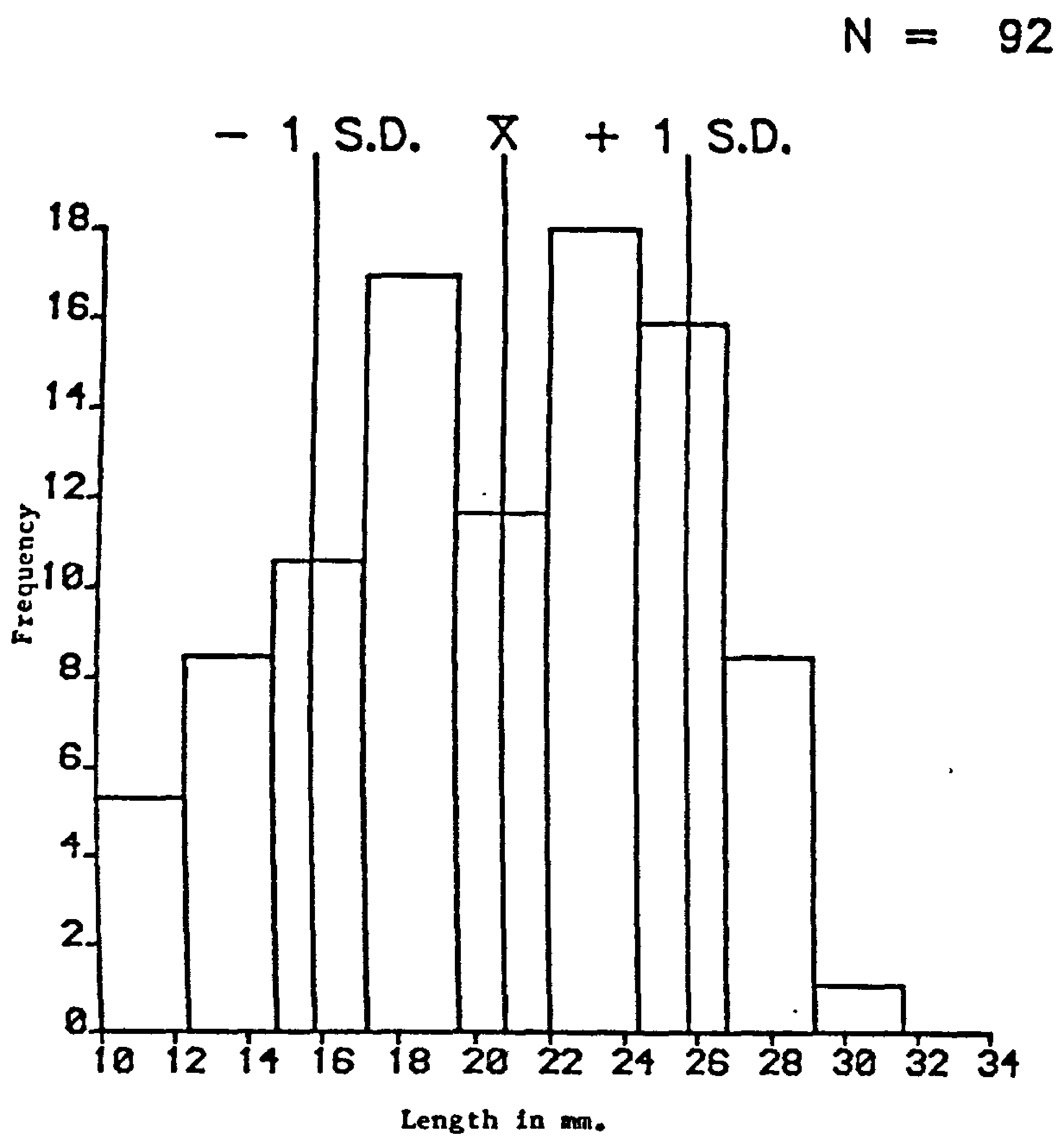


FIG. 8.21

THE SIZE DISTRIBUTION OF MURICID BORED <u>ASTARTE</u> FROM THE RED CRAG.

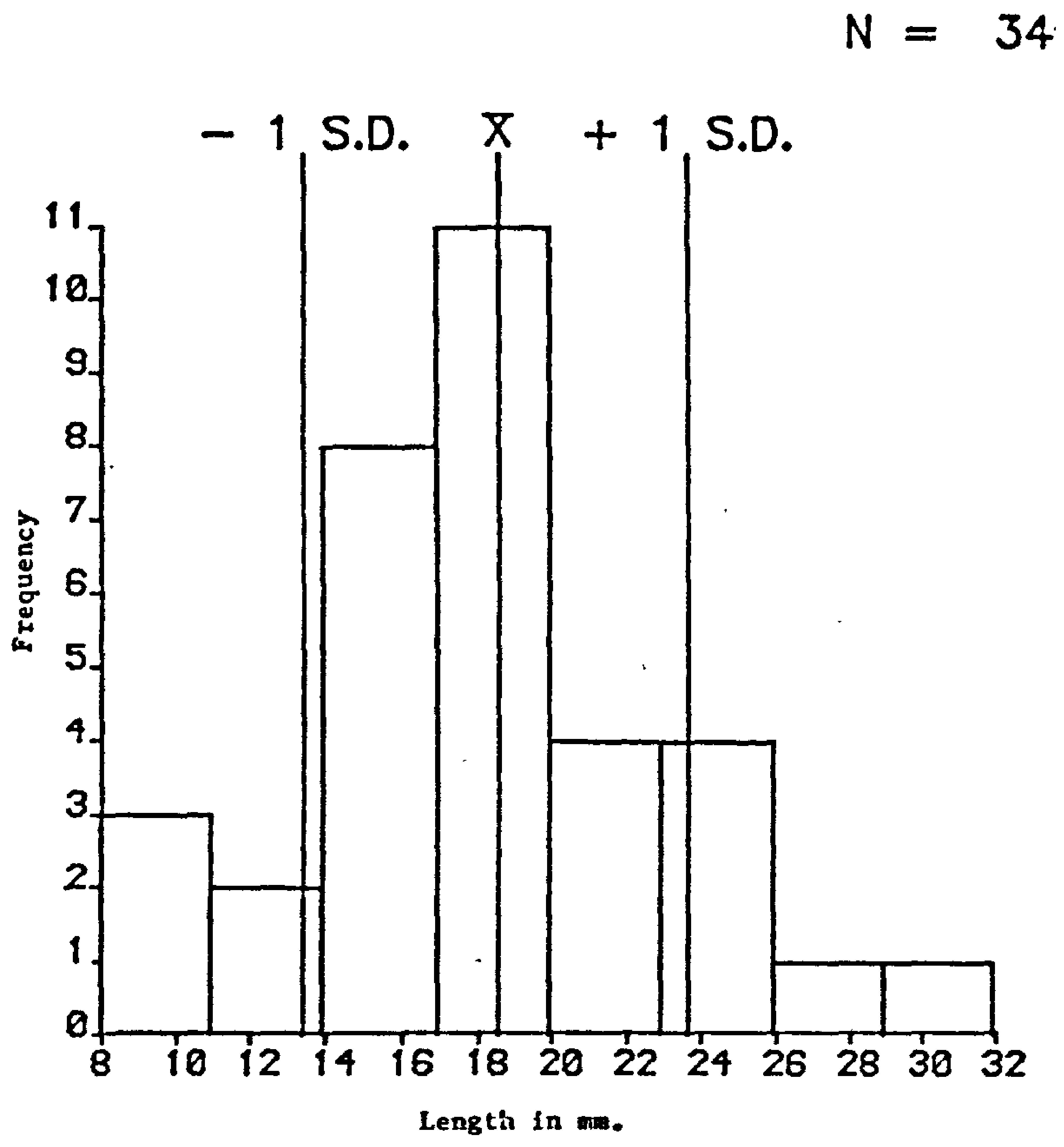


FIG. 8.22

THE SIZE DISTRIBUTION OF <u>GLYCYMERIS</u> FROM THE RED CRAG.

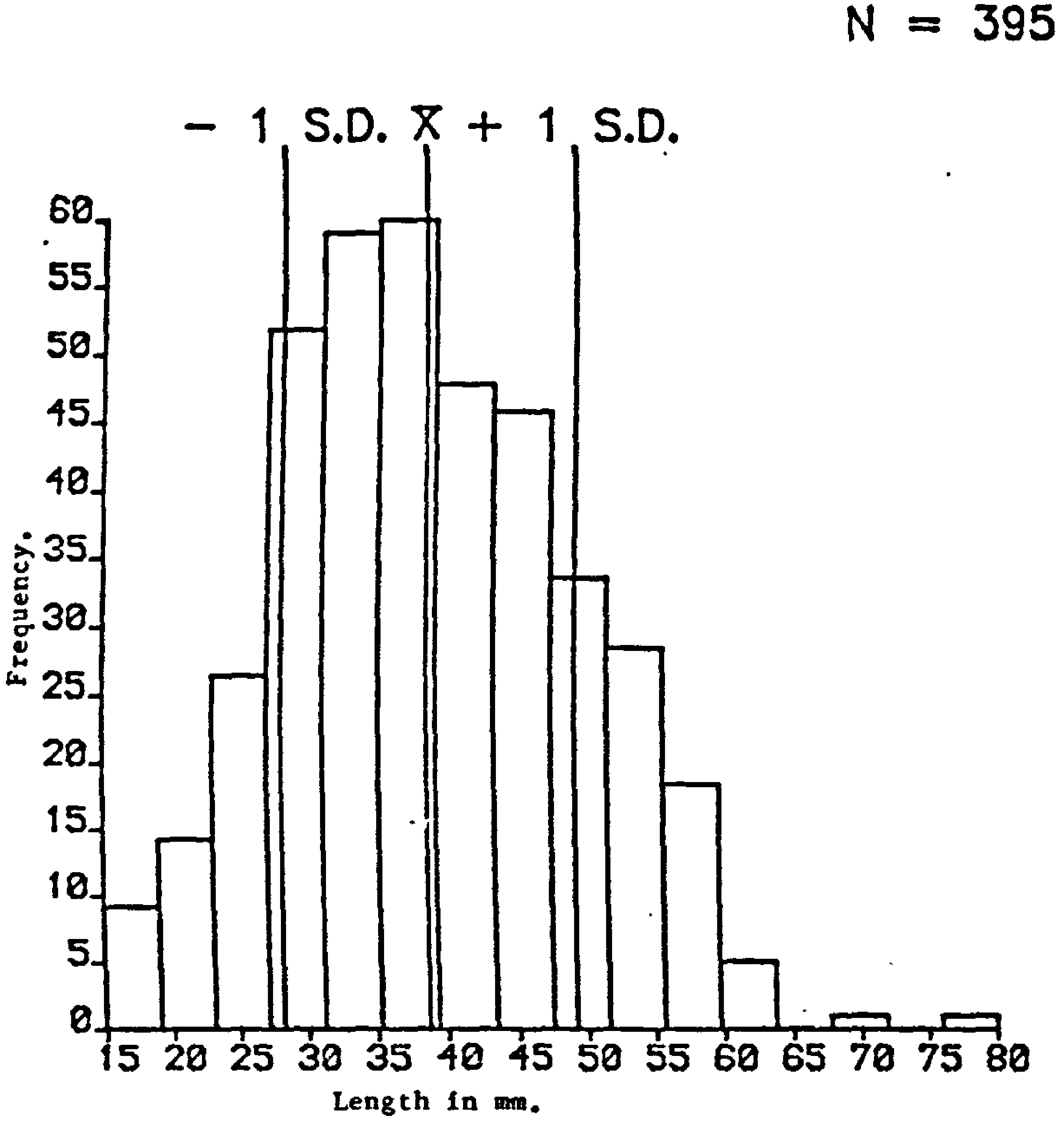


FIG. 8.23

THE SIZE DISTRIBUTION OF MURICID BORED <u>GLYCYMERIS</u> FROM THE RED CRAG.

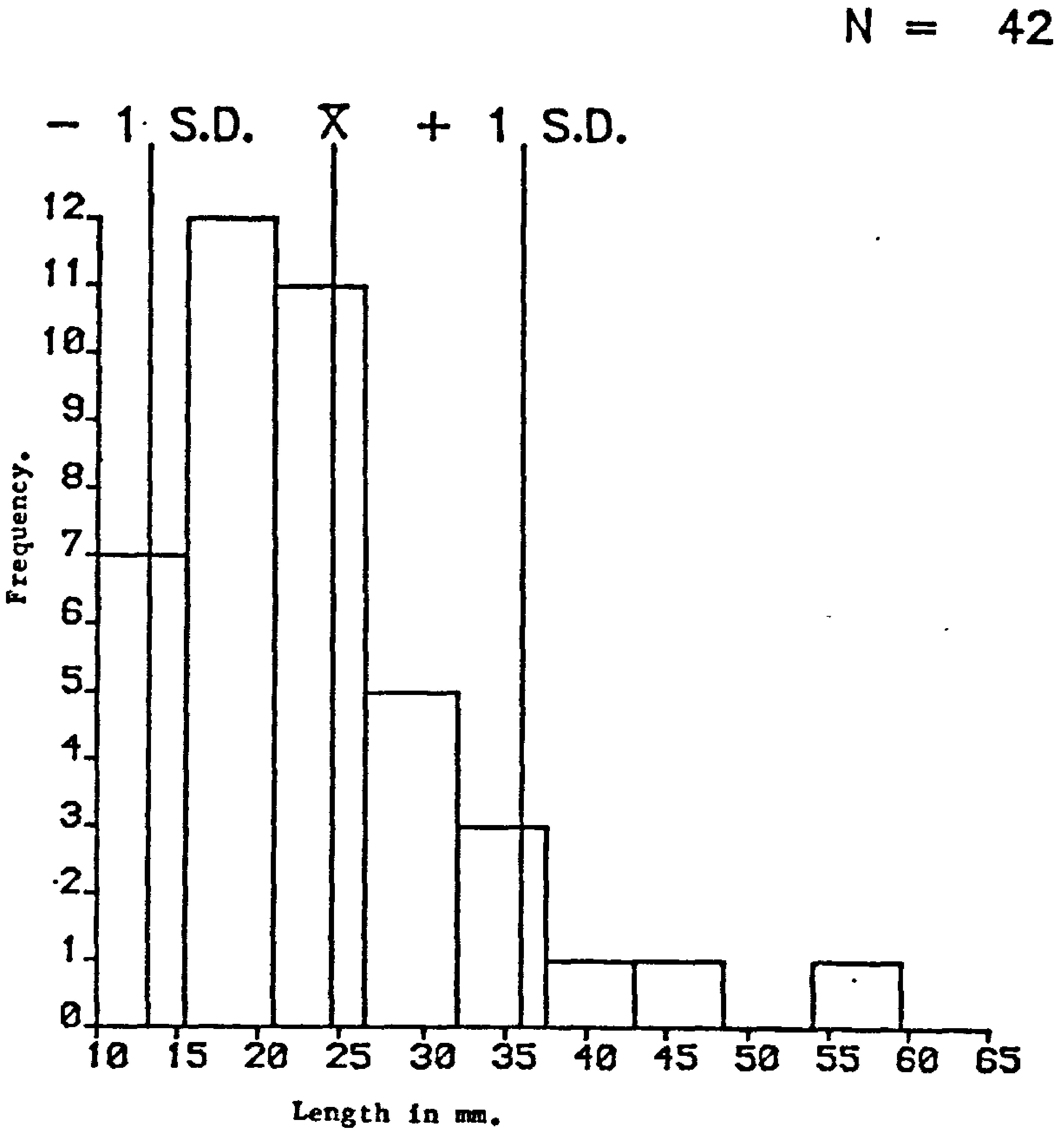


FIG. 8.24

THE SIZE DISTRIBUTION OF THE DIAMETERS OF MURICID BORES ON THE VALVES OF ASTARTE.

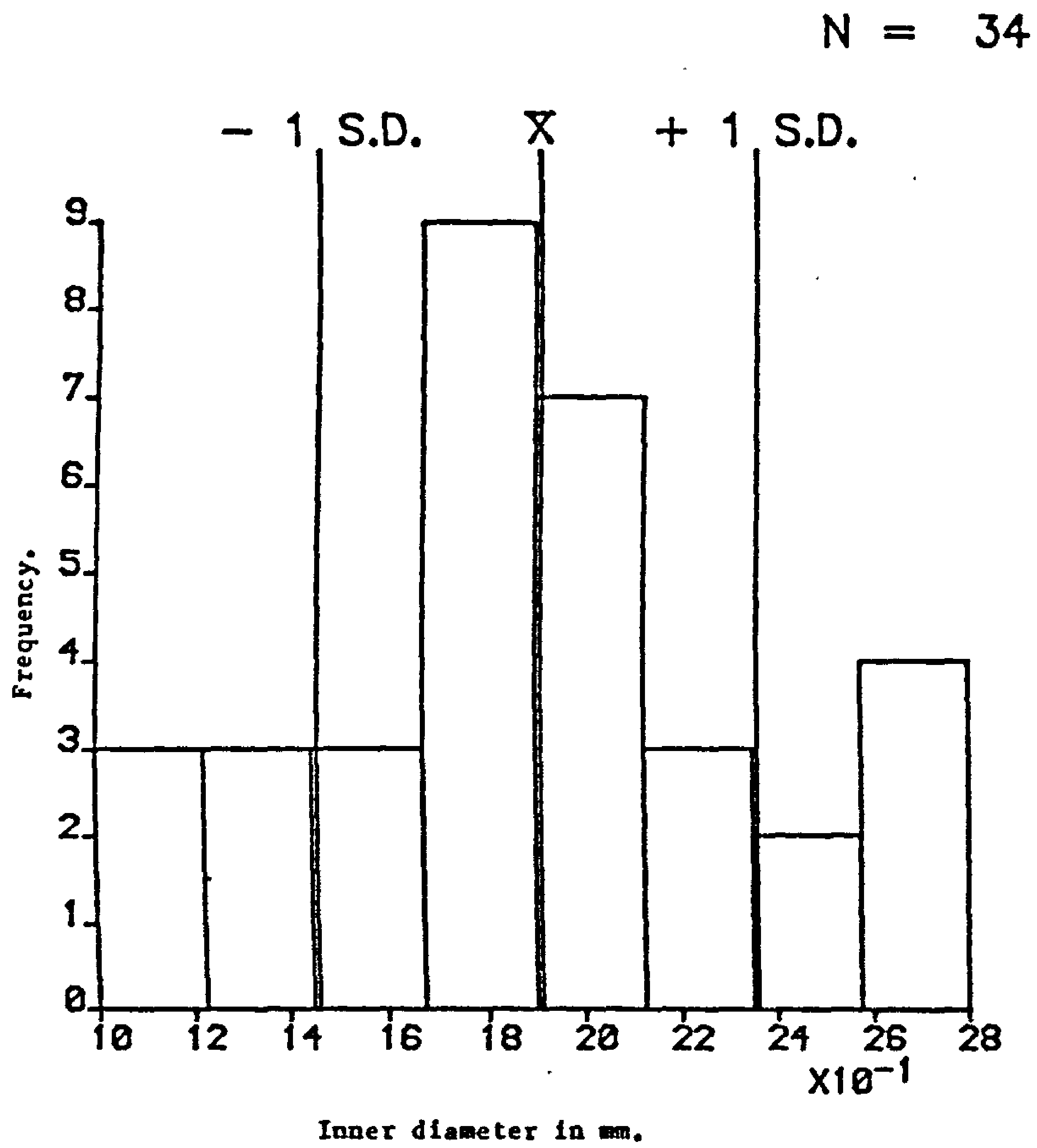


FIG. 8.25

THE SIZE DISTRIBUTION OF MURICID BOREHOLE DIAMETERS ON THE VALVES OF GLYCYMERIS.

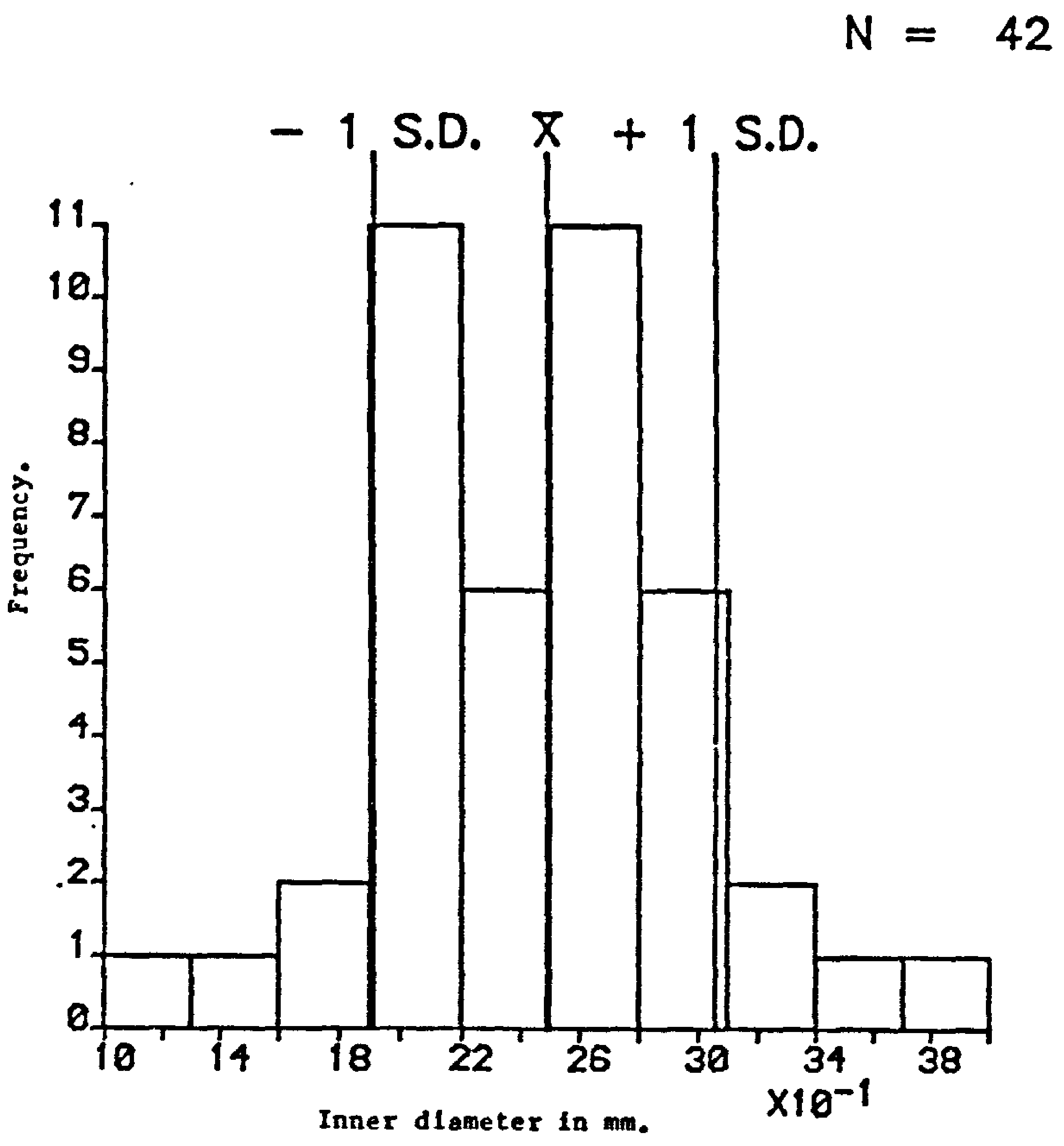


FIG. 8.26

MURICID BOREHOLE DIAMETERS
AGAINST SIZE OF BORED *ASTARTE.*

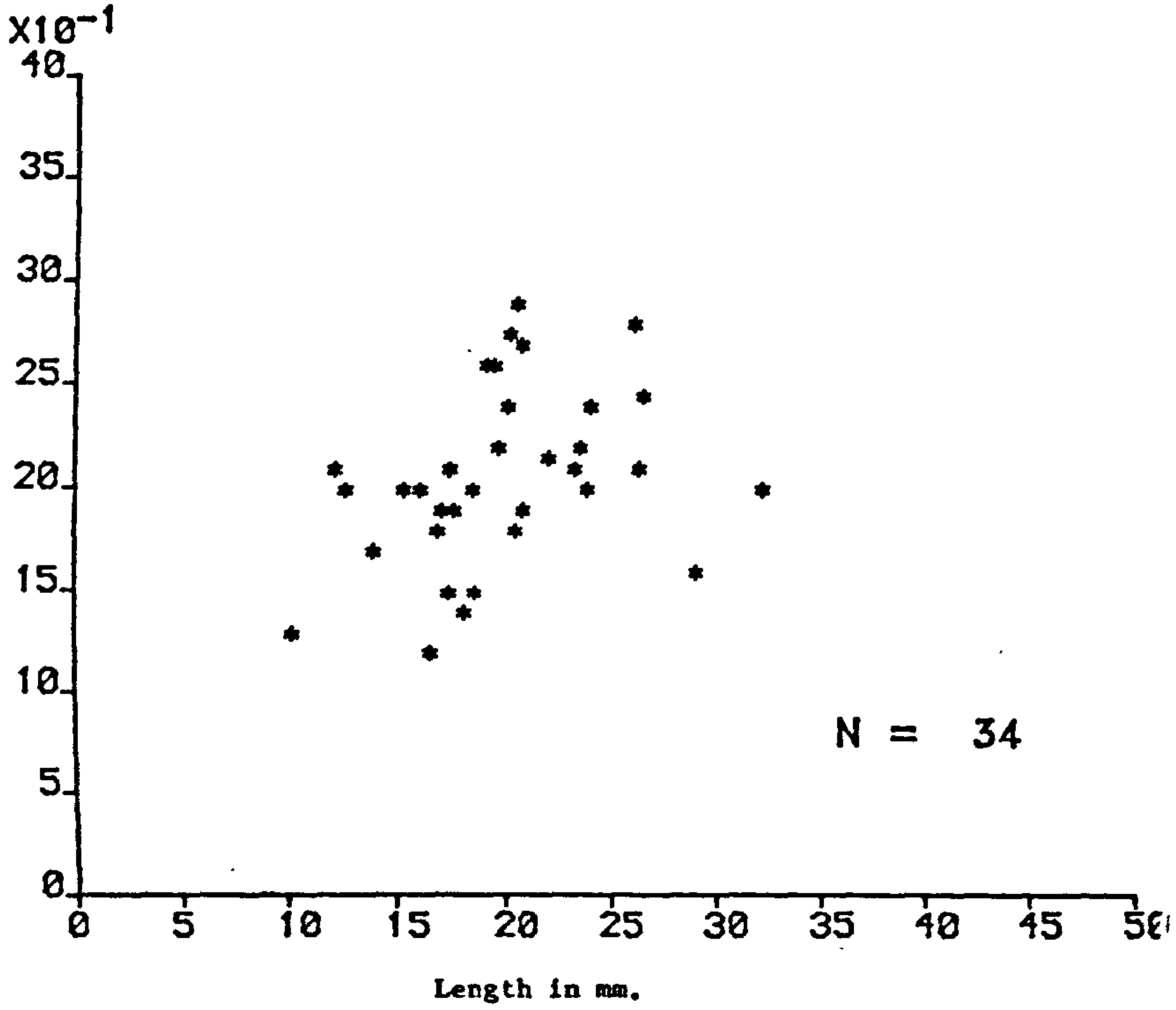
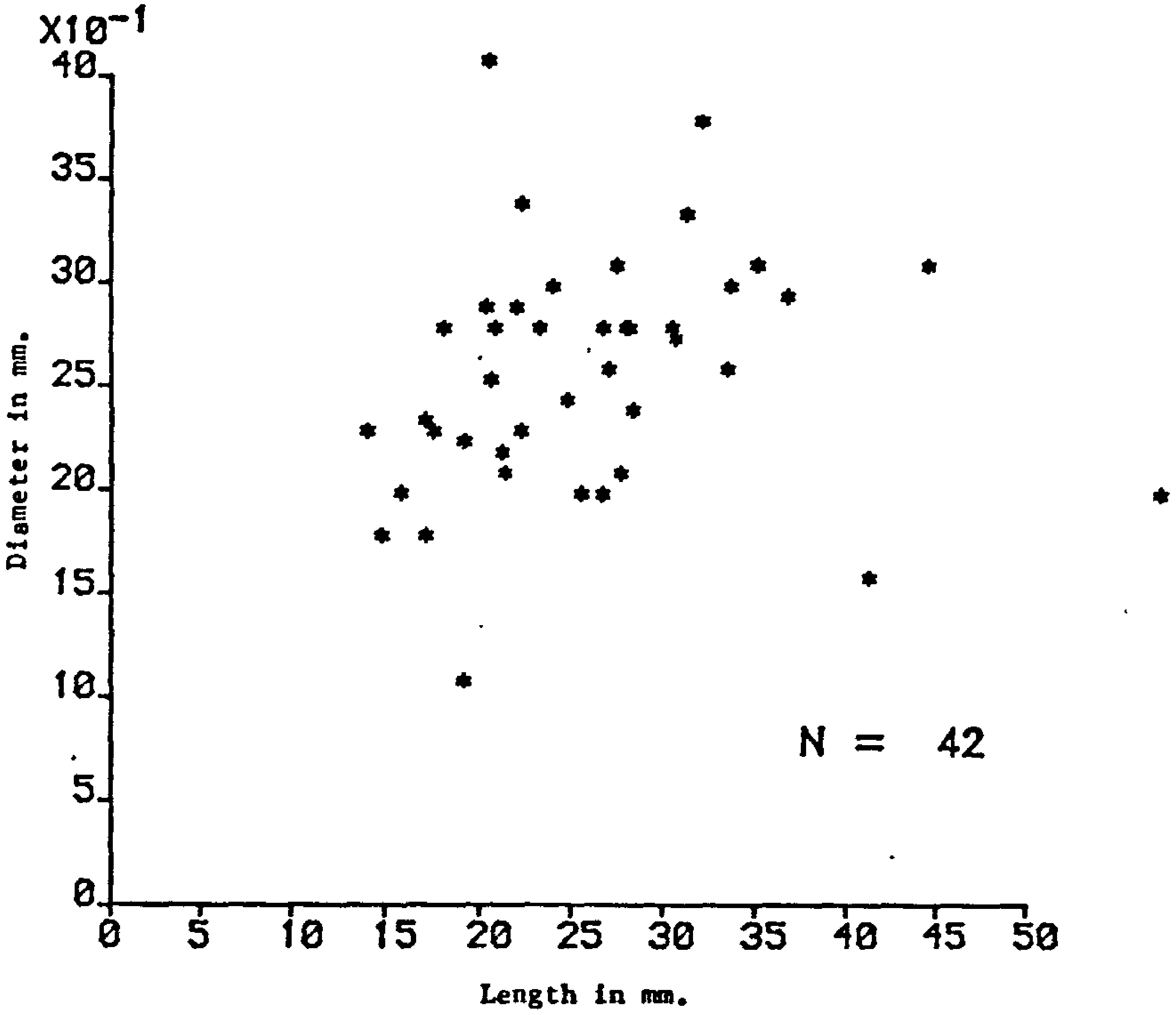


FIG. 8.27

MURICID BOREHOLE DIAMETERS
AGAINST BORED *GLYCYMERIS* SIZE.



significant at the 95% level and the former at the 99% level also. So assuming the diameter of the borehole is proportional to the size of predator (Mace 1978) then the muricids of the Red Crag were size selective in the prey that they chose. The size of prey chosen by a muricid was governed by its own size, a small muricid could not succesfully drill individuals that were preyed upon by larger muricids. Because of this Astarte and Glycymeris reached a partial refuge from muricid predation during the later stages of ontogeny. The larger muricids however had a tendency to attack larger individuals of the two prey genera than smaller muricids.

Even smaller muricid bores can be seen on the sample of Turritella prey, a mean borehole diameter of 1.48mm which is significantly (99% level) smaller than those on Astarte. These could possibly be juveniles attacking a small gastropod which has weak escape responses or it could be a species of small hole drilling muricids which specialize in feeding on Turritella. The highest degree of multiple boring is exhibited in specimens of Turritella (see 8.5). There are 11 specimens of drilled Turritella with a total of 27 muricid holes in them. This could be a juvenile feeding behaviour or one peculiar to a particular species of muricid, Nucella tetragona possibly.

8.4.2 Naticids.

There was a different size relationship between predator and prey where the naticids were concerned. In Spisula there was no significant difference at the 95% level between the mean length of bored and non-bored individuals with means of 16.9mm and 17.6mm respectively (see figs. 8.28 and 8.29). Macoma which have been bored by naticids have a larger mean length, 26.05mm, than the non-bored

FIG. 8.28

THE SIZE DISTRIBUTION OF <u>SPISULA</u> FROM THE RED CRAG.

N = 300

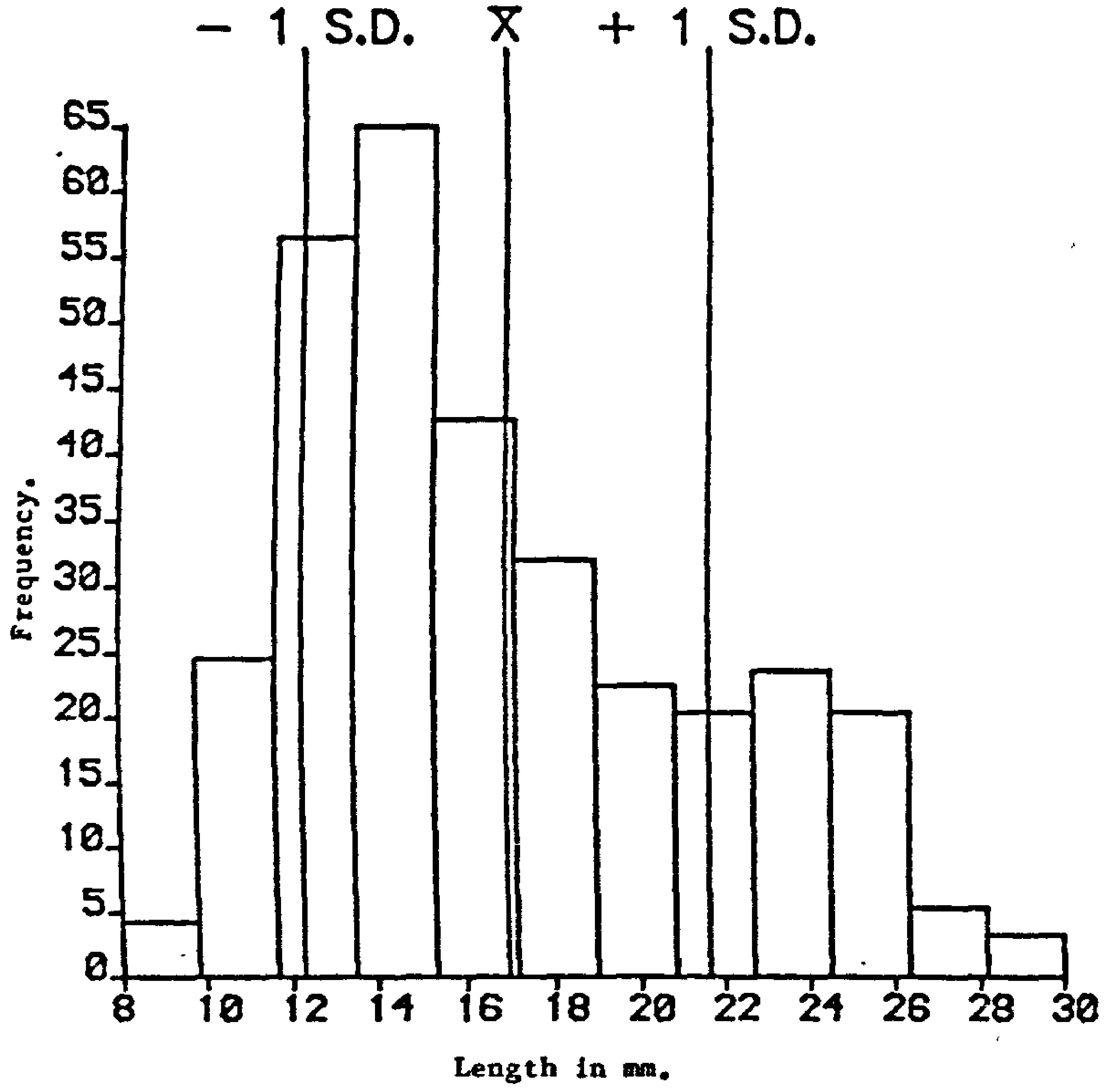
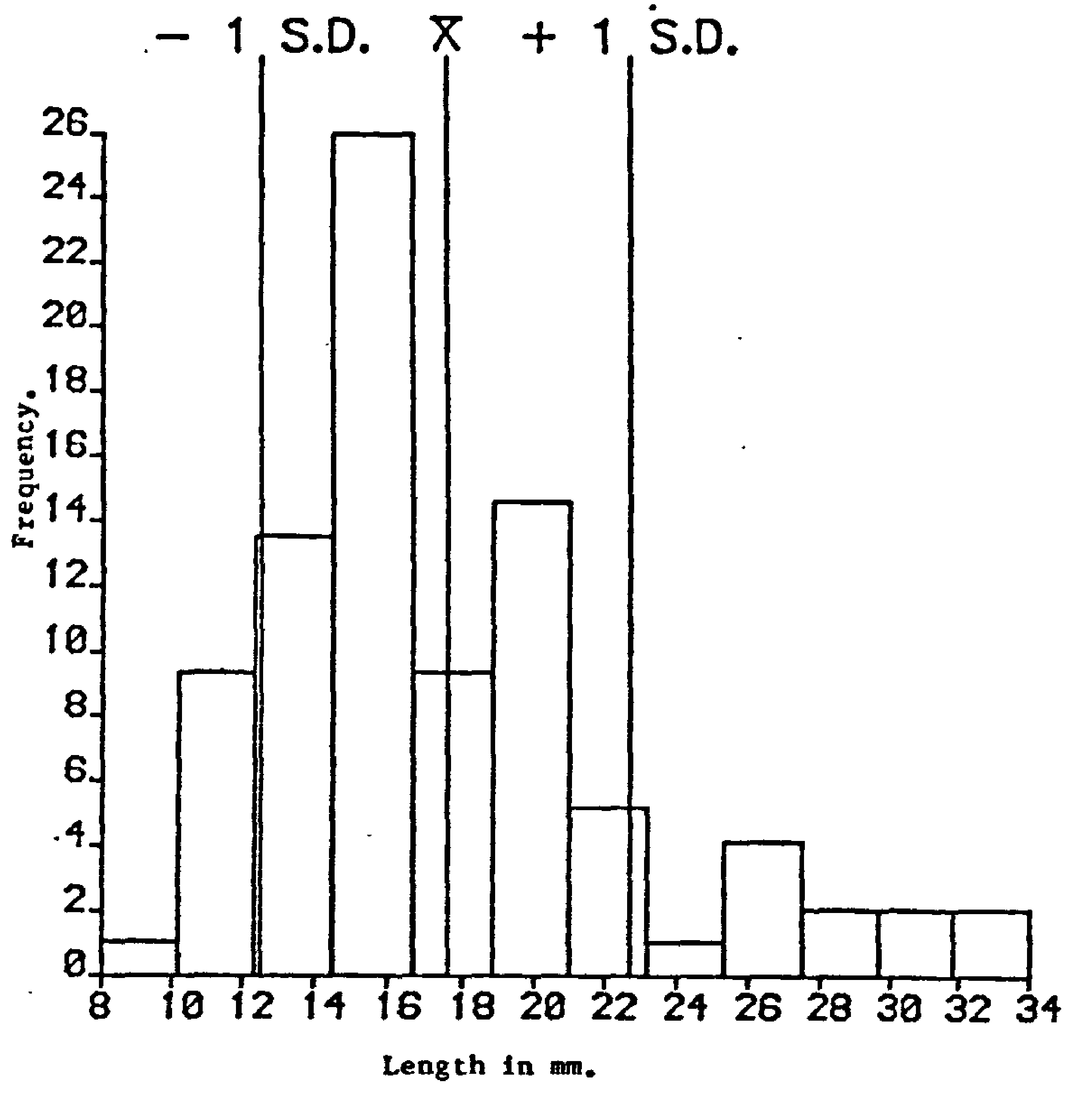


FIG. 8.29

THE SIZE DISTRIBUTION OF NATICID BORED <u>SPISULA</u>.

N = 87



ones: 23.6mm (see figs. 8.30 and 8.31) which is significant at the 95% but not the 99% level. Neither Spisula nor Macoma reached a size refuge to naticid predation during ontogeny and the predators could deal with the largest individuals of these two genera.

The mean diameter of naticid boreholes in Macoma (2.51mm) is significantly larger at the 99% level than in Spisula (1.82mm) (see figs. 8.32 and 8.33). Macoma is significantly larger than Spisula (99% level) (see figs. 8.28 and 8.30) suggesting that the larger naticids were attracted towards the larger prey genus. The correlation between borehole size and length of prey shows that there is a significant (99% level) positive correlation for Spisula of R=0.52 (see fig. 8.34) and a non-significant negative correlation for Macoma of R=-0.01 (see fig. 8.33). There was a proportional relationship between the size of naticid predator and Spisula prey during the Red Crag but no such relationship in Macoma.

It seems probable that Macoma and Spisula were drilled by different species of naticid with different predation behaviour towards their prey.

8.5 Multiple bores.

Examples of multiple bores can be seen on a number of specimens from the Red Crag. A specimen of G. glycymeris from Waldringfield Heath [18] has two muricid bores in one valve (see pl. 3F). Several specimens of Turritella have been penetrated by more than one muricid hole. One specimen from Bawdsey [27] has been pierced by six muricid

FIG. 8.30

THE SIZE DISTRIBUTION OF <u>MACOMA</u>
FROM THE RED CRAG.

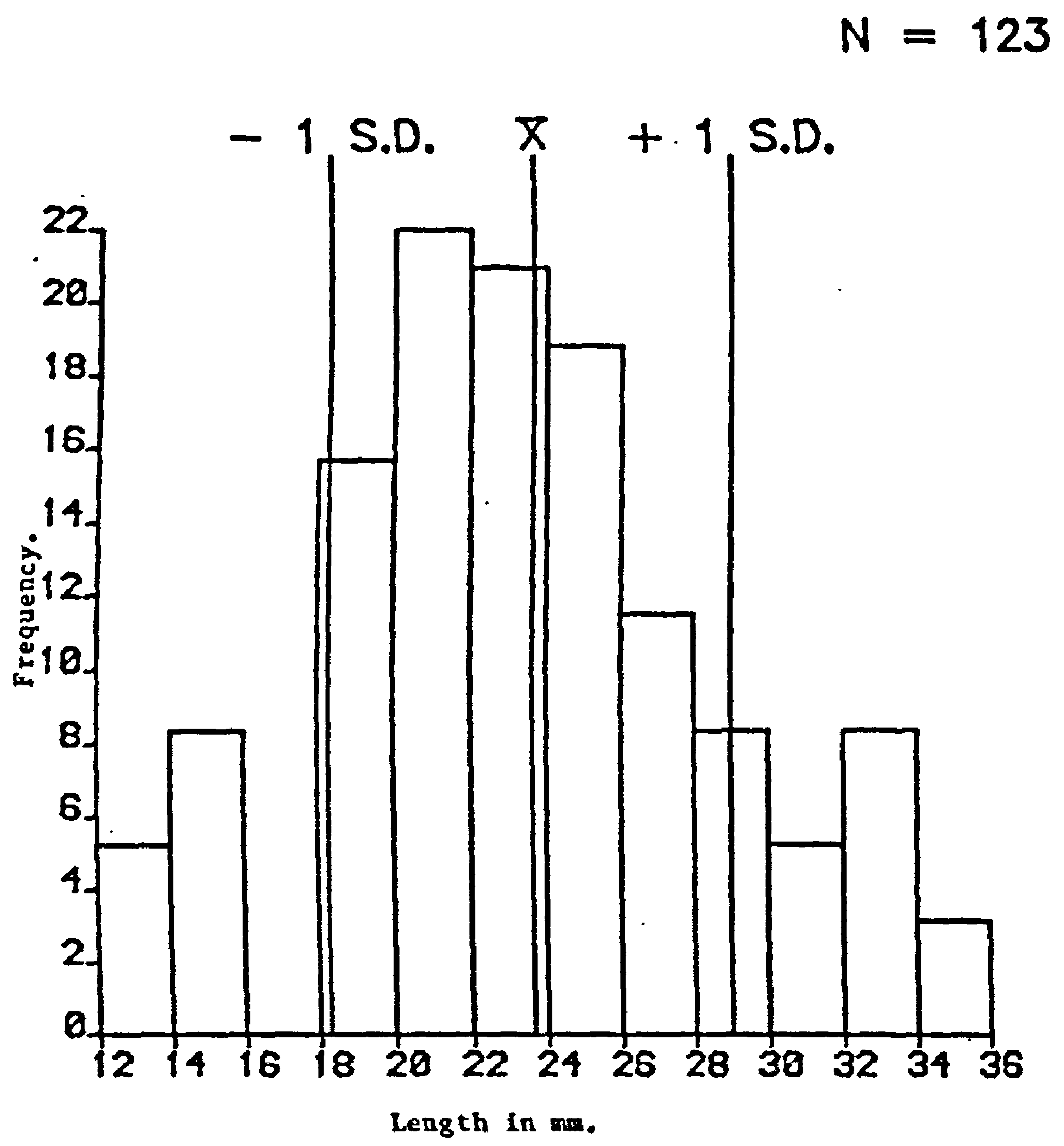


FIG. 8.31

THE SIZE DISTRIBUTION OF NATICID
BORED <u>MACOMA</u>.

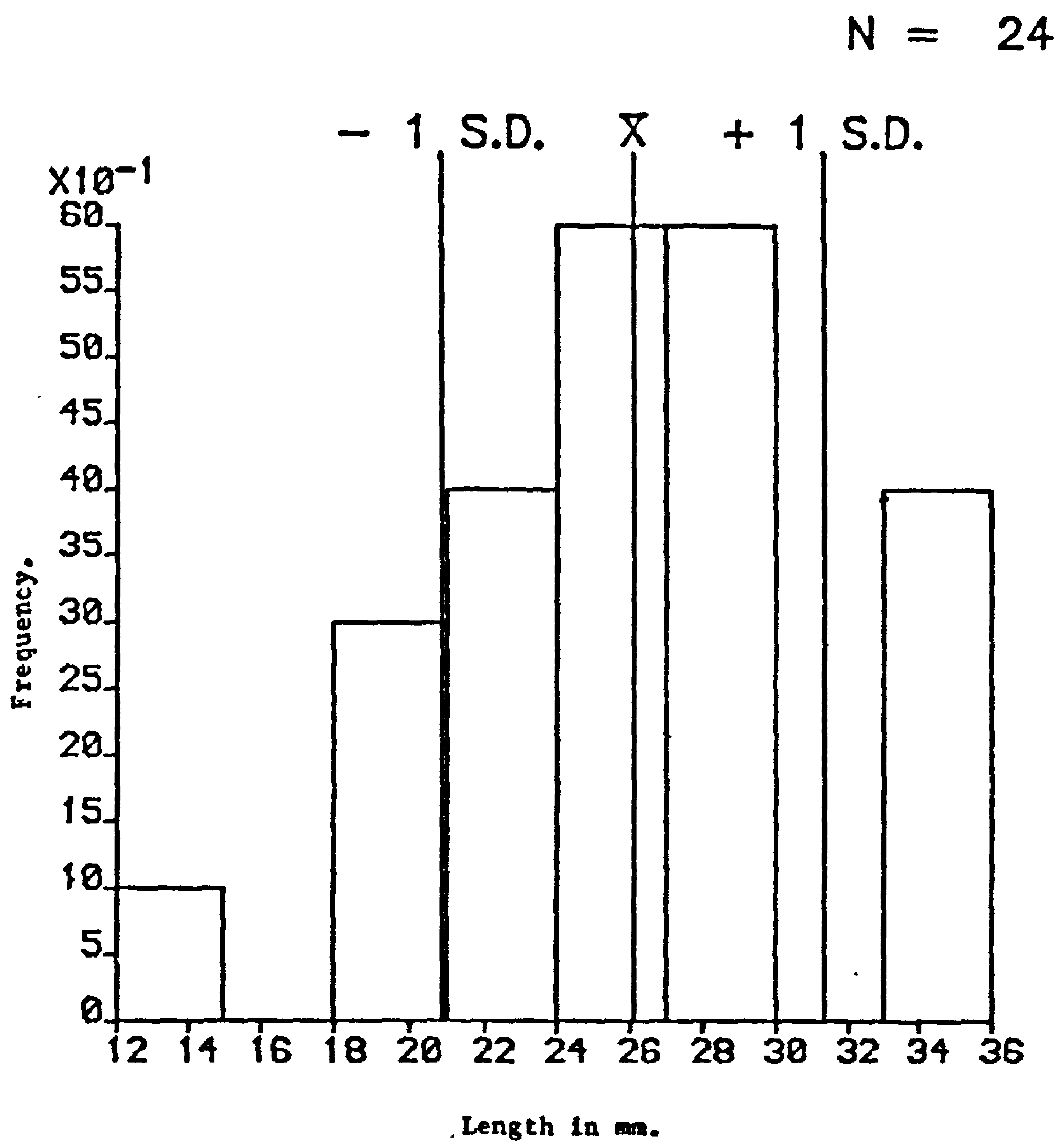


FIG. 8.32

THE SIZE DISTRIBUTION OF NATICID BOREHOLE DIAMETERS IN THE VALVES OF <u>MACOMA</u>.

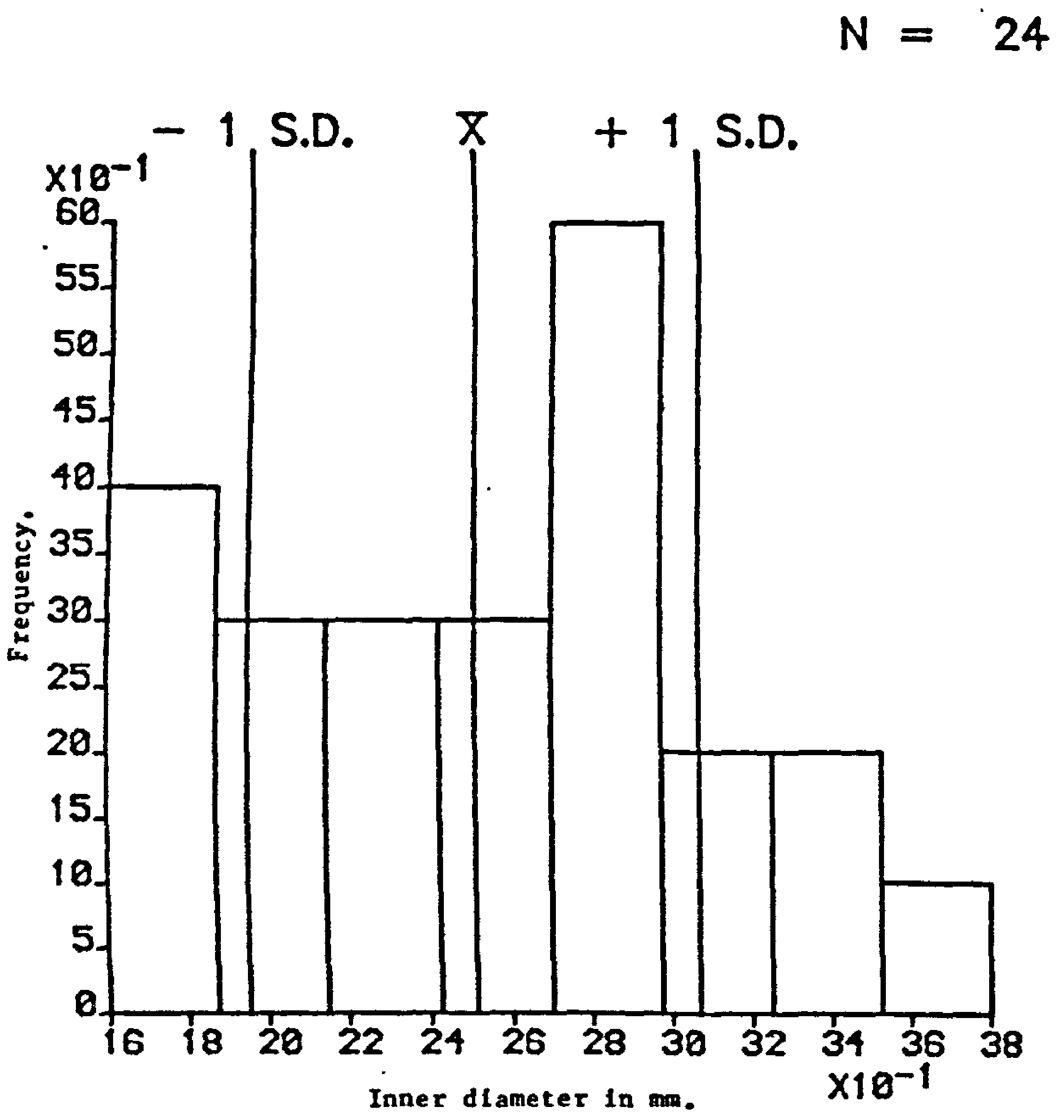


FIG. 8.33

THE SIZE DISTRIBUTION OF NATICID BOREHOLE DIAMETERS IN THE VALVES OF <u>SPISULA</u>.

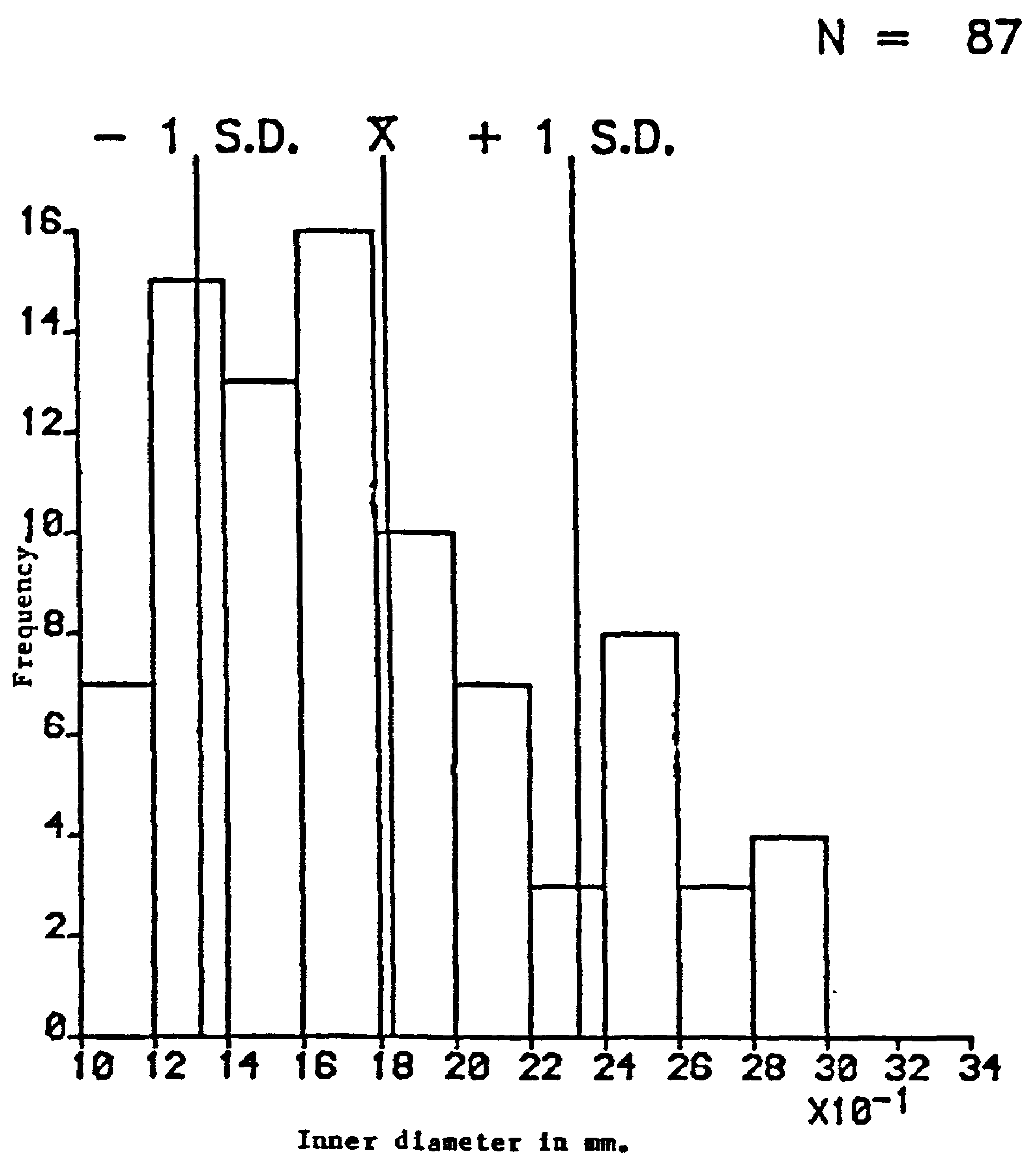


FIG. 8.34

NATICID BOREHOLE DIAMETERS
AGAINST BORED SPISULA SIZE.

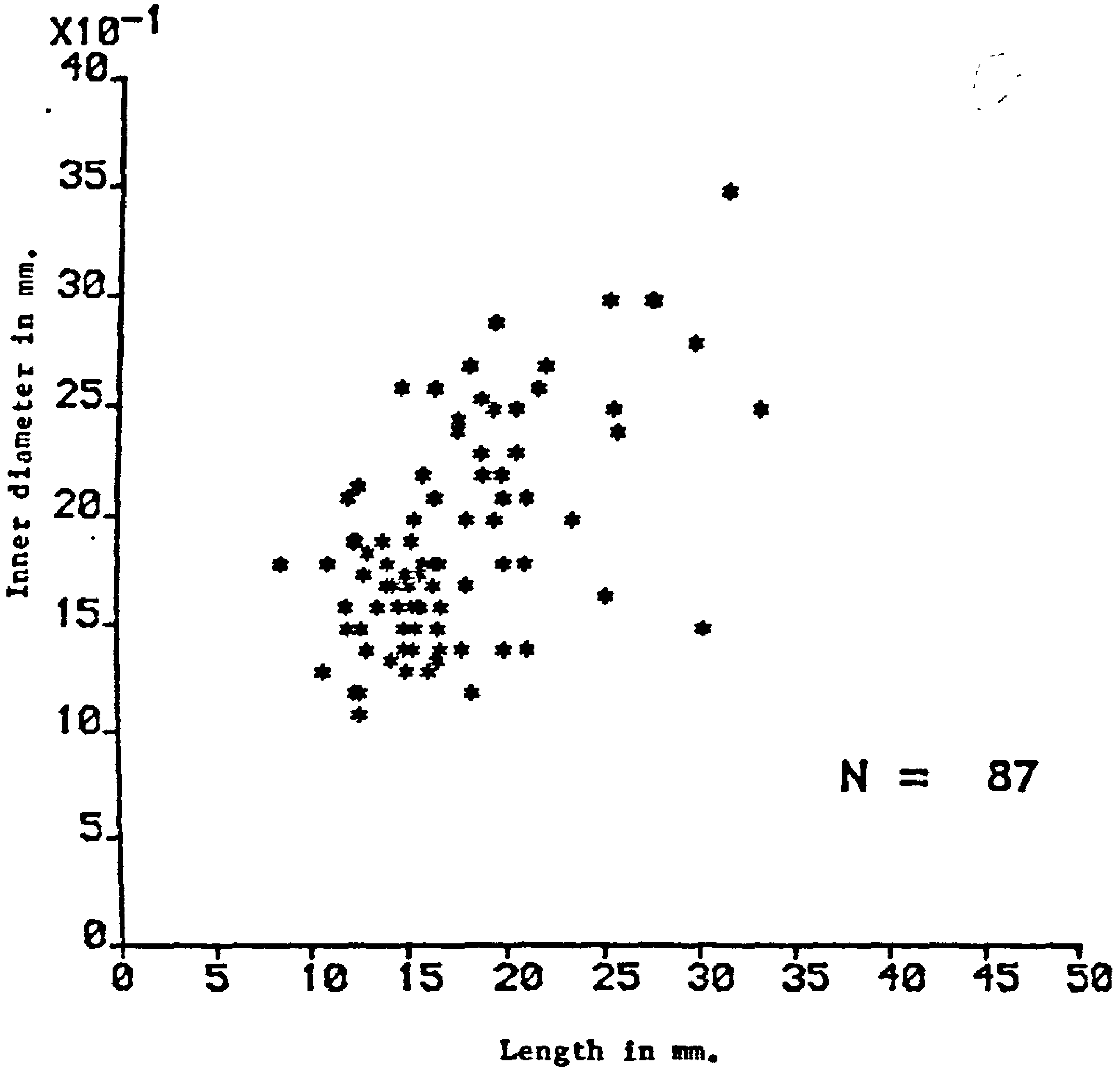
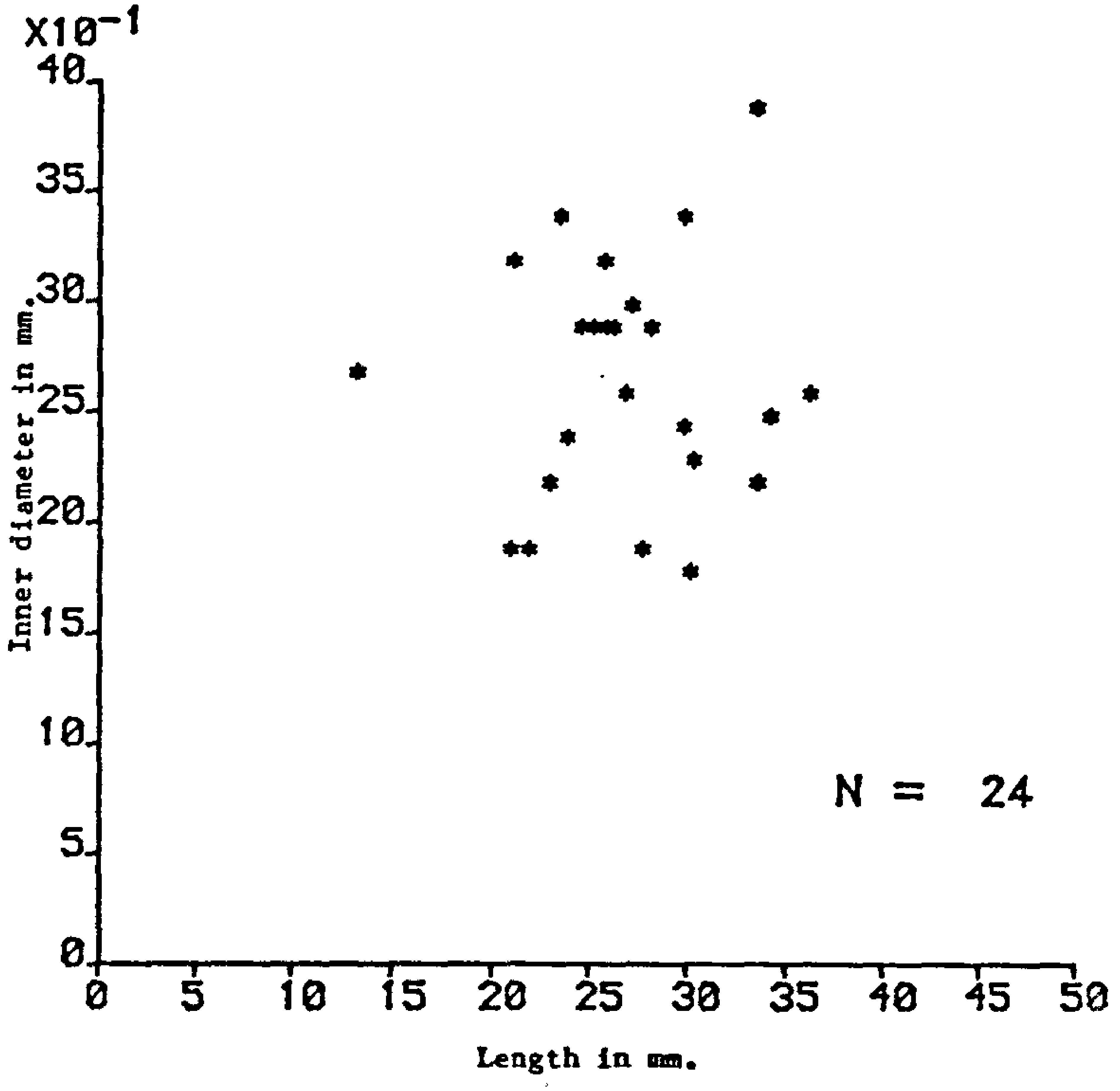


FIG. 8.35

NATICID BOREHOLE DIAMETER
AGAINST SIZE OF BORED MACOMA.



bores. This phenomenon is due to the tendency of muricids to attack in gangs (Hoffman et al. 1974).

This behaviour is not exhibited by naticids but there are occasional examples of multiple naticid bores. A specimen of Spisula arcuata from Virtue's Farm [28] has two failed naticid bores on a single valve (see pl. 3B). There are two successful naticid bores on a specimen of Turritella incrassata from Stratton Hall [6] as well as four successful muricid bores. This situation could only have arisen if one or both of the naticids had bored an empty shell or all four muricids and one naticid had bored an empty shell. It is impossible for more than one naticid to bore at the same time as the victim is completely engulfed within the predator's foot (Fretter and Graham 1962, p. 247). Similarly the muricids could not have bored at the same time as the naticid, for the same reason, and because naticids bore their prey beneath the sediment surface therefore the empty shell must have been bored at least twice.

CHAPTER 9.

Predation on gastropods.

9.1 Octopus boreholes in gastropod shells.

9.2 Decapod attack? aperture damage and the potential causes.

9.1 *Octopus* boreholes in gastropod shells.

A few specimens of gastropods from the Red Crag exhibit boreholes which look remarkably like the ones made by *Octopus* (Pilson and Taylor 1961, Wodinsky 1969, Nixon 1979, Nixon *et al.* 1980, Boyle and Knobloch 1981). The borehole in *Nucella lapillus* from Vale Farm [21] being the best example (see pl. 3D). This is the first record of Red Crag *Octopus*.

The boreholes made by *Octopus* are small, less than 1mm (Pilson and Taylor 1961), elliptical holes with striations visible parallel to the long axis of the ellipse at the terminations of this long axis. These bores are not for the removal of flesh from the prey, as are the boreholes of gastropods, but to inject the prey with an anaesthetic. This relaxes the muscles of the gastropod or bivalve and allows the *Octopus* to force open the valves or operculum and extract the flesh (Pilson and Taylor 1961).

The distribution of present day *Octopus* is widespread. The common octopus, *Octopus vulgaris* Lamark ranges from the North Atlantic to the Mediterranean (Campbell 1976, p. 192) and the lesser octopus, *Eledene cirrhosa* (Lamark) is also an Atlantic dweller, its range extends into the English Channel and the northern North Sea (Campbell 1976, p. 192). *Octopus vulgaris* occupies sandy and rocky bottoms (George and George 1979, p. 108) making *N. lapillus* ideal prey.

9.2 Decapod attack? aperture damage and the potential causes.

There are two kinds of aperture damage that can be easily recognised in gastropods from the Red Crag. There are those which are damaged at the final lip of the aperture and so the damage was either fatal or caused by post-mortem activity. The second category of aperture damage is that which was caused during the life of the gastropod and was not fatal; this is apertural damage that has been repaired (see pl. 3E).

The first kind of damage must have been caused by a fatal predation incident, by current action causing death, by post mortem current action or by the activity of other organisms after the gastropods death, for example hermit crabs. The second category of damage, the non-fatal variety, could have been caused by the breakage of the shell in a strong current and the impact with other sedimentary debris or the substrate. It could have been caused by an unsuccessful predation attempt by a crab (see 2.4.2). It could also have been due to the predation behaviour of the gastropod itself as described by Colton (1908), Clench (1939) and Neilson (1975) (see 2.4.2).

In table 9.1 and 9.1a the gastropods studied are listed and the number of breaks and repaired breaks at the aperture are recorded. The species with the highest number of non-fatal aperture breaks is Neptunea contraria: 49 individuals with a total of 64 repaired aperture breaks, which is 42.1% of the total number of aperture breaks (both repaired and non-repaired). Whatever caused these breaks did not prove to be fatal to the gastropod in nearly a half of the incidents. N. antiqua and N. despecta show no examples of repaired

Table 9.1 Aperture damage in gastropods from the Red Crag.

Species.	Total.	Broken apertures.	Individuals with one or more breaks.	With two or more breaks.	Total breaks.	Total number of repaired breaks.
B. undatum	3	2	0	0	2	0
N. antiqua	30	7	0	0	7	0
N. contraria [18]	92	20	19	9	50	30
N. contraria	488	88	49	13	152	64
N. despecta	13	3	0	0	3	0
N. lapillus [6]	193	38	1	0	39	1
N. lapillus [42]	76	13	3	0	16	3
N. lapillus	498	69	5	0	74	5
N. tetragona	22	1	1	0	2	1
Turritella sp.*	50	0	4	1	6	6

*Number of aperture breaks not recorded as many were damaged during collection and in the laboratory.

Table 9.1a Percentage of Red Crag gastropods with aperture damage.

Species.	% broken.	% of total sample broken and repaired.	% broken and repaired more than once.	% of breaks which non-fatal.	% of which are fatal or post mortem.
B. undatum	66.66	0.0	0.0	0.0	100.0
N. antiqua	23.33	0.0	0.0	0.0	100.0
N. contraria [18]	54.34	20.65	9.78	60.0	40.0
N. contraria	31.14	10.04	2.66	42.1	57.9
N. despecta	23.07	0.0	0.0	0.0	100.0
N. lapillus [6]	19.68	0.52	0.0	2.56	97.44
N. lapillus [42]	17.1	3.94	0.0	18.75	81.25
N. lapillus	13.85	1.0	0.0	6.75	93.25
N. tetragona	4.54	4.54	0.0	50.0	50.0
Turritella sp.*	12.0	8.0	2.0	0.0	0.0

*See table 9.1.

breaks but 23% of the sample show evidence of damage at the final aperture lip, therefore being fatal or post-mortem. Only three specimens of *B. undatum* were collected and two had damaged aperture lips.

Turritella shows a small number of repaired breaks 8% of the total sample display them. A count was not made of the specimens with broken final aperture lips as much damage was caused during collection and in the laboratory to these fragile apertures, consequently most of them are broken.

Nucella tetragona was rarely damaged at the lip of the aperture and only one specimen from 22 demonstrated this phenomenon. Similarly only one of the 22 shells of *N. tetragona* has a repaired apertural break. On the other hand 13.85% of the sample of *Nucella lapillus* have broken final aperture lips but only 1% repaired breaks. The breakage factor in *N. lapillus* was nearly always fatal or post-mortem (93.25%).

Of the 64 repaired breaks in the sample of *N. contraria* most of them were made in the fifth and sixth whorl of the shell, 49 out of the 64 were in these two whorls (see fig. 9.1). Whatever caused the damage it either happened more often at this size, approximately 40mm to 55mm, or they were more able to survive it. The specimens with the breaks on the final aperture lip have a similar distribution as the repaired ones (see fig. 9.1a). This infers that the damage was being caused at this size and that the gastropod had a 42% chance of survival.

FIG. 9.1

DISTRIBUTION OF REPAIRED, NON FATAL,

APERTURE BREAKS IN NEPTUNEA CONTRARIA.

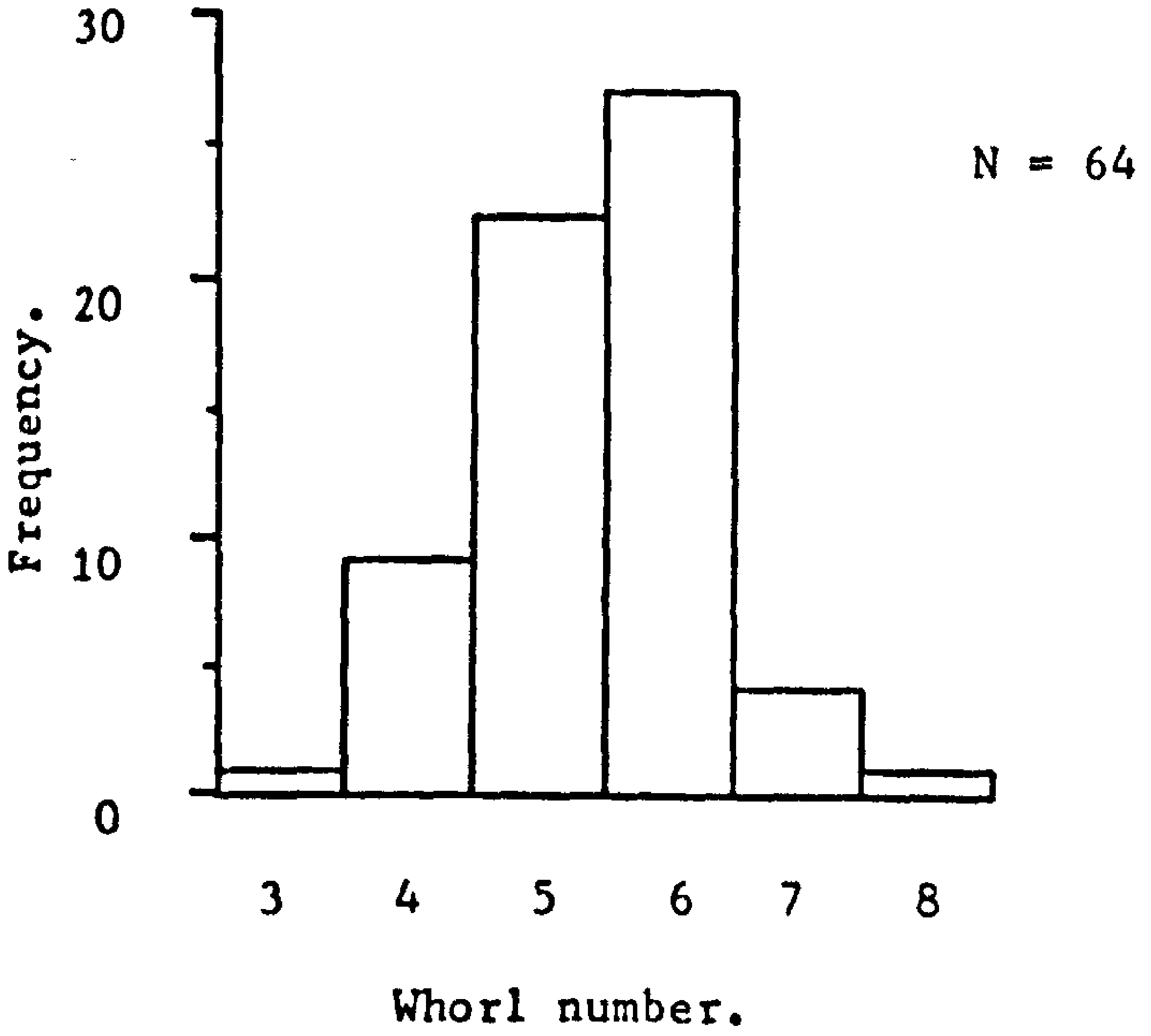
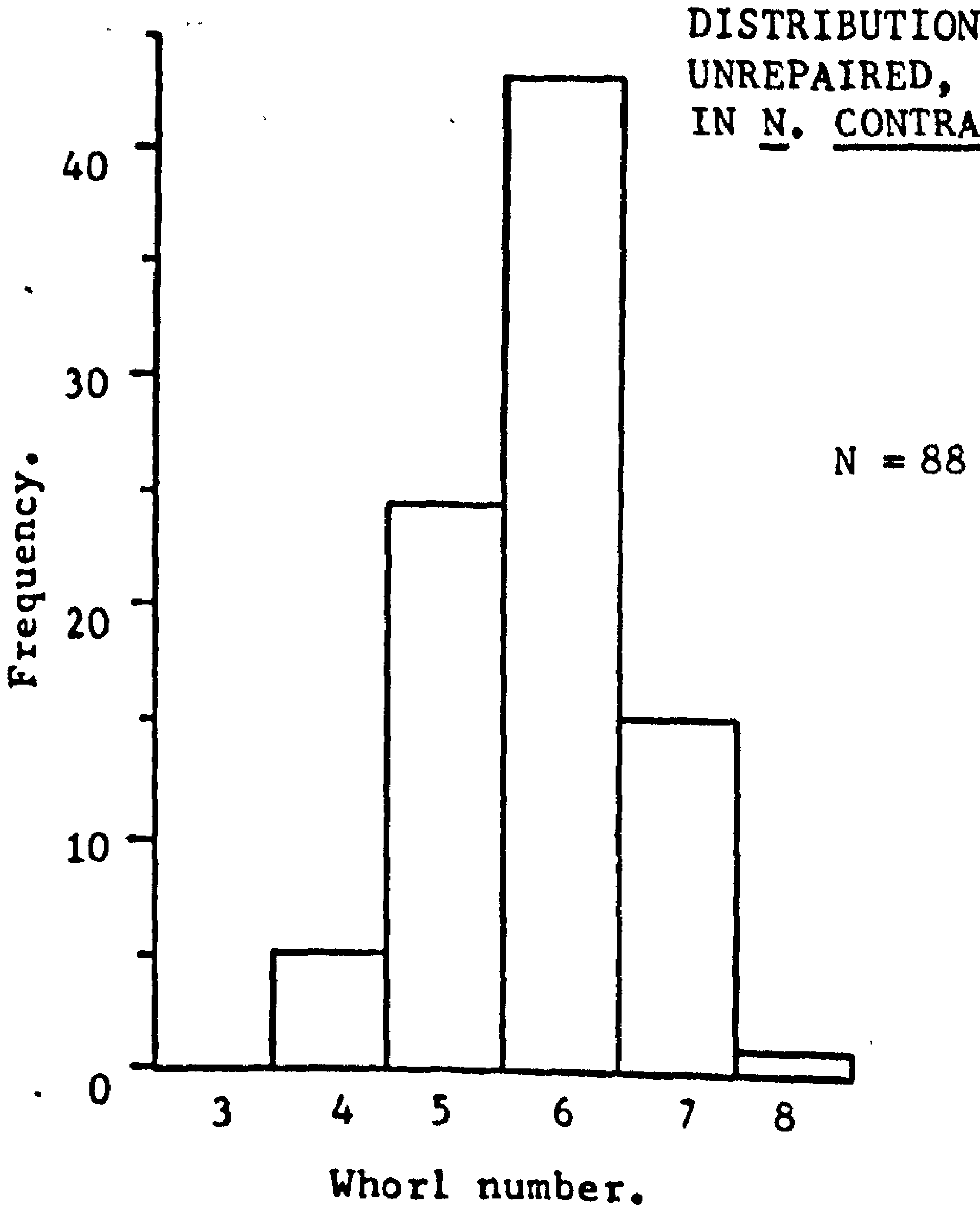


FIG. 9.1a

DISTRIBUTION OF BROKEN, UNREPAIRED, APERTURE LIPS IN N. CONTRARIA.



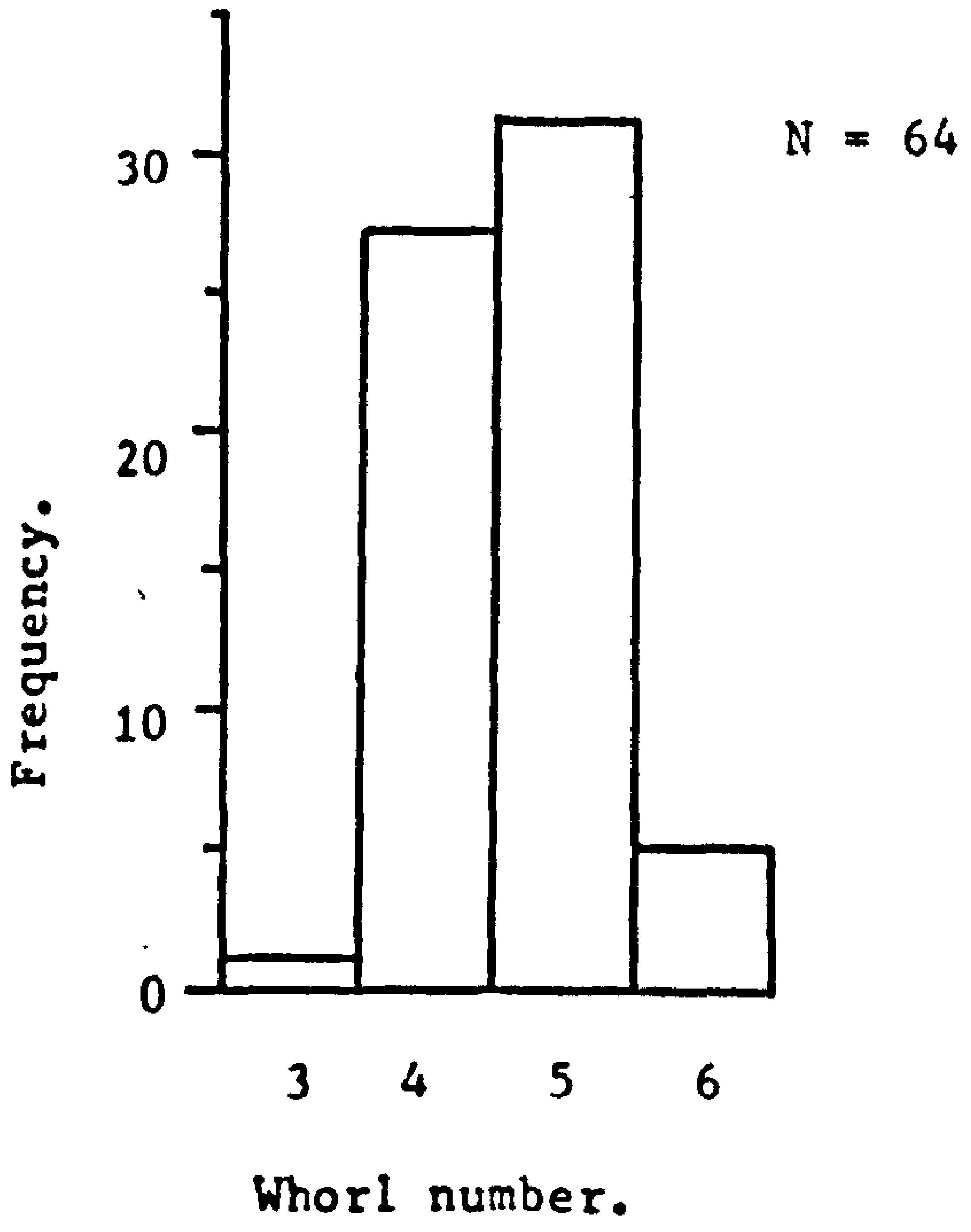
In N. despecta the three recorded breaks occur in the fifth and sixth whorls. Similarly for N. antiqua the seven breaks are distributed between the fifth and sixth whorls. In N. tetragona both the final and repaired breaks occur in the fifth whorl. The poor preservation of Turritella makes the whorl number a difficult thing to estimate.

In N. lapillus the repaired breaks occur in the fourth and fifth whorls: one in the fourth and four in the fifth. Similarly the breaks in the final aperture outer lip occur mostly in the fourth and fifth whorl (see fig. 9.2).

So was the breakage of these shells due to current action, predation or both. By using a breakage experiment in a tumbler (see appendix 3) it may be possible to ascertain which of these two factors was the more important. If the shells break readily at the aperture the natural breaks may have been caused by post-mortem transport. If however they do not break at the aperture and they break at the spire first we must conclude that the aperture breakage was due to their interaction with other organisms; either predation attempts on them or by them on other organisms (see 2.4.2).

FIG. 9.2

DISTRIBUTION OF BROKEN, UNREPAIRED, APERTURE LIPS IN <u>NUCELLA LAPILLUS</u>.



PART V.

CONCLUSIONS.

CH. 10. Summary and conclusions.

CHAPTER 10.

Summary and conclusions.

10.1 A Red Crag invertebrate food web.

10.2 Summary.
    10.2.1 Methods.
    10.2.2 Shell shape.
    10.2.3 Predation.

10.1 A Red Crag invertebrate food web.

It is certain that naticids preyed upon *Macoma* and *Spisula*. These two genera of bivalve were the main diet of Red Crag naticids that have been preserved. Muricids on the other hand preyed upon *Astarte* sp. and *Glycymeris glycymeris* as can be proved by the many boreholes in their valves. This is also true of the gastropod *Turritella*. It is also likely that *Mytilus edulis* and barnacles figured significantly in the diet of *Nucella lapillus* as they do at the present time. *M. edulis* is present in the Red Crag but is never in large enough fragments to preserve predation boreholes (see 1.4.3).

The Buccinidae family of gastropods do not leave feeding traces and so it is difficult to make suggestions about their diet. If they behave as they do today it is likely that they preyed and scavenged on amongst other things bivalves. Being epifaunal they are more likely to have fed on the same species as the muricids.

The aperture scars on both the Buccinidae and Muricidae are to some extent the result of crab predation. Modern crabs commonly prey on *M. edulis* as well as gastropods (Ebling *et al.* 1964), and this is likely to have been the case in the Red Crag.

The discovery of *Octopus* sp. feeding traces leads one to wonder what apart from *N. lapillus* it ate. It is likely that they preyed on the other epifaunal gastropods the Buccinidae and the larger bivalves such as *G. glycymeris* and *Astarte* sp. Boyle and Knobloch (1981) reported that modern *Octopus* preyed upon crabs and this is likely to have occurred in the Red Crag. Star fish figure significantly as predators of bivalves in the modern marine environment (Carter 1968). Cardium, Mactra corallina cinerea, Macoma balthica and Mytilus edulis are listed amongst their prey (Schafer 1972, p.92). It is probable that star fish were a major predator of Red Crag molluscs, but they do not leave a feeding trace.

Amongst the vertebrate predators of Red Crag molluscs fish must have played a major role. Gadus morrhua (the Cod) for example is a voracious consumer of molluscs in the present marine environment (Schafer 1972, p.159). These fish, however, break the shells of molluscs into small fragments and these can not be recognised as evidence of predation in the fossil. Intertidal molluscs are eaten in large numbers, at present, by sea birds, such as Herring Gulls. The shells of the prey of these birds are broken into small fragments (Schafer 1972, p.414) and as with the fish predation can not be recognised in the fossil.

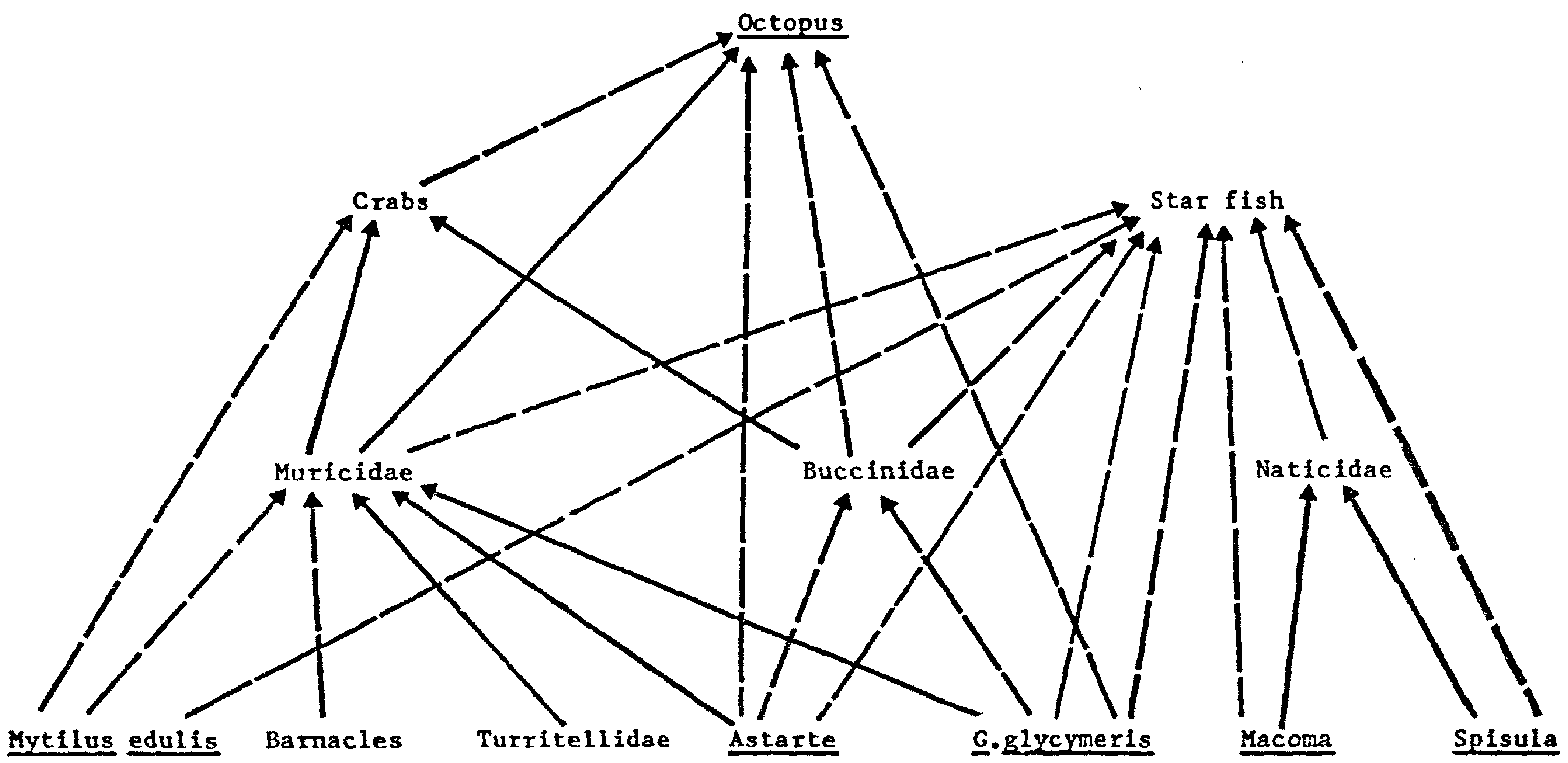
See fig. 10.1 for a summary of the food web, solid lines show definite predation associations and dashed lines probable ones.

10.2 Summary.

10.2.1 Methods.

The work for this thesis was based on the more common gastropods from the Red Crag. These are the families Buccinidae, Muricidae, Naticidae and Turritellidae. The Red Crag is a fully marine shelly sandstone of the Lower Pleistocene which outcrops in south-east Suffolk and north-east Essex. The aim of the thesis was to discover more of the

FIG. 10.1 A RED CRAG INVERTEBRATE FOOD WEB.



palaeoecology of the Red Crag and the palaeoethology of the above gastropods.

A large number of mollusc shells were collected from the area and used in the laboratory for this purpose. Crothers' (1973) regression was calculated from simple measurements of Nucella lapillus and was used to determine the severity of wave action on the Red Crag coastline. A method of shadow casting the shells of gastropods was devised in order to record the Raupian parameters which define their shell shape.

A new method of plotting boreholes of gastropods, on composite diagrams of bivalve shells was developed using the computer. Also with the aid of the computer a statistical test for randomness for the distribution of these boreholes was devised. An estimation of predation rates on bivalves by gastropods was attempted.

Several computer programs were specially written for this study to analyse the data collected and to present the results in the form of graphical output diagrams. Histograms, scatter diagrams, composite shell diagrams and cumulative distribution diagrams were produced by these programs.

10.2.2 Shell shape.

The shape of Nucella lapillus shows that the severity of wave action was low during Red Crag times in the study area. They show a length to length of aperture ratio of 1.503 which gives a value of 7.21 on Ballantine's (1961) exposure scale, where 7 is very sheltered and 8 extremely sheltered. The results of this study from the various localities were within a small range of this overall figure.

Neptunea contraria does not appear to demonstrate sexual dimorphism in the shape of its shell. The only parameter to show a bimodal distribution was translation and it is very unlikely that this is related to sex.

The study of encrusting organisms has shown that N. contraria was not very efficient at removing soft bodied encrusting organisms and tended to overgrow them resulting in uncoiling. Nucella lapillus , Neptunea antiqua and Neptunea despecta are all commonly encrusted with Balanus sp. inferring that they inhabited among other habitats rocky substrates in shallow water. Barnacles are however very rare on Neptunea contraria showing that this species of whelk inhabited a different niche from the above species, probably soft substrates and or deeper water. Nucella tetragona does not suffer encrusting barnacles and may have lived on soft substrates unless the ornamentation of its shell prevented barnacle attachment.

10.2.3 Predation.

Muricid predators preferred the shallow burrowing bivalves Astarte sp. and Glycymeris glycymeris whilst the naticids preferentially drilled the fully infaunal Macoma sp. and Spisula sp. This was due to the depth of burial, muricids being epifaunal and naticids infaunal, and the substrates preferred: G. glycymeris and Astarte sp. prefer coarse substrates as do muricids; Macoma sp. and Spisula sp. along with naticids prefer finer grained sediments. Of the gastropods which fell prey to the drills Turritella was the most popular and was mainly attacked by muricids. The predation rates on these prey are comparable to present-day examples.

The distribution of muricid boreholes is random on the valves of *Astarte* but clustered in the dorsal half of the valves of *G. glycymeris*. This suggests *Astarte* had a variety of life positions whereas *G. glycymeris* favoured sitting upright in the sediment bringing the dorsal half of the valves closest to the surface and therefore more susceptible to attack from above from the epifaunal muricids. *Macoma* was bored preferentially by naticids in the central part of its shell and *Spisula* very close to the umbo. This stereotypy is common in modern naticids and was also so during the Red Crag. Neither the muricids nor the naticids favoured one valve over another and all four of the common bivalve prey genera were bored equally on their left and right-hand valves.

Both the bored samples of *G. glycymeris* and *Astarte* sp. are smaller than the non-bored sample. There is also a significant positive correlation between borehole diameter and the size of prey in these two genera. It seems that the larger the predator the larger the prey it could take and also that both prey reached a partial size refuge, from predation, through ontogeny. The smallest muricid boreholes were found in specimens of *Turritella* suggesting that they were attacked by juveniles or a species which made smaller boreholes than those which preyed on *Astarte* and *Glycymeris*. *Turritella* was also the most susecptable to multiple borings by muricids, out of the species of prey studied.

Larger naticid boreholes are found in *Macoma* than *Spisula*. *Macoma* are larger than *Spisula* showing that either separate naticid species preyed on these two bivalves or that larger prey were taken by larger predators of the same species. The larger the *Spisula* prey the larger the naticid which bored it but there is no such relationship in the sample of *Macoma* prey. It seems likely that these bivalves were preyed upon by separate species of naticids. Neither *Spisula* nor *Macoma* reached a size refuge from naticid predation during ontogeny.

Probable *Octopus* bores are recorded on *Nucella lapillus* showing the first account of Red Crag octopods.

A large number of non-fatal aperture breaks are recorded on *Neptunea contraria* which probably represents a high incidence of crab predation on this species. An alternative hypothesis is that they were damaged in current activity but as has already been established they were soft sediment dwellers, it is therefore unlikely that they were exposed to strong currents.

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Plate descriptions.

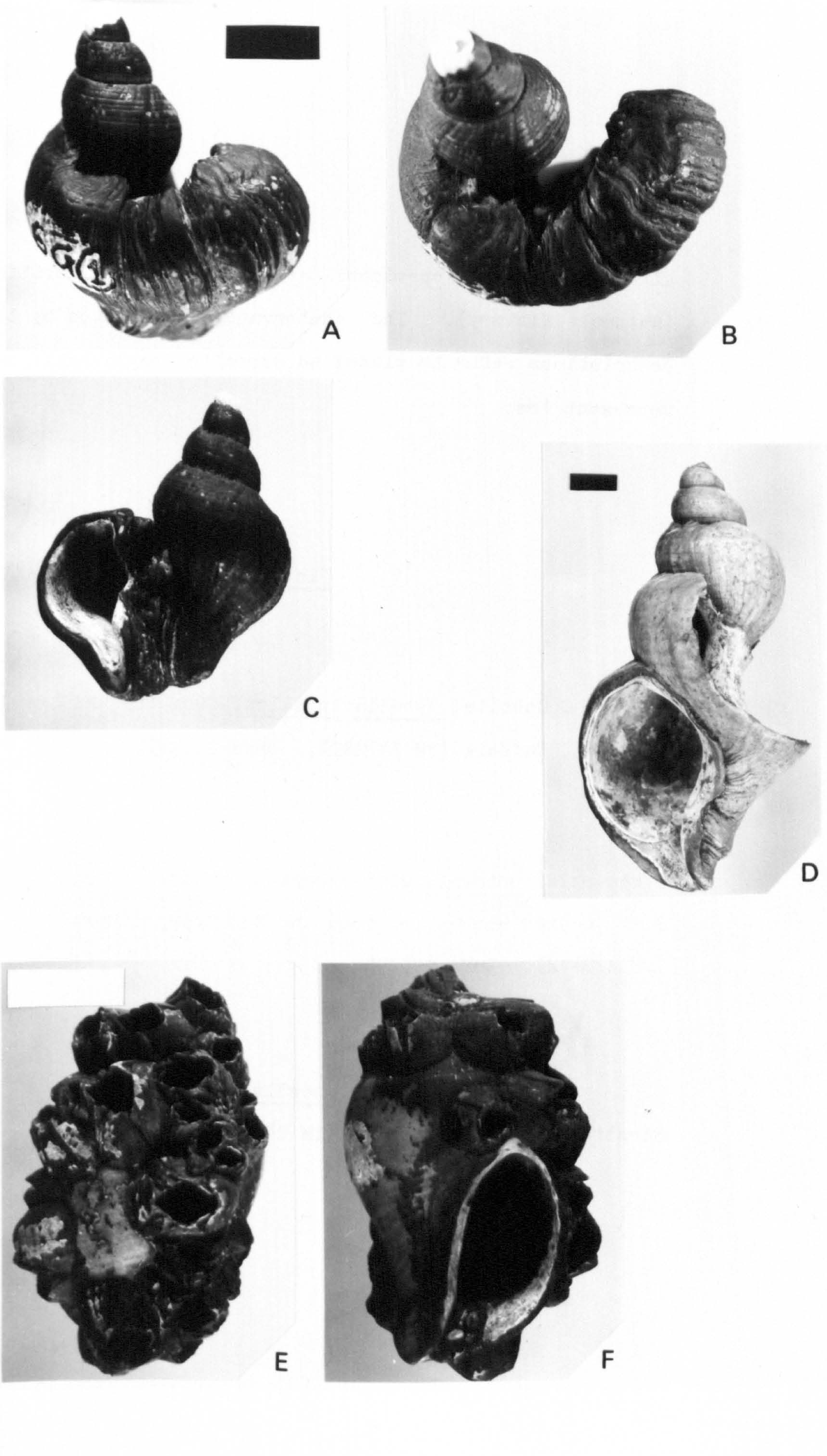
All of the figured specimens are held by the British Museum (Natural History). The photographs were taken by the author. Descriptions refer to plates on opposite page, all scale bars represent 1cm.

Plate 1.

A,B and C Uncoiled *Nucella lapillus*, from the Red Crag, Stratton Hall [6], Suffolk (TM 247382). BMNH GG9349.

D *Neptunea contraria* with a bent spire due to the overgrowth of a soft bodied encruster, from the Red Crag, Alderton [26], Suffolk (TM 328412). BMNH GG9350.

E and F Barnacle encrusted *Nucella lapillus*, from the Red Crag, Stratton Hall [6], Suffolk (TM 247382). BMNH GG9351.


GG1
A
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F

Plate 2.

A and B *Neptunea antiqua* overgrowing *Polydora ciliata*, from the beach at Southend-on-Sea, Essex. BMNH GG9352.

C *Neptunea contraria* showing a cavity once occuppied by a soft bodied encruster, from the Red Crag, Stratton Hall [6], Suffolk (TM 328412). BMNH GG9353.

D *Turritella* with a bent spire due to the overgrowth of an encrusting organism, from the Red Crag, Stratton Hall [6], Suffolk (TM 328412). BMNH GG9354.

E *Neptunea contraria* showing a tubular overgrowth structure, probably caused by an encrusting annelid, from the Red Crag, Stratton Hall [6], Suffolk (TM 328412). BMNH GG9355.

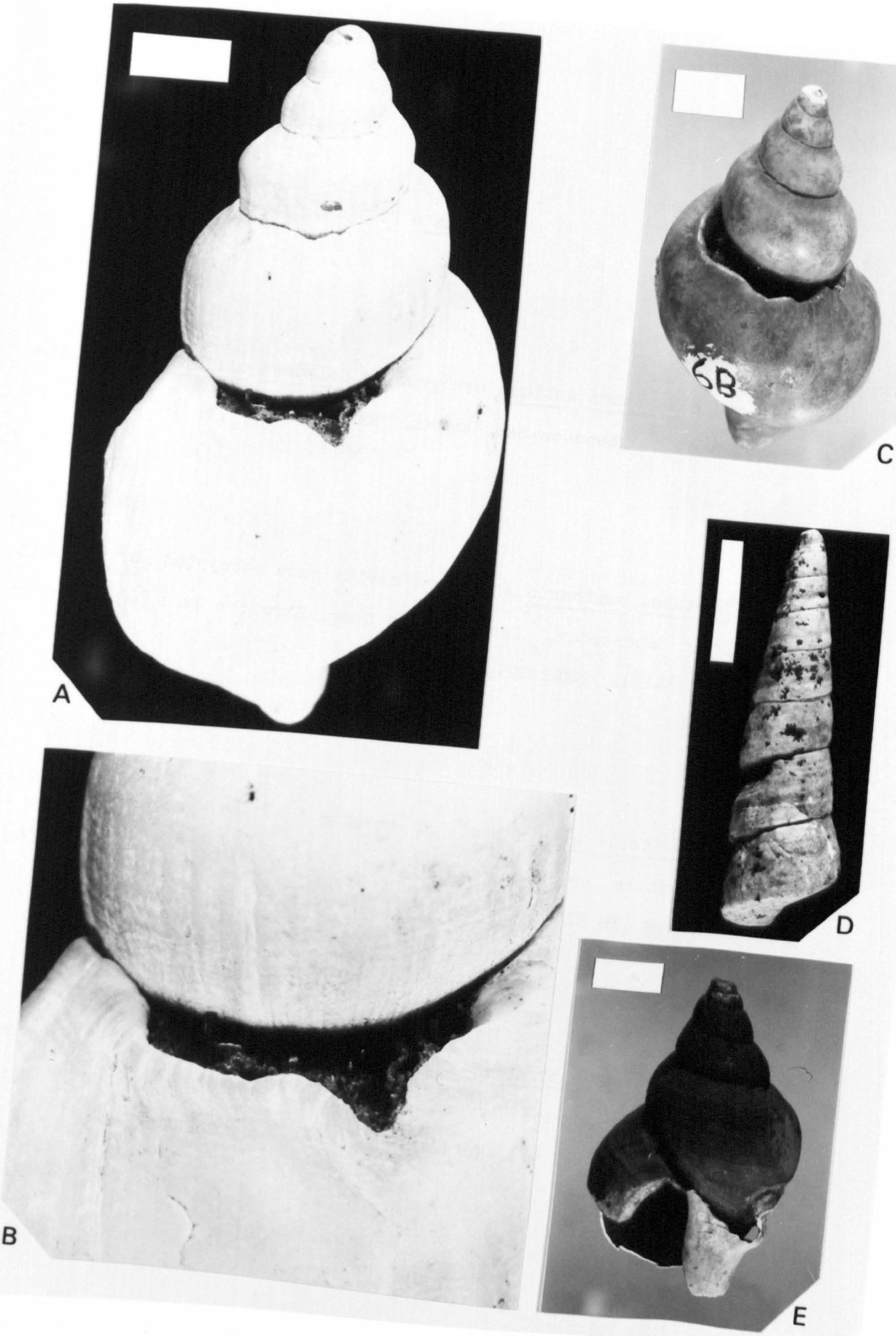

A
6B
C
D
B
E

Plate 3.

A Naticid borehole in Tellina crassa, from the Red Crag, Alderton [26], Suffolk (TM 328412). BMNH LL18751.

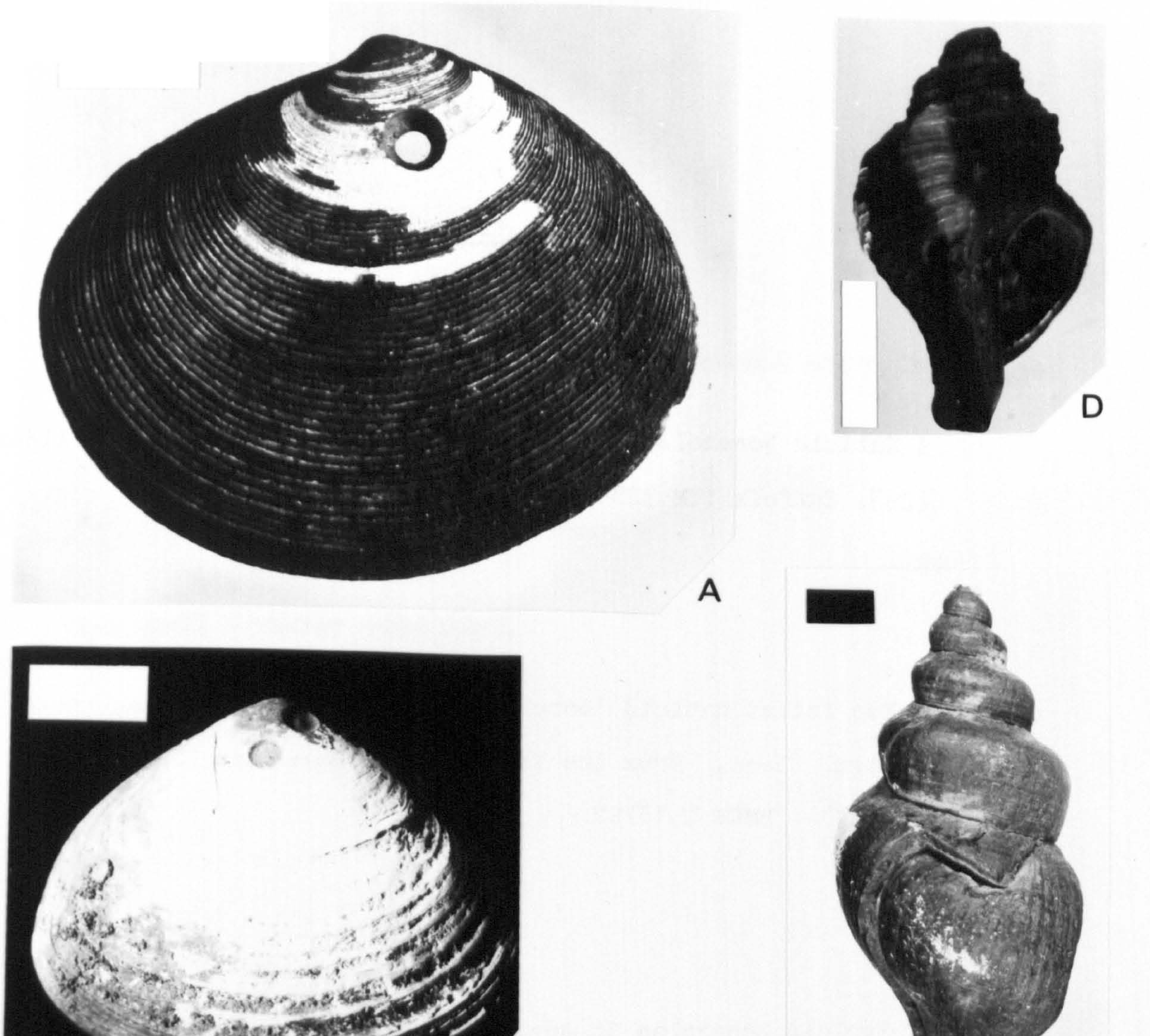
B Two failed naticid boreholes in Spisula arcuata, note the central boss. From the Red Crag, Virtues Farm [28], Suffolk (TM 340434). BMNH LL18752.

C Muricid boreholes in specimens of Astarte, from the Red Crag, Brightwell [14], Suffolk (TM 250430). BMNH LL18753-LL18757.

D Octopus borehole in Nucella lapillus, from the Red Crag, Vale Farm [21], Suffolk (TM 319455). BMNH GG9356.

E Repaired crab damage in Neptunea contraria, from the Red Crag, Waldringfield Heath [18], Suffolk (TM 257446). BMNH GG9357.

F Two muricid boreholes in Glycymeris glycymeris, from the Red Crag, Waldringfield Heath [18], Suffolk (TM 257446). BMNH LL18758.


A
D
B
E
C
F

APPENDICES

A.1 Shell shape of Nucella lapillus from modern and raised beach deposits in eastern Scotland.

A.2 Bivalve shell shape variation.

A.3 Shell breakage experiment.

A.4 Red Crag pollen.

Appendix 1.

Shell shape of <u>Nucella lapillus</u> from modern and raised beach deposits in eastern Scotland.

Shell shape of *Nucella lapillus*.

Empty shells of *Nucella lapillus* were collected by M. A. Whyte and the author in August and September 1982 in order to compare the shell shape of dog-whelks from the recent and modern British east coast with those of the Red Crag. Shells were collected from Gardenstown (Banff), Ardross in Fife and Belhaven Point near Dunbar in East Lothian. The Gardenstown shells were collected from the modern beach deposits below high water mark in Gamrie Bay which is north-west facing. The modern beach deposits from Belhaven Point were collected below high water mark, the eastern side of the point is north facing and the western side west facing. The raised beaches are approximately 3m above present high water mark and the Ardross coastline faces south-east.

The shells of these dog-whelks were measured in the same way as described in section 3.3 and the regression equation recalculated from Crothers (1973) was used in the computer program NUCELA (see 4.2.2) to derive an estimate of exposure to wave action. The BEV or Ballantine's (1961) Exposure Value is described in sections 2.3.3 and 3.3.

The results shown in table A.1 show slightly higher exposure values than those of the Red Crag (see table 5.1 and 5.2). The overall BEV for the Red Crag is 7.21 (7 is very sheltered) whereas the Scottish east coast *N. lapillus* show BEVs ranging from 5.66 to 6.66 (6 is sheltered).

Table A.1 Samples of dog-whelk shells from beaches and raised beaches in eastern Scotland.

Locality with grid reference.	Mean length.	Mean length of aperture.	Mean L/LA.	1 S.E.M.	BEV.	N.
Gardenstown NJ 793645	25.3	17.63	1.435	0.036	5.78	24
Ardross raised beach NO 508006	22.48	15.78	1.429	0.035	5.66	16
East side of Belhaven point NT 665793	23.56	16.15	1.459	0.035	6.27	19
Raised beach, west side Belhaven point NT 663789	26.64	18.06	1.477	0.023	6.66	35
West side of Belhaven point NT 662789	25.04	17.33	1.439	0.012	5.86	87

Although these BEVs are higher than those from the Red Crag it is not by a great deal and coastlines inhabited by N. lapillus during recent and modern times at these sites in eastern Scotland are not drastically different from ones of Red Crag times in Suffolk, in terms of exposure to wave action.

Ballantine (1961) describes shorelines which are sheltered (that is of value 6, on his scale) in the Dale area as being open to fetches of less than 10 miles over at least 60°; with a refraction of 90° required to bring waves of more than 50 miles fetch to bear. The Scottish east coast examples given above are all open to waves with a fetch of over 50 miles when the waves are coming from a particular direction. Most of them however are probably only subjected to these infrequently. The localities are mostly situated so that usually they would only be subjected to waves with fetches of less than or little more than 50 miles. Gardenstown faces north-west giving a maximum fetch in that direction of 60 miles across the Moray Firth although waves refracted into Gamrie Bay from the north-east would have much greater fetches. The coastline at Ardross faces south-east and in that direction would face waves with a fetch of less than 20 miles across the Firth of Forth although refracted waves from the east would have much greater fetches. The west side of Belhaven Point is a sheltered site facing north-east across the Firth of Forth and waves of only 40 miles fetch would affect this locality, only considerable amounts of refraction would allow waves of great fetch to come to bear on this coastline. The east side of Belhaven Point however is much more exposed and would usually be affected by waves with a fetch in excess of 100 miles.

These are however not the most exposed sites on the east coast of Britain and a study of more exposed sites would probably indicate a greater degree of exposure to wave action. The shells collected were not from a living population and there is thus no gaurantee that they were collected from their orginal habitat. It is likely that exposure values are generally lower on the east coast even when comparing them with coastline of a similar fetch on the west coast; due to the prevailing westerly wind systems which affect Britain. Ballantine's description of a sheltered coastline for the Dale area therefore could be valid for east coast localities which are exposed to waves with larger fetches.

Appendix 2.

Bivalve shell shape.

A.2.1 *Glycymeris glycymeris*.

A.2.2 *Macoma*.

A.2.3 *Spisula*.

A.2.1 Glycymeris glycymeris Linne.

Glycymeris glycymeris is an extant marine bivalve which is very common in the Red Crag.

Thomas (1975) showed that the shape of the Glycymerididae was conservative in its range since they appeared in the Cretaceous. To see if this was the case in the Red Crag and the Coralline Crag the shape of a sample of 405 valves was studied, 9 of which were from the Coralline Crag at Ramsholt Beach [47].

Eight measurements were taken from each valve, these were based on the ones taken by Thomas (1975). They were length (L), width (W), height (H), umbo to inner hinge (UIH), umbo to a line joining the lowest part of the muscle scars (UMS), width of ligament area (WLA), width of dentition (WD) and width of lower margin (WLM) (see fig. A2.1). These measurements were all graphed one against the other and they all show a strong positive correlation.

It was then decided to plot the shapes of the G. glycymeris sample on a diagram which represented length, width and height of the valves. On this diagram a comparison of the mean shapes of samples taken from three separate Red Crag localities and the Coralline Crag sample is made. As it can be seen from fig. A2.2 there is very little difference in the shape of these samples. Conservatism in the shape of G. glycymeris was evident during Red Crag and Coralline Crag times as would be expected from the work of Thomas (1975).

FIG. A2.1 The measurements taken from *Glycymeris glycymeris*.

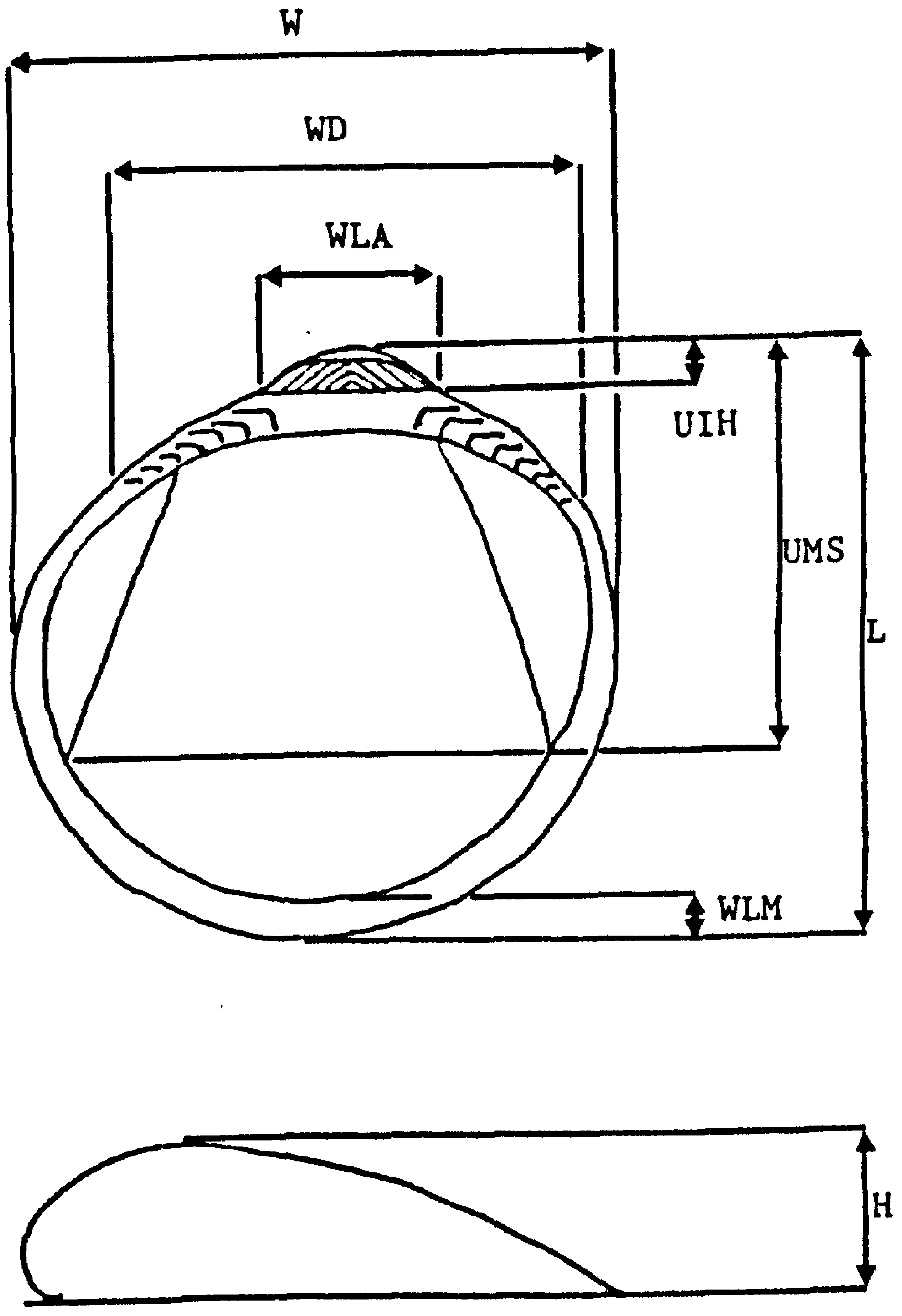
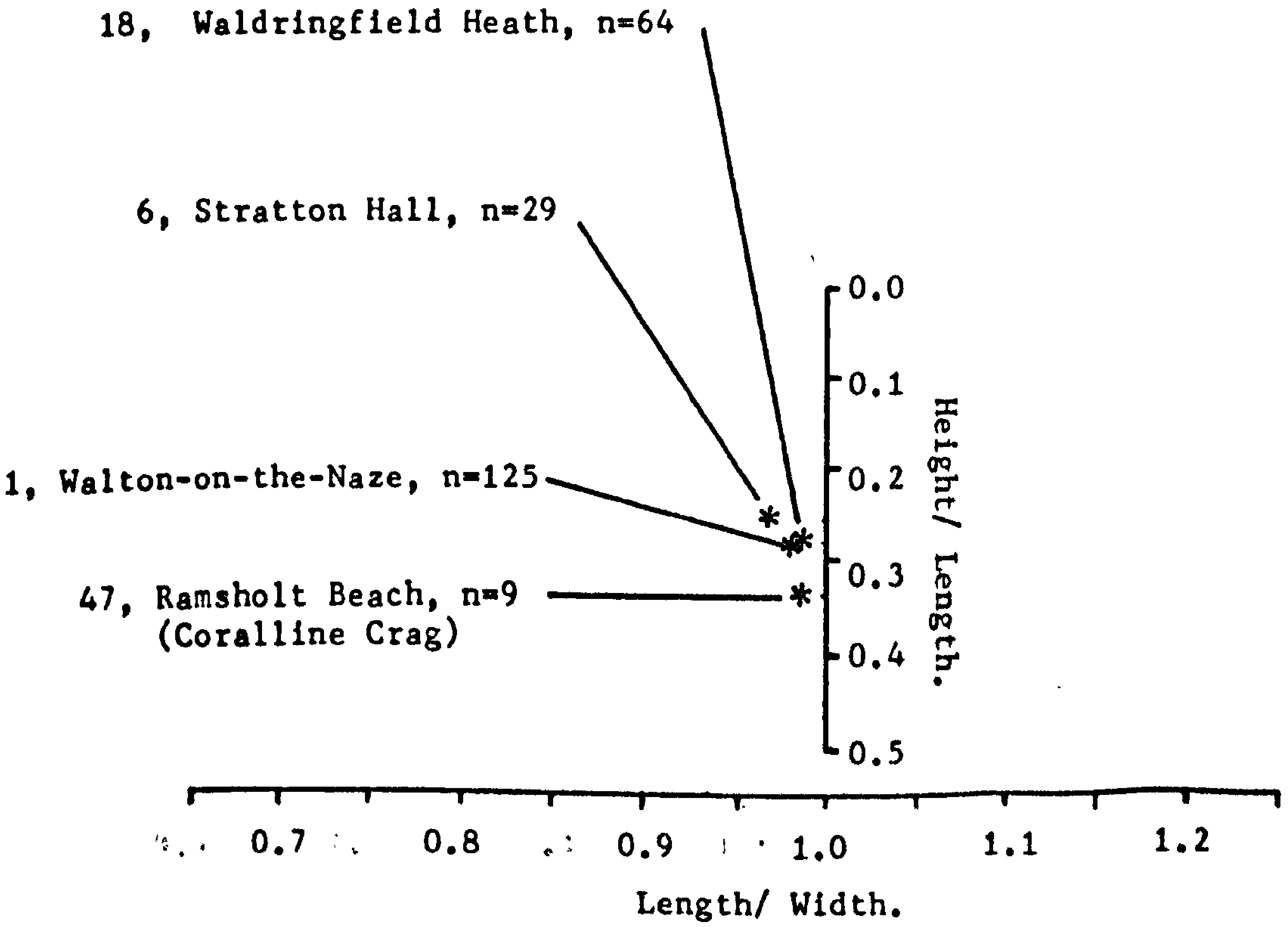


FIG. A2.2 The shape variation between four samples of <u>Glycymeris glycymeris</u> from the Red Crag and the Coralline Crag.



A.2.2 *Macoma*.

Macoma is an extant marine bivalve which burrows in soft sediment. Wood's monograph (1848-82) lists ten species of Red Crag *Macoma* whereas Dixon (1977) lists only two: *Macoma obliqua* J. Sowerby and *Macoma praetenuis* (Woodward). In addition to these two common Red Crag species the author recognises *Macoma calcarea* Gmelin as well. The other species listed by Wood (1848-82) are either very rare or so similar to the above three that it is difficult to distinguish them.

An attempt is made here to separate the species using the computer as a tool. 123 valves of *Macoma* sp. were collected from 11 Red Crag localities, of these 63 were right-hand valves and 60 left-hand ones. Each was measured using vernier calipers and the length, width and height were recorded to the nearest mm.

The computer program HISTO (see 4.2.1) was used to graph various parameters and ratios between parameters in an attempt to separate the species statistically. Due to the asymmetry of the valves it was found that only left or right-hand valves could be considered at any one time.

The three parameters: length, width and height were plotted against one another on a scatter diagram produced by ORIGIN (see 4.2.7) to test if they were positively correlated and they were.

The plots from HISTO (see figs. A2.3-A2.8) show polymodal distributions of length/ height, width/ length and width/ height. It is quite probable that these peaks coinside with the different species recognised as most of these distributions have three distinct peaks. Each of the three graphs for the left-hand valves of Macoma sp. (see figs. A2.3, A2.5 and A2.7) have peaks of similar heights: 2, 9, 12; 2, 11, 17; and 2, 10, 14. In the right-hand valves similarly the peaks are of the same magnitude in the three plots (see figs. A2.4, A2.6 and A2.8): 19, 4, 6; 13, 6, 8; and 24, 4, 8.

The largest population is the species M. praetenuis which is the most common of the three species, the next largest population is M. obliqua and the smallest the less common M. calcarea.

Further collections of Macoma sp. from the Red Crag will add credence to this thesis that the various Macoma species can be separated using this method of graphing the distributions of certain ratios of their parameters. The other species described by Wood (1848-82), may show separate peaks on such a plot, if indeed they are separate species. This method of species separation may be useful in dealing with other problematic bivalve genera.

FIG. A2.3

THE LENGTH TO HEIGHT RATIO DISTRIBUTION
OF <u>MACOMA</u> (LEFT VALVES). N = 60

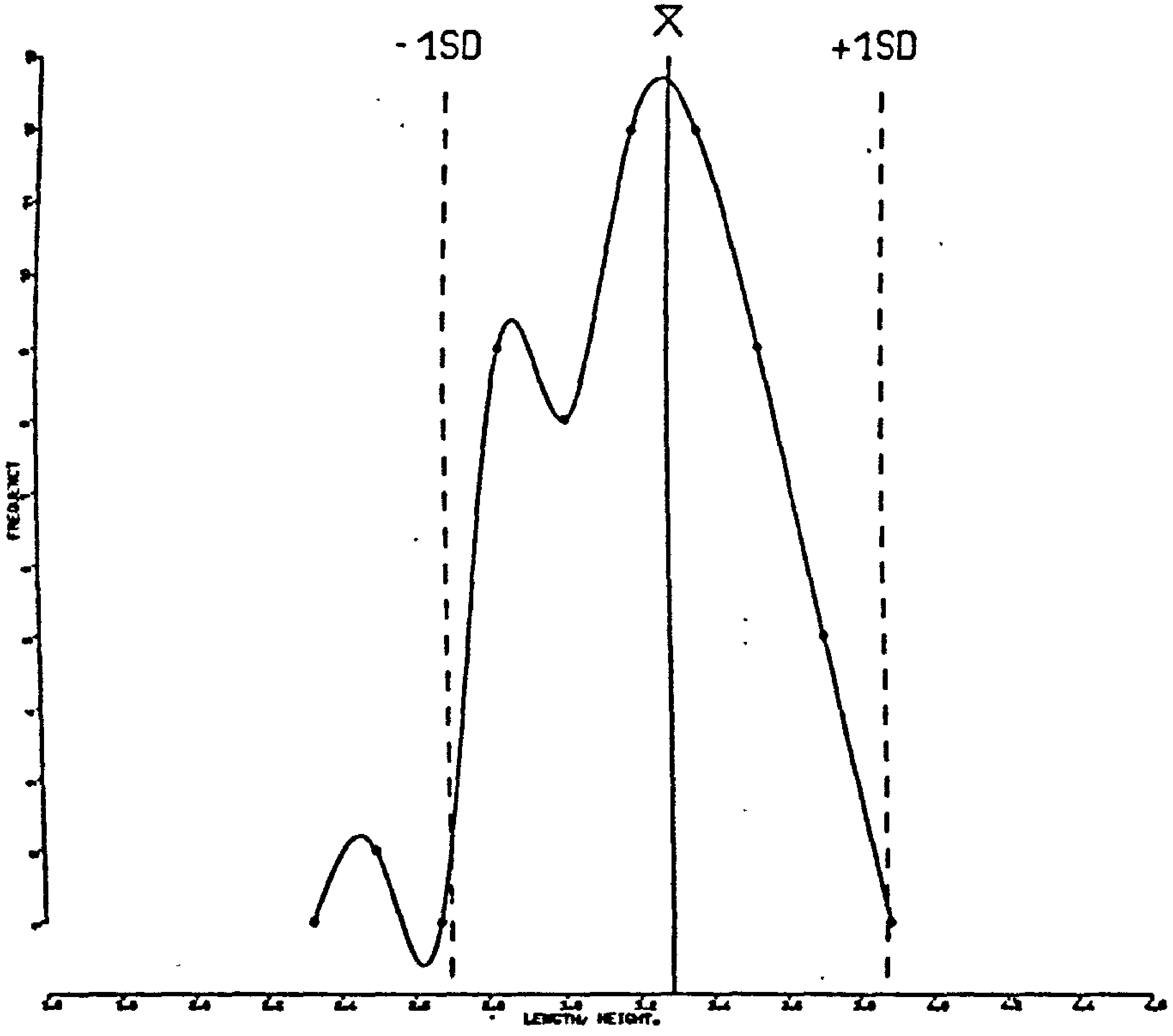


FIG. A2.4

THE LENGTH TO HEIGHT RATIO DISTRIBUTION
OF <u>MACOMA</u> (RIGHT VALVES). N = 63

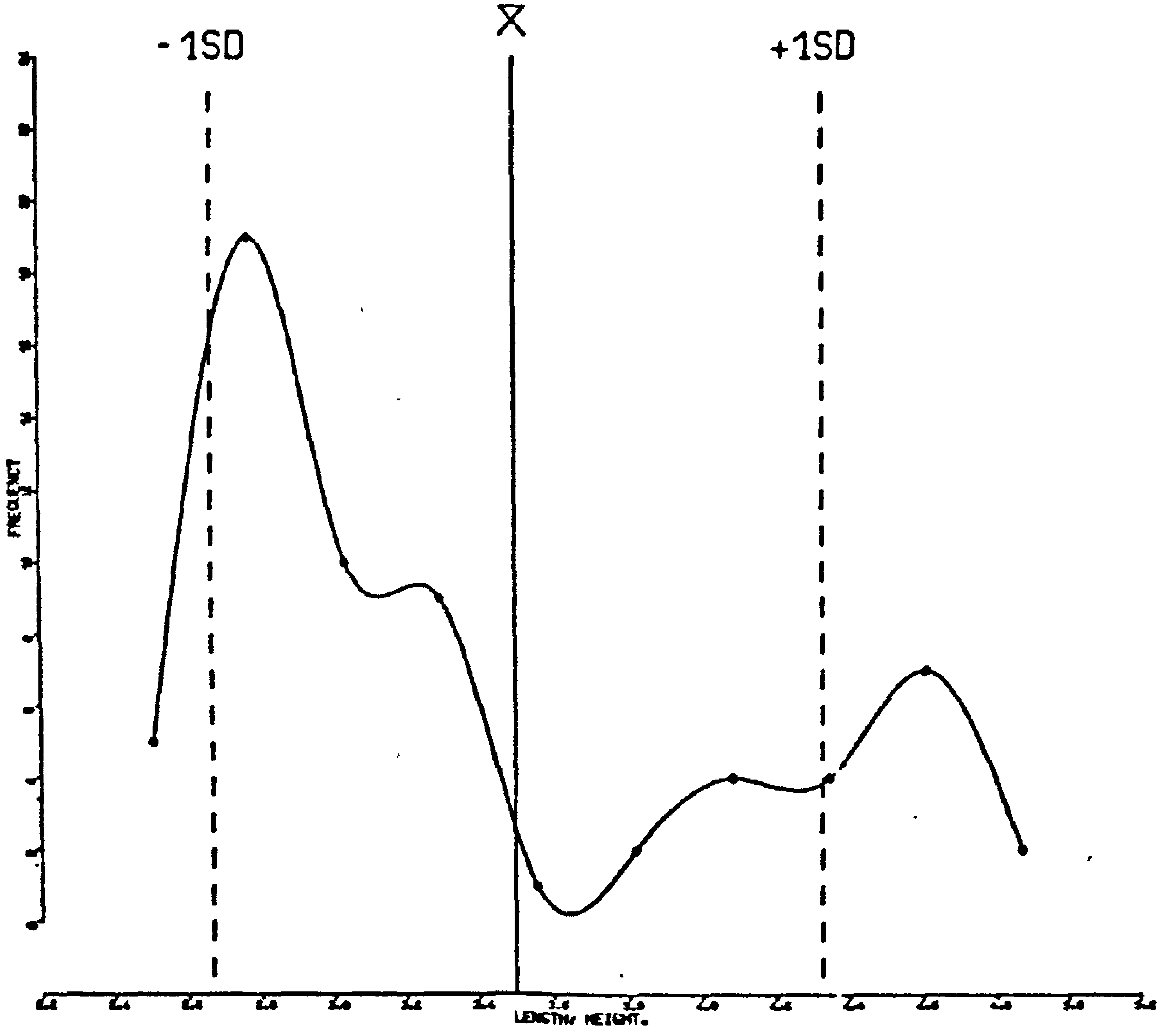


FIG. A2.5

THE WIDTH TO LENGTH RATIO OF <u>MACOMA</u> FROM THE RED CRAG (LEFT VALVES). N = 60

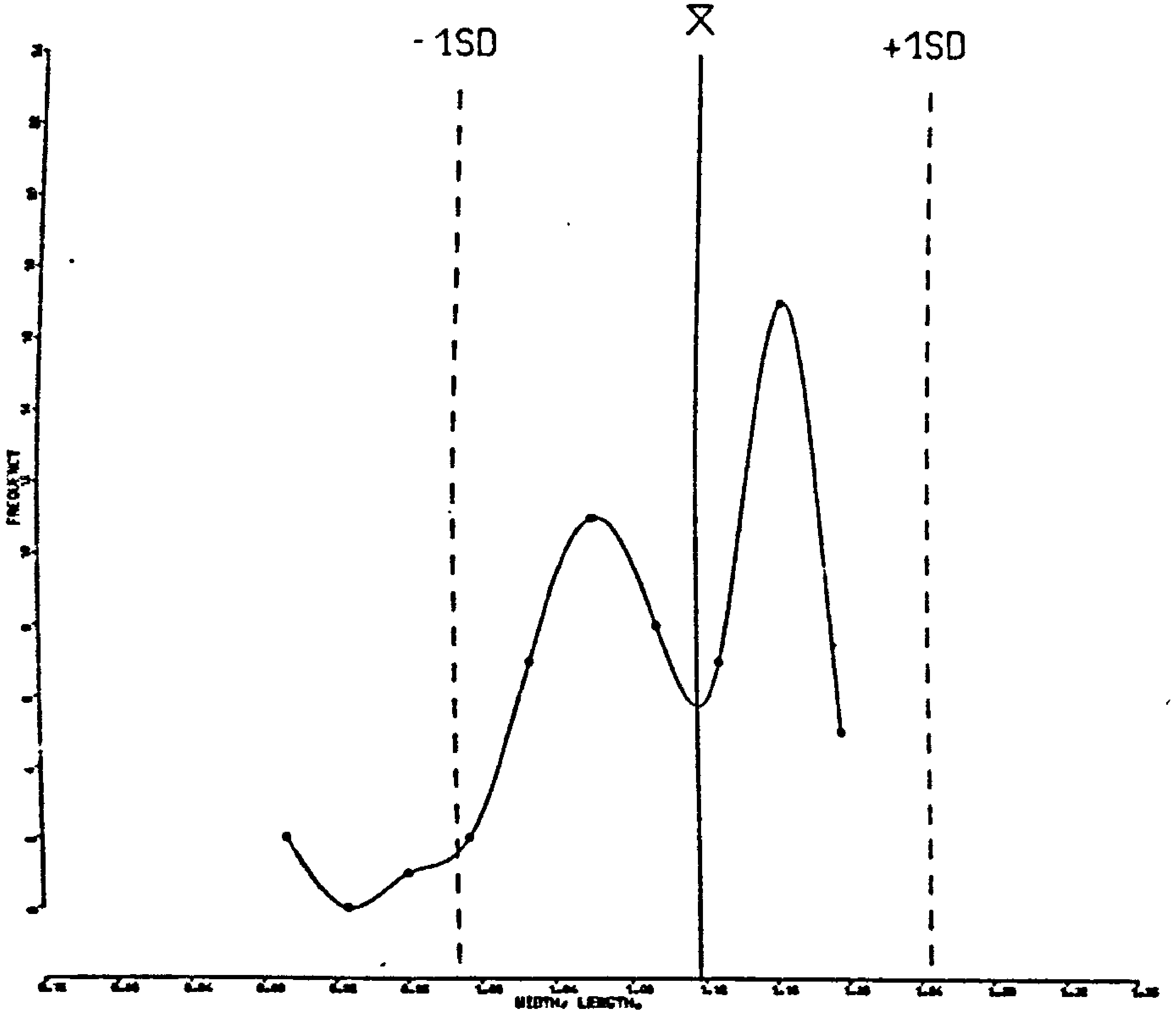


FIG. A2.6

THE WIDTH TO LENGTH RATIO OF <u>MACOMA</u> FROM THE RED CRAG (RIGHT VALVES). N = 63

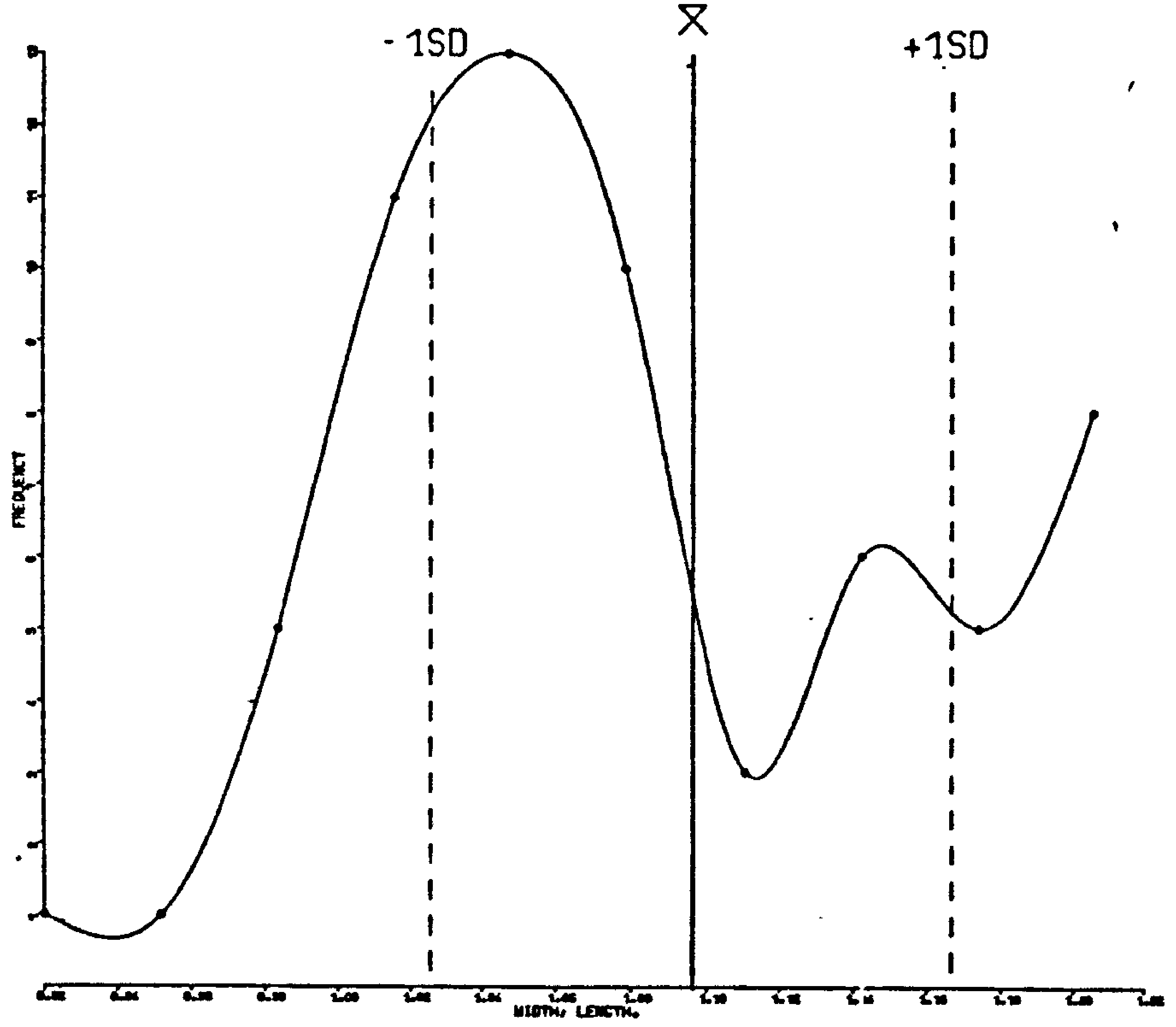


FIG. A2.7

THE WIDTH TO HEIGHT RATIO DISTRIBUTION OF *MACOMA* FROM THE RED CRAG(LEFT VALVES N = 60

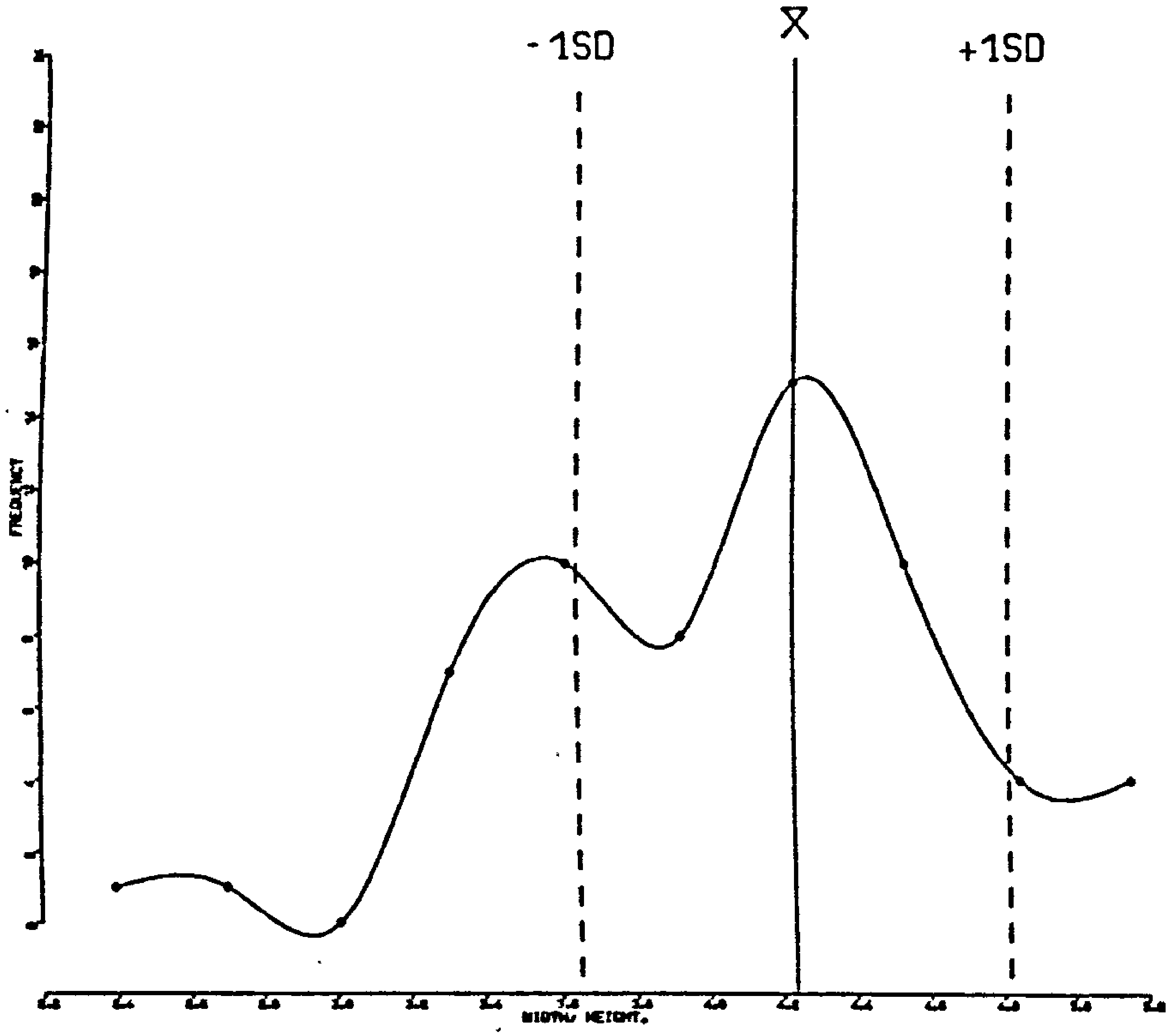
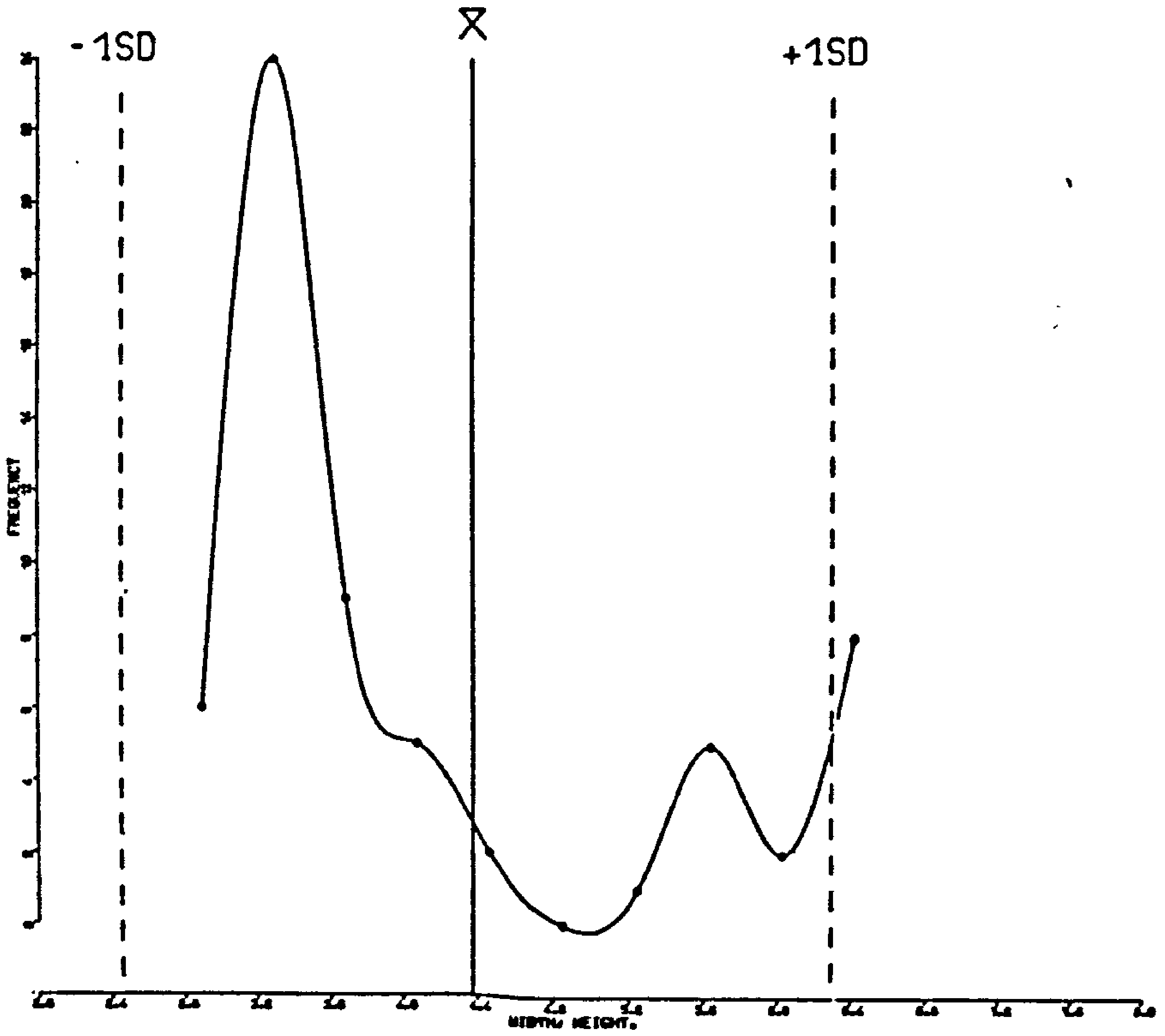


FIG. A2.8

THE WIDTH TO HEIGHT RATIO DISTRIBUTION OF *MACOMA*(RIGHT VALVES). N = 63



A.2.3 Spisula.

Spisula is an extant genus of marine bivalve. It is well represented in the Red Crag being one of the most common bivalves and altogether 297 valves were recovered from 14 localities for this study. Wood (1848-82) recognised 12 separate species of Spisula while Dixon (1977) mentions only four: Spisula constricta, Spisula arcuata, Spisula obtruncata and Spisula ovalis. The author however has only managed to distinguish two species from the valves collected, these are the large form Spisula arcuata and the more common smaller form Spisula ovalis.

Each valve was measured to the nearest mm using vernier calipers and the length, height and width of each valve was recorded in the same way as for Macoma (see A.2.2). In addition the width of the dentition was taken. These parameters were plotted against one another using ORIGIN (see 4.2.7) and all had strong positive correlations with one another.

HISTO (see 4.2.1) was then used to produce graphs of the distribution of these parameters (see figs. A2.9, A2.10 and A2.11). As can be seen these the two populations stand out very well indeed giving bimodal distributions: the larger peak representing S. ovalis and the smaller peak S. arcuata. The figures A2.12-A2.15 show the ratios of these parameters plotted on histograms, again a bimodal distribtuion is evident with a large population and a small one representing the two species of Spisula.

FIG. A2.9

THE WIDTH DISTRIBUTION OF SPISULA FROM THE RED CRAG OF SUFFOLK.

N = 297

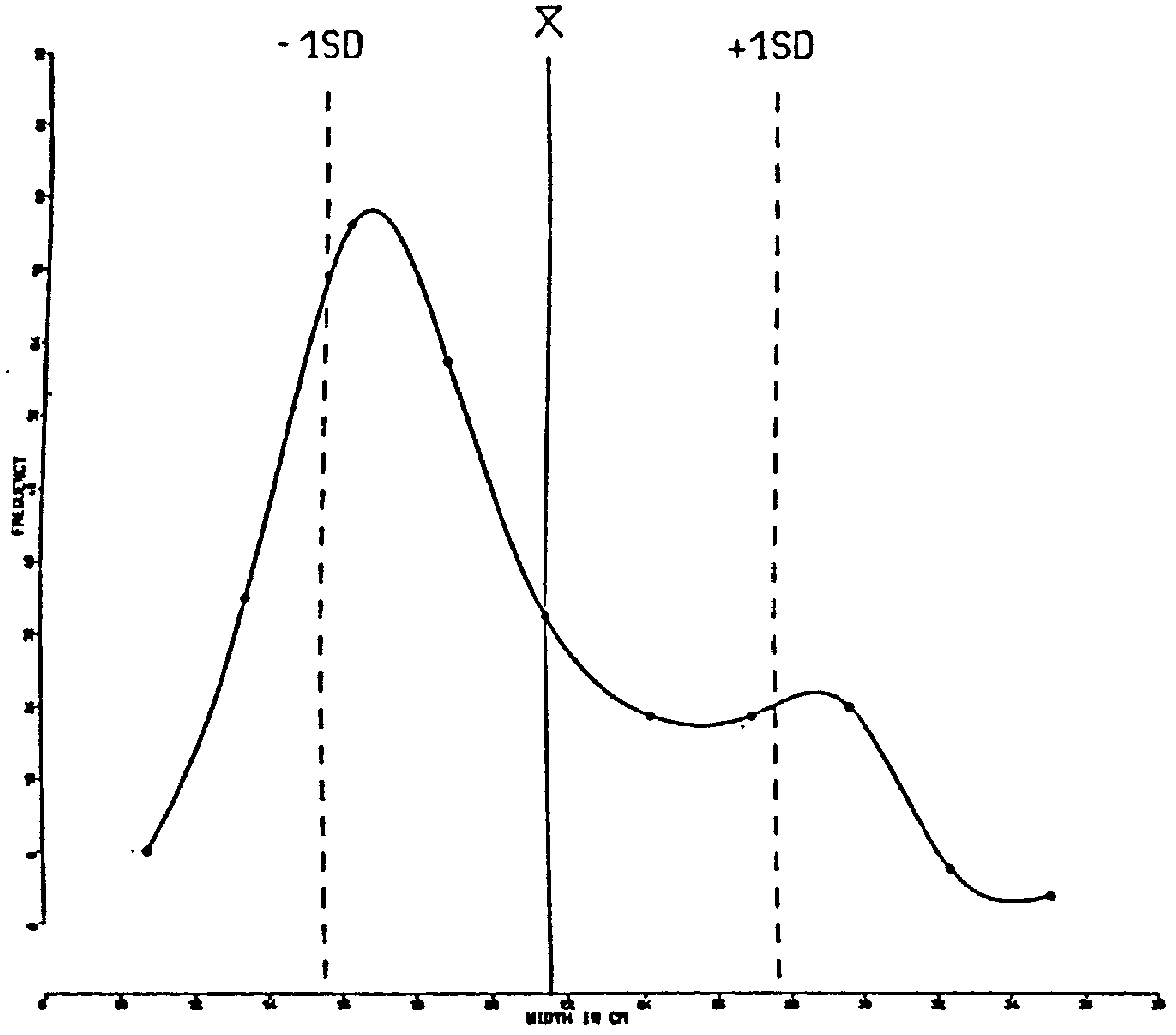


FIG. A2.10

THE LENGTH DISTRIBUTION OF SPISULA FROM THE RED CRAG OF SUFFOLK.

N = 297

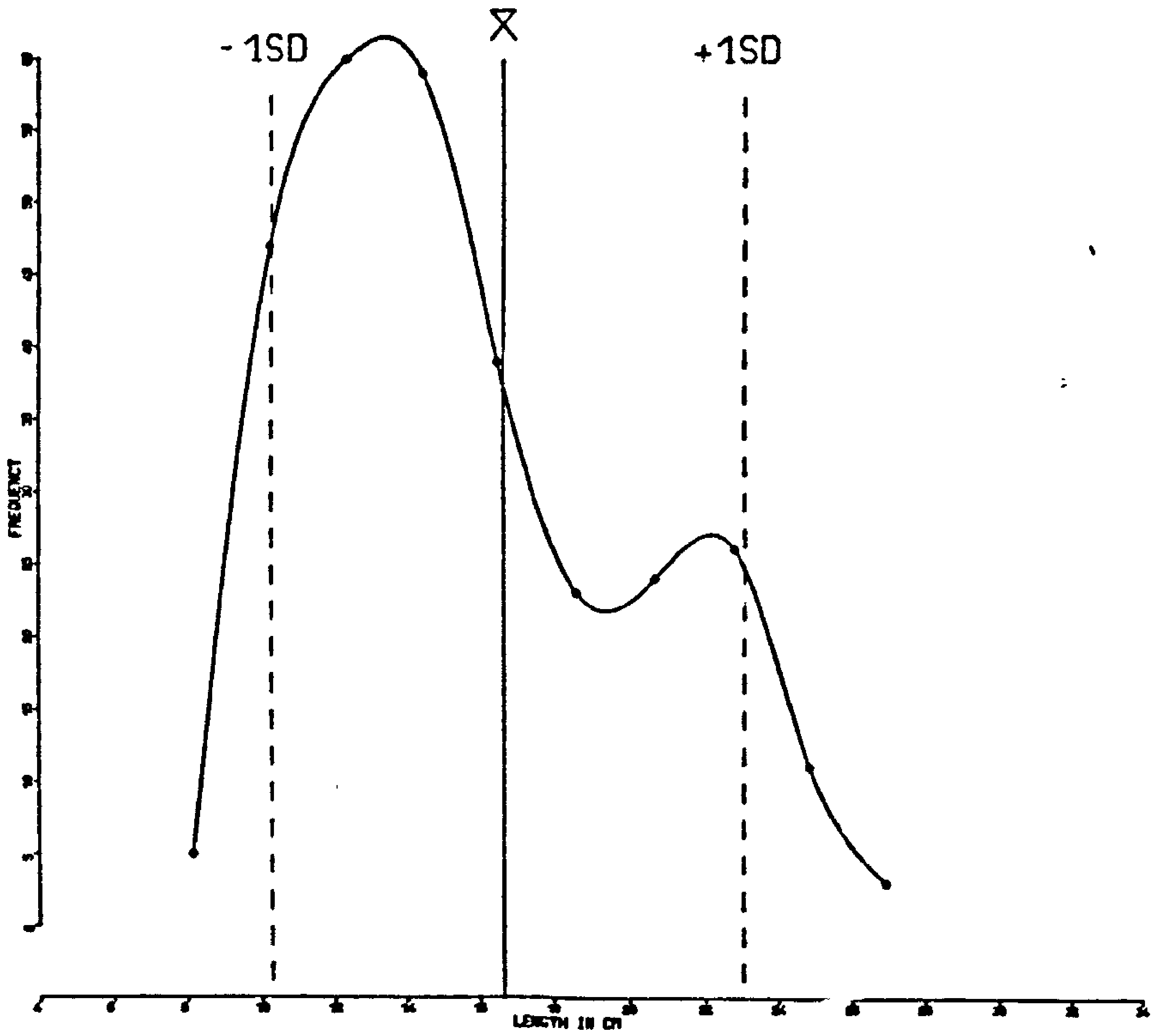


FIG. A2.11

THE HEIGHT DISTRIBUTION OF SPISULA FROM THE RED CRAG OF SUFFOLK. N = 297

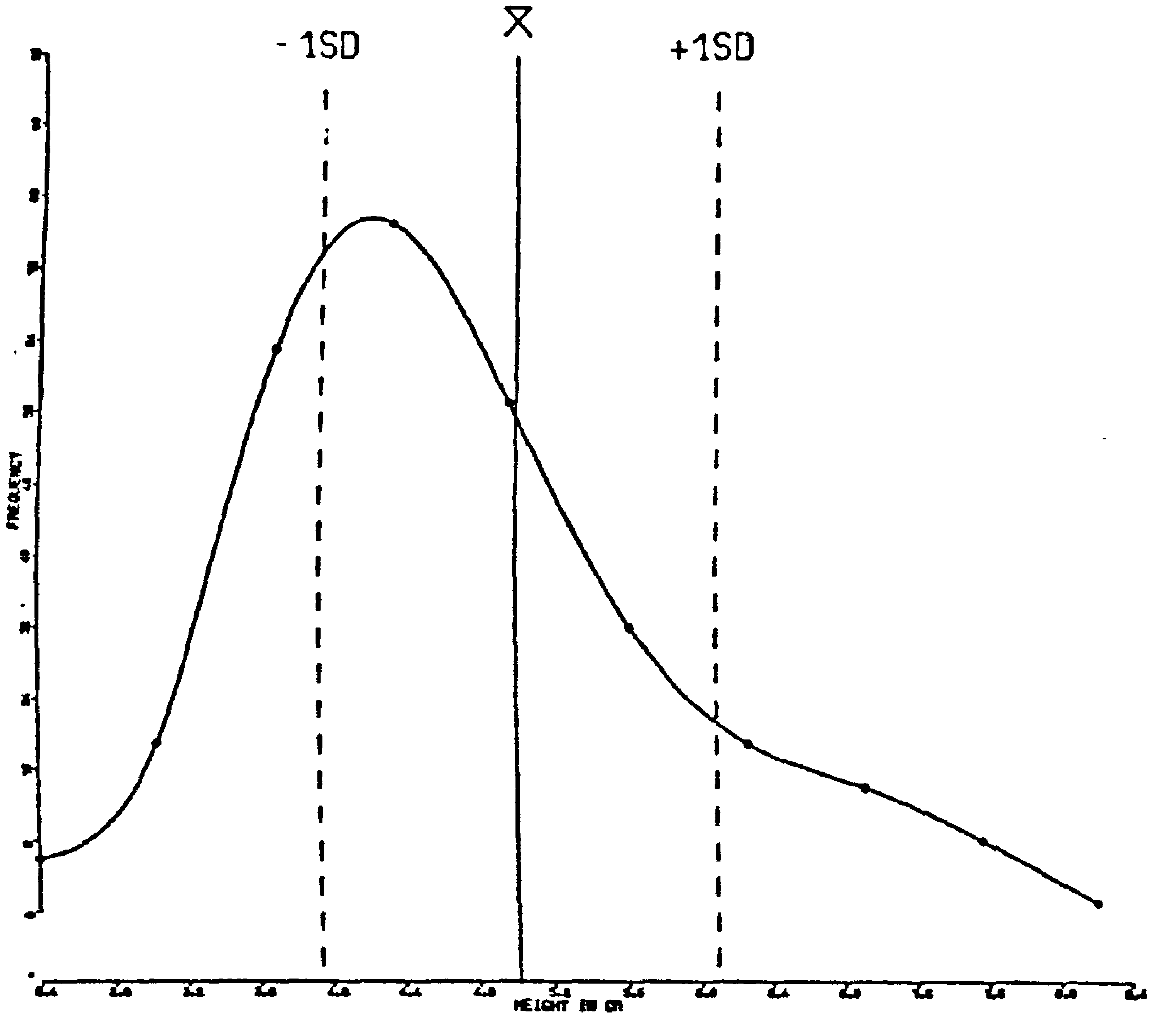


FIG. A2.12

THE WIDTH TO LENGTH RATIO OF SPISULA FROM THE RED CRAG. N = 297

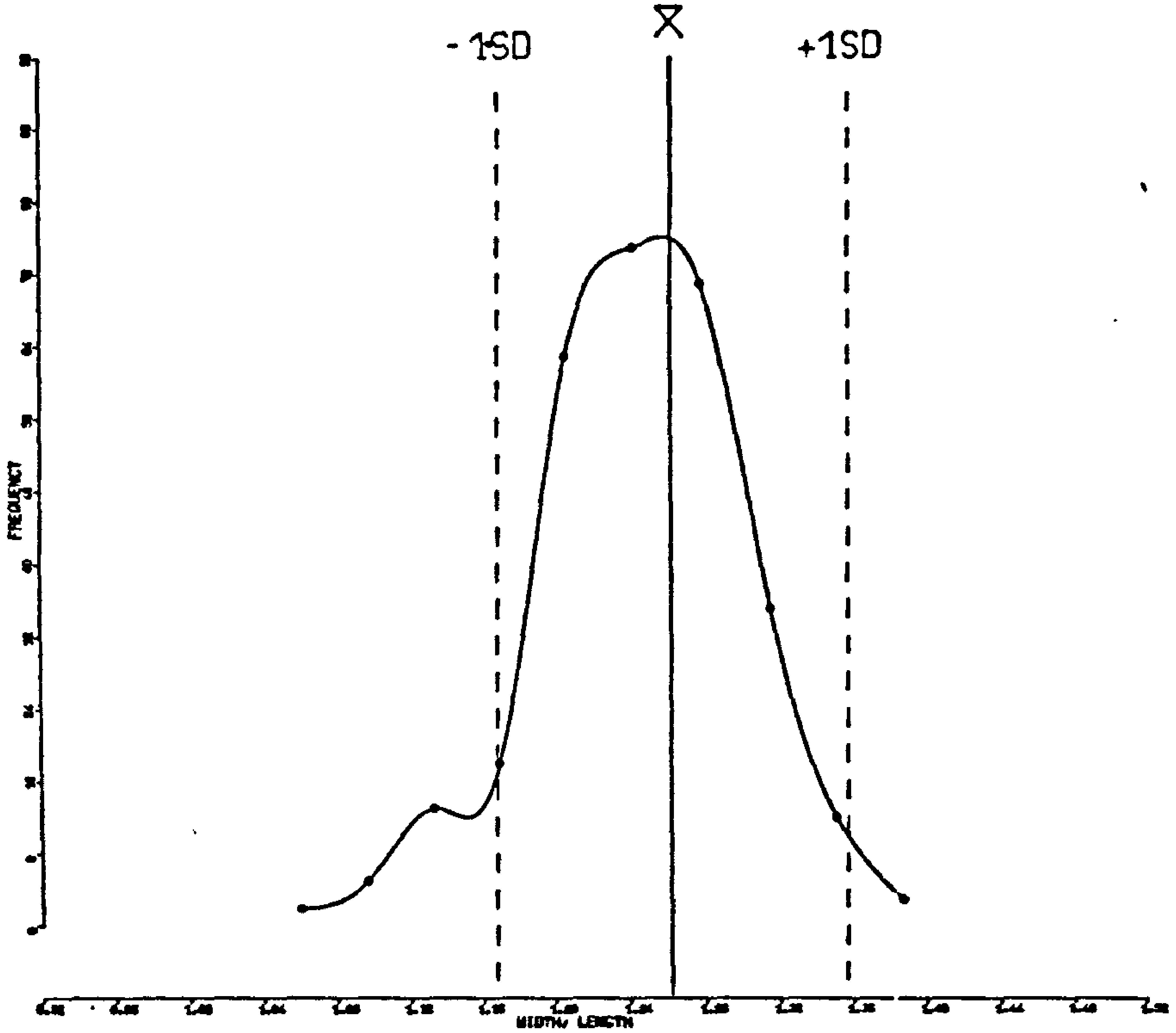


FIG. A2.13

THE LENGTH TO WIDTH OF DENTITION RATIO OF <u>SPISULA</u>.

N = 297

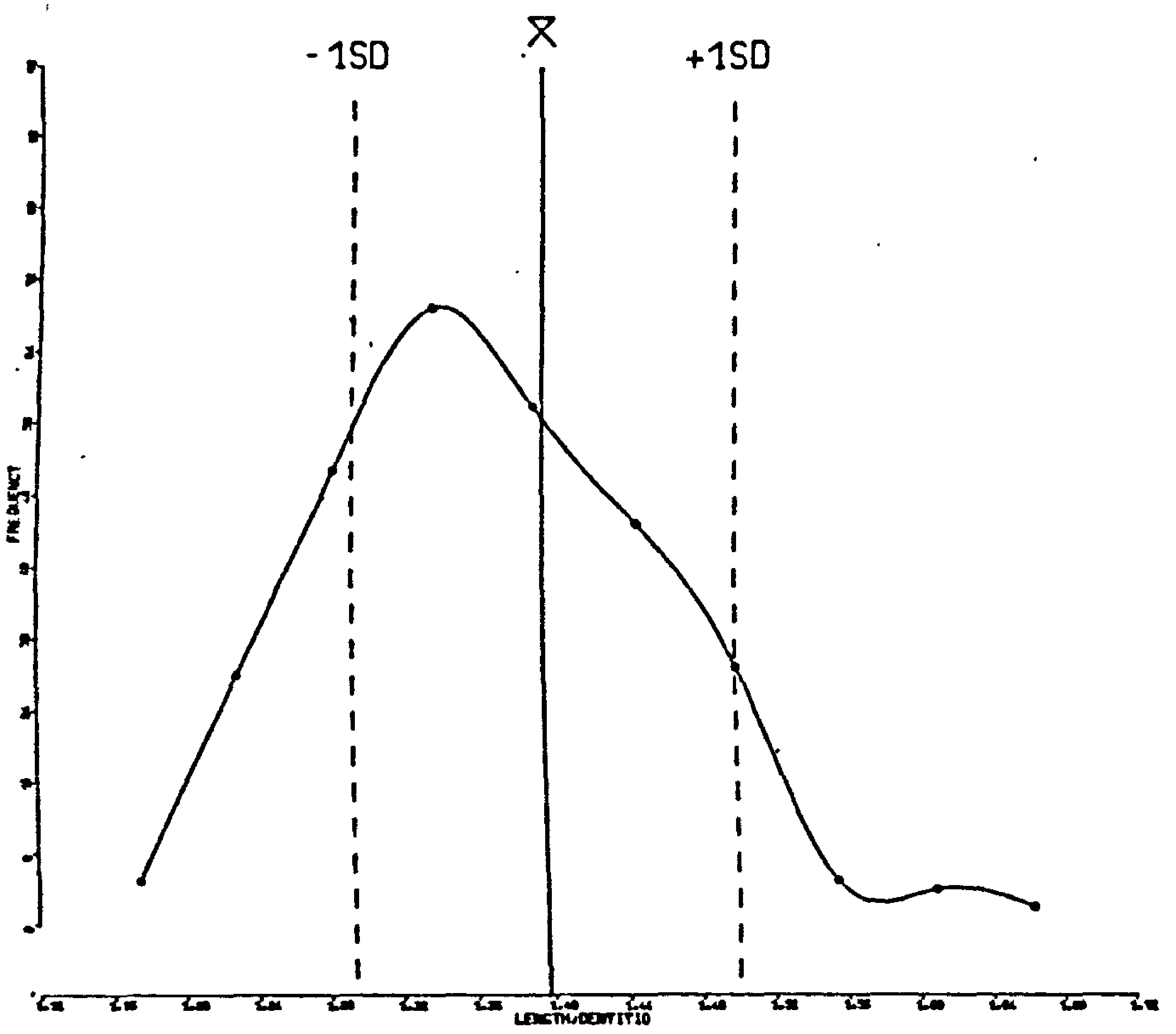
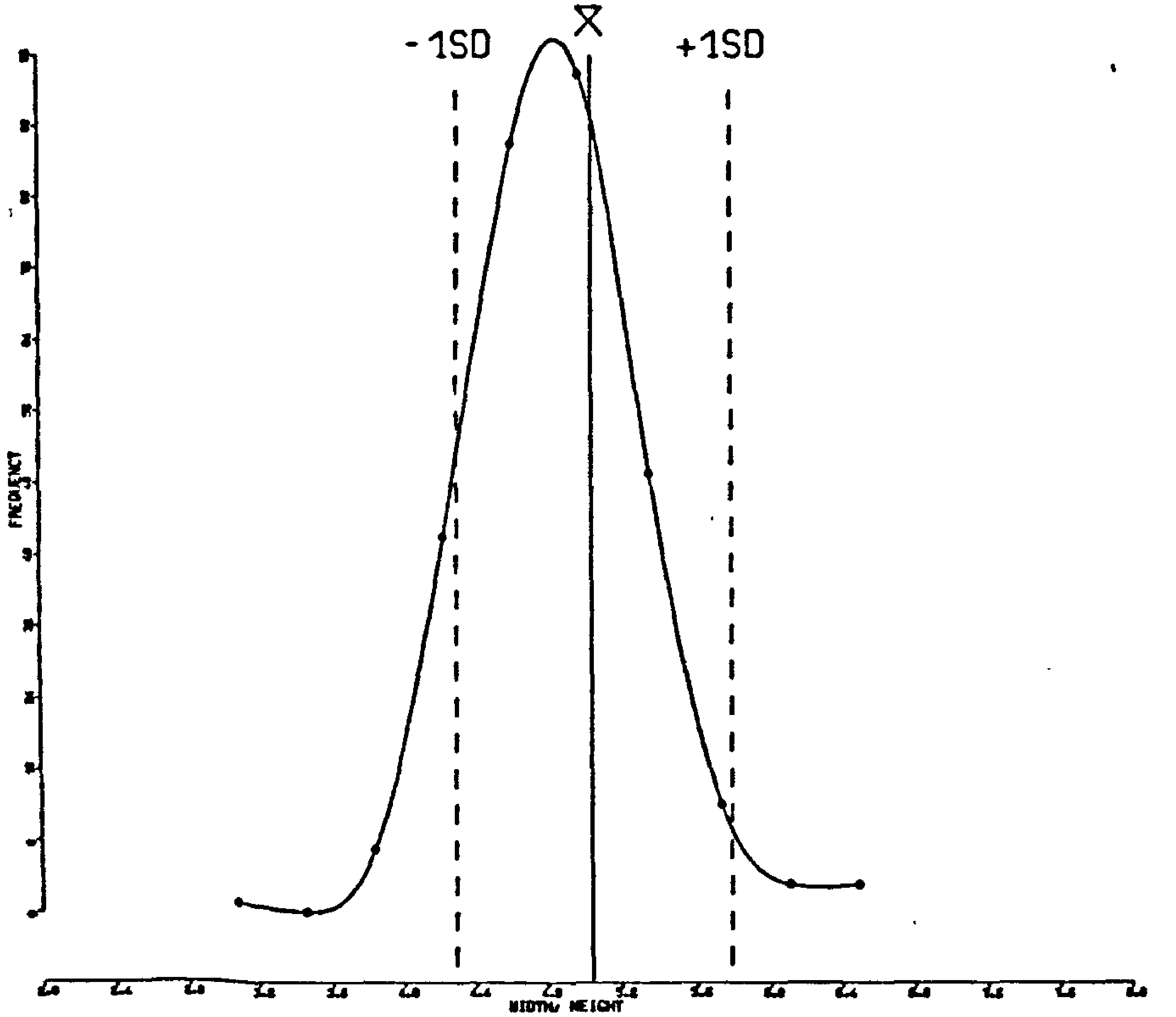


FIG. A2.14

THE WIDTH TO HEIGHT RATIO OF <u>SPISULA</u> FROM THE RED CRAG.

N = 297



As with Macoma there is a need to collect more specimens of Spisula from the Red Crag in an attempt to find the species mentioned by Dixon (1977) and Wood (1848-82) and these would presumably show up as different peaks on the histograms.

Appendix 3.

Shell breakage.

A3.1 The tumbler experiments.

A3.2 Breakage with pliers.

A3.3 Conclusions and future work.

A3.1 The tumbler experiments.

The apparatus for the tumbler experiments consisted of two rollers connected to an electrical motor by a pulley and belt drive system and two polythene jars, 240mm long and 170mm in diameter, with screw tops. The jars could be placed onto the rollers and with the motor running they rotated at 31.5 r.p.m.

In the first experiment ten shells of Neptunea contraria and ten Nucella lapillus shells, from the Red Crag, were used. These were placed in one of the jars with 1,947g of Red Crag sand and 1 litre of water. Ten modern shells of Neptunea antiqua and ten modern Nucella lapillus shells were placed in the second jar with 1,719g of Red Crag sand and 1 litre of water. Both of the jars were then rotated on the tumbling apparatus for a total of 80 hours. This time was divided into 16 five hour periods of continous tumbling. For the first 40 hours the contents of the jars were sieved every five hours of tumbling time. During the second 40 hours of tumbling time the contents of the jars were sieved every ten hours. The amount of wear on the shells was recorded on each succesive sieving. The modern shells in the second jar were used as a control experiment, as even though the fossil shells were composed of their original material, the affects of diagenesis on shell durability was not known.

Very little breakage of either set of shells was induced in this experiment although most of the shells had their apices chipped and abraded. Their aperture margins were not affected. Abrasion wore roughly circular holes in the central parts of some of the larger whorls of the shells. The shells without holes showed wear in the same places.

A further experiment was carried out using the equipment described above but in this experiment bivalve shells were studied. Ten valves of Glycymeris glycymeris, ten valves of Astarte omalli, 20 valves of Macoma praetenuis and 20 valves of Spisula ovalis were placed in a tumbling jar with one litre of water and 2,012g of Red Crag sand. The fossil valves selected for this experiment were ones which showed little evidence of abrasion. Half of the valves of each species selected had been perforated by the boreholes of predatory gastropods. The Glycymeris valves ranged in size from 2cm (width) to 4cm, with bored and non-bored valves of similar sizes. Similar care was taken to select Astarte valves where width dimensions, which ranged from 1cm to 3cm, were similar for the bored and non-bored valves. The valves of Spisula and Macoma used in the experiment were, due to availability, all of approximately the same size, which was 2cm and 3cm in width respectively. The valves of Macoma chosen were equally divided between left and right valves so that any variation in durability due to the asymmetry of the two valves could be detected.

These shells were tumbled continuously for periods of six hours at a time, until they had undergone a total of 120 hours of tumbling. For the first 60 hours of tumbling the contents of the jar were sieved every six hours and the amount of breakage recorded (see table A3.1). This sieving and recording of of breakage was reduced to every 12 hours of tumbling during the second 60 hours.

Glycymeris proved to be the most durable of the shells in the experiment. Only one of the smaller bored valves broke, but even then a large easily recognisable fragment (>50% of the valve) was observed. All of the valves of Glycymeris showed considerable abrasion after 120

Table A3.1 Shell durability of four Red Crag bivalve species in a tumbler experiment. Figures refer to the number of identifiable valves recovered after periods of tumbling.

Hours.	0	6	12	18	24	36	48	60	72	84	96	108	120
Glycymeris													
Bored	5	5	5	5	5	5	5	5	5	5	5	4	4
Non-bored	5	5	5	5	5	5	5	5	5	5	5	5	5
Others	-	-	-	-	-	-	-	-	-	-	-	1	1
Total	10	10	10	10	10	10	10	10	10	10	10	10	10
Astarte													
Bored	5	5	5	5	5	5	5	5	5	5	5	5	5
Non-bored	5	5	5	5	4	4	4	4	4	3	3	3	3
Others	-	-	-	-	1	1	1	1	1	2	2	2	2
Total	10	10	10	10	10	10	10	10	10	10	10	10	10
Spisula													
Bored	10	10	9	7	7	7	7	7	7	7	7	7	7
Non-bored	10	10	10	8	7	7	7	7	7	7	7	7	7
Others	-	-	-	2	3	3	1	1	1	1	1	1	1
Total	20	20	19	17	17	17	15	15	15	15	15	15	15
Macoma													
Bored	10	8	4	4	3	2	2	2	2	2	2	1	1
Non-bored	10	10	6	4	4	4	4	4	4	4	3	3	3
Others	-	-	3	5	4	2	2	2	2	2	3	1	-
Total	20	18	13	13	11	8	8	8	8	8	8	4	4

N.B. "Others" refers to fragments which can be recognised as having formed one valve but where it was not possible to determine from the fragments whether or not the valve had been bored.

hours, one of the larger valves having had a hole worn into its centre.

The valves of Astarte were similarly abraded although in none of them did the wear produce holes. Two of the non-bored valves had broken into two and three pieces respectively, although these were still recognisable as fragments of Astarte. The valves of Astarte in the experiment tended to crack and break rather than simply wear down; three of the remaining whole valves exhibited large cracks after 120 hours of tumbling.

After the early disintegration of six of the 20 Spisula valves the remaining valves demonstrated a high degree of resistance to abrasion. Fourteen of the original 20 were still identifiable after 120 hours of tumbling. This resistance to breakage was also reported by Chave (1960 and 1964). The breakage that did occur was around the ventral margins of the valves and all of the remaining identifiable fragments exhibited a certain degree of this breakage. The bored valves did not break across the bore but at the ventral margin along growth lines.

Macoma proved, in this experiment, to be the least durable shell with respect to abrasion. Only four of valves, out of the original 20, could be identified as pieces of Macoma after 120 hours of tumbling. The valves broke both at their margins and across the valves, one of the bored valves broke across the borehole. No difference in durability was observed between left or right-hand Macoma valves.

A3.2 Breakage with pliers.

A simulation of the breakage caused by crabs at the apertures of gastropods was carried out on five specimens of Neptunea contraria and Nucella lapillus from the Red Crag. In addition, as a control, five specimens of modern Neptunea antiqua and Nucella lapillus were used. The selected shells were broken at their aperture margins with a pair of sharp nosed pliers. This was thought to be a reasonable approximation for the mechanism employed by crabs when breaking gastropod shells.

The breaks in all three species used in this experiment, both modern and fossil, were of similar form. They tended to break, for the most part, along a single growth line and then across the growth lines to the margin at a high angle, approximately 90°, to the growth lines. The breakage thus produced by this experiment appeared very angular.

A3.3 Conclusions and future work.

The tumbler experiments simulated damage to the shells due to abrasion over a short period of time and in a fairly low energy environment. Any impaction was minor and no real breakage was induced in the gastropods, abrasion being the major factor in the breakage of the bivalves. An experiment which produces a more violent action may give different results in the future. The shell wear observed in these experiments is in evidence in some of the Red Crag gastropod and bivalve shells (Pratje 1929), but not in all of the shells. Many are preserved with less abrasion which is surprising as one would have expected that they would have been available for post-mortem transport for longer periods than those simulated in these experiments. The recycling of fossil material in the Red Crag submarine dune environment may be important here, with the valves involved in only one or two episodes of transportation being less abraded than those involved in several cycles of transportation.

The experiment with the bivalve shells demonstrated that the valves of certain species are more durable than those of others; Glycymeris being stronger than Macoma for example. This enforces the arguements raised in the taphonomic section (1.4.2) that sedimentary processes have probably biased the fossil record in the Red Crag in favour of the more robust shells.

The wear produced on the shells in the tumbler experiments is comparable to the wear exhibited by the fossil shells in the Red Crag. There are shells which show less wear in the Red Crag but few which show more. Those which have suffered much more wear than those in the tumbler experiments have disintegrated. The experiments therefore have simulated approximately the maximum amount of wear sustained by the valves collected in this study.

If it is assumed that the conditions of sedimentary transport were correctly simulated in the tumblers, then the time spent in the tumbler is similar to the time spent in sedimentary transition. Therefore the shells showing the maximum amount of wear in the Red Crag have been a part of the mobile fraction of the sediment for up to 120 hours.

If it is further assumed that during this 120 hours of transportation the shells were under the influence of a unidirectional current and they were being transported up to 100m per hour, then they could have been moved as much as 12Km. This figure is based on several assumptions and is therefore open to debate but it is felt that the figure of 12Km for a maximum distance of shell transportation of the fossil shells in the Red Crag is of the right magnitude.

The experiment also demonstrated that differential breakage between valves of bored and non-bored bivalves was probably not a significant factor in the species considered in the Red Crag with little difference in the durability between the bored and the non-bored valves (see Table A3.1). The experiment however only simulated abrasion and not impaction which may have produced different results.

The crude experiment of breaking the gastropod apertures with pliers shows, how the shells break when subjected to the kind of predation behaviour displayed by crabs. The breaks are of a distinctive shape and are very similar to the ones which can often be seen in Red Crag specimens both repaired and non-repaired (see chapter 9 and plate 3E).

Appendix 4.

Red Crag pollen.

A.4 Red Crag pollen.

The use of pollen as a technique applied to the palaeoecology of the Red Crag has not been used in the past due to the oxidized state of the deposit. Collections from the thin clay beds of Vale Farm [21] have however yeilded pollen grains in moderate numbers.

Of the grains identified so far the tree species are dominant, especially <u>Pinus</u> (Pine). Of the other tree species present Oak (<u>Quercus</u>), Alder (<u>Alnus</u>) and small amounts of Lime (<u>Tilia</u>) are the most significant. Pine pollen grains are often over represented in marine deposits as they are transported great distances in the sea (Groot 1966). Even so a conclusion that the adjacent land area of the time was, almost certainly, forested can be made.

The presence of Oak, Alder and Lime infers that the climate was at least as warm as the present day. More work is planned for the future and at the moment no further conclusions are possible. This avenue of research may well help to reconstruct a palaeoclimatic picture of the Red Crag and if, as is suspected, it can be found at other localities it may well be of great use in stratigraphic correlation within the Red Crag.