STUDIES ON THE BIOLOGY OF THE BEACH CLAM, DONAX (BIVALVIA, DONACIDAE) IN THE WEST INDIES

STUDIES ON THE BIOLOGY OF THE BEACH CLAM, *DONAX* (BIVALVIA, DONACIDAE) IN THE WEST INDIES

by

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ABSTRACT

Donax denticulatus (Linné) and Donax striatus (Linné) are beach clams which live in the intertidal zone of exposed sandy beaches throughout the West Indies. They occur in the saturated region of the wash zone and migrate synchronously with the tides to maintain their zonation. They are found mostly on clean alluvial beaches near the mouths of rivers and swamps. Populations from different localities vary greatly in density, size of clams, and colour of shells, and there are wide fluctuations in population densities from one year to the next.

In Jamaica D. denticulatus breeds continuously throughout the year with peak activity between November and January. Growth of the clams is rapid in the first seven months of life but slows down and ceases when the gonads mature and spawning commences. Food supply is the main limiting factor on growth and at different localities clams grow to varying sizes because of the differences in the food content of the sea. Mortality is high in the first four months of life when approximately 70% of the spat die and again in the eleventh and twelvth months when the adults spawn and die.

The Tellinacea as a group are deposit feeders, but D. denticulatus and D. striatus show a reversion to a suspension feeding habit. The form and function of the siphons, mantle organs, and alimentary canal are adapted for dealing with finely particulate material suspended in the sea water although many of the deposit-feeding structures persist. Some of these structures enable the clams to establish a fixed zonation on the beach and consequently to maintain permanent populations.

D. denticulatus is regarded as having achieved a high degree of success in the West Indies.

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SECTION A

GENERAL INTRODUCTION

I. INTRODUCTION

Beach clams of the genus Donax are small active bivalve molluscs which live in the intertidal zone of sandy beaches throughout the world. They are interesting animals for several reasons and are known to show at least two unusual biological features. Firstly, they are almost unique in their ability to develop and maintain populations in the precarious environment of a wave-swept beach, and secondly, some species are known for enormous populations which develop periodically and then suddenly die off. Commercially, these clams are also of interest as they have formed the basis of small fisheries in many parts of the world, and among conchologists, are highly favoured because of the rich variety of colour and pattern of their shells. As a result of the range of interest in Donax, much attention has been focused on it and some of the more unusual aspects of the clam have been reported on frequently. Most of the published work, however, has been in the form of short notes on specific topics, and previously, there has been no comprehensive study of the biology of any one species.

Two species of Donax, D. denticulatus (Linné) and D. striatus (Linné) are common inhabitants of beaches in the West Indies and are available for study throughout the year, but no previous investigation has been made of them. They have therefore been examined in this study with the following aims:

(1) To investigate their ecology, and in particular, to elucidate those morphological features which enable the clams to maintain themselves in such a difficult environment.

(11) To find out what factors in the environment may regulate the populations, and the reasons for periodic population explosions followed by sudden mass mortality.

(111) To determine what ecological differences exist between the local tropical species and the subtropical and temperate species, and the reasons for these differences.

The results of this study are reported in separate sections on the ecology, life history, and nutrition of the clams, and comprise the major part of this thesis.

II. REVIEW OF THE GENUS DONAX

1. Classification and distribution

The genus Donax is a member of the order Tellinacea[1], family Donacidae (Thiele, 1935). It was first described by Linnaeus (1758) who named and classified it with the order Testacea, class Vermes. The genus was also given the names Cuneus, by Da Costa in 1758, and Capisteria, by Meuschen in 1789; but none of these ever came into common usage.

Linnaeus described the genus only in terms of the shape of the shell and the structure of the hinge:

> " Tefta bivalvis, margine antico obtufiffimo.
> Cardo Dentibus duobus; marginalque folitario,
> fubremoto, fub ano".

He listed eight species in his original description, but later (1767) added more.

Following this original account of the genus was a more detailed and accurate description by Reeve (1841) who added further information on the structure of the hinge and ligament, and the position of the pallial sinus. Like Linnaeus, however, Reeve made the mistake of regarding

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[1]Most systematists now regard the Tellinacea as a super-family, and it is this system which will be adopted throughout this thesis.

the short, abbreviated end as anterior. This error kept recurring in the literature for another hundred years as may be seen from a description of the genus by Smith (1945), although Thiele (1935) correctly described the shorter end as posterior. Thiele's description of the genus is one of the most recent and includes information on the shell, siphons, mantle, and gills. A translation from the German follows:

The shell is triangular or elongated, the posterior end is shorter than the anterior, the umbo is rather small, the ligament is partly intruded, the lateral teeth are more or less prominent, there are two main teeth on each side, the pallial sinus is deep and rounded, the margins are unequal, the mantle edge is covered with papillae; the gills vary, sometimes they are smooth and with identical filaments, sometimes they are folded with large internal border filaments, the outer lamella is broadened, the foot is without a byssus.

Figure 1 shows some of the features of a typical Donax shell.

Because the genus is so strongly characterised by the short truncated wedge-shaped form of the shell, it has remained nearly as entire as in Linnaeus' day although several new species have been added. Recently, however, the genus has been undergoing some revision, and several species and sub-species have been grouped together to form larger species. Approximately eighty species are now included in the genus.

Figure 1.

A, left lateral, and B, posterior views of a typical Donax shell showing its general orientation and dimensions.

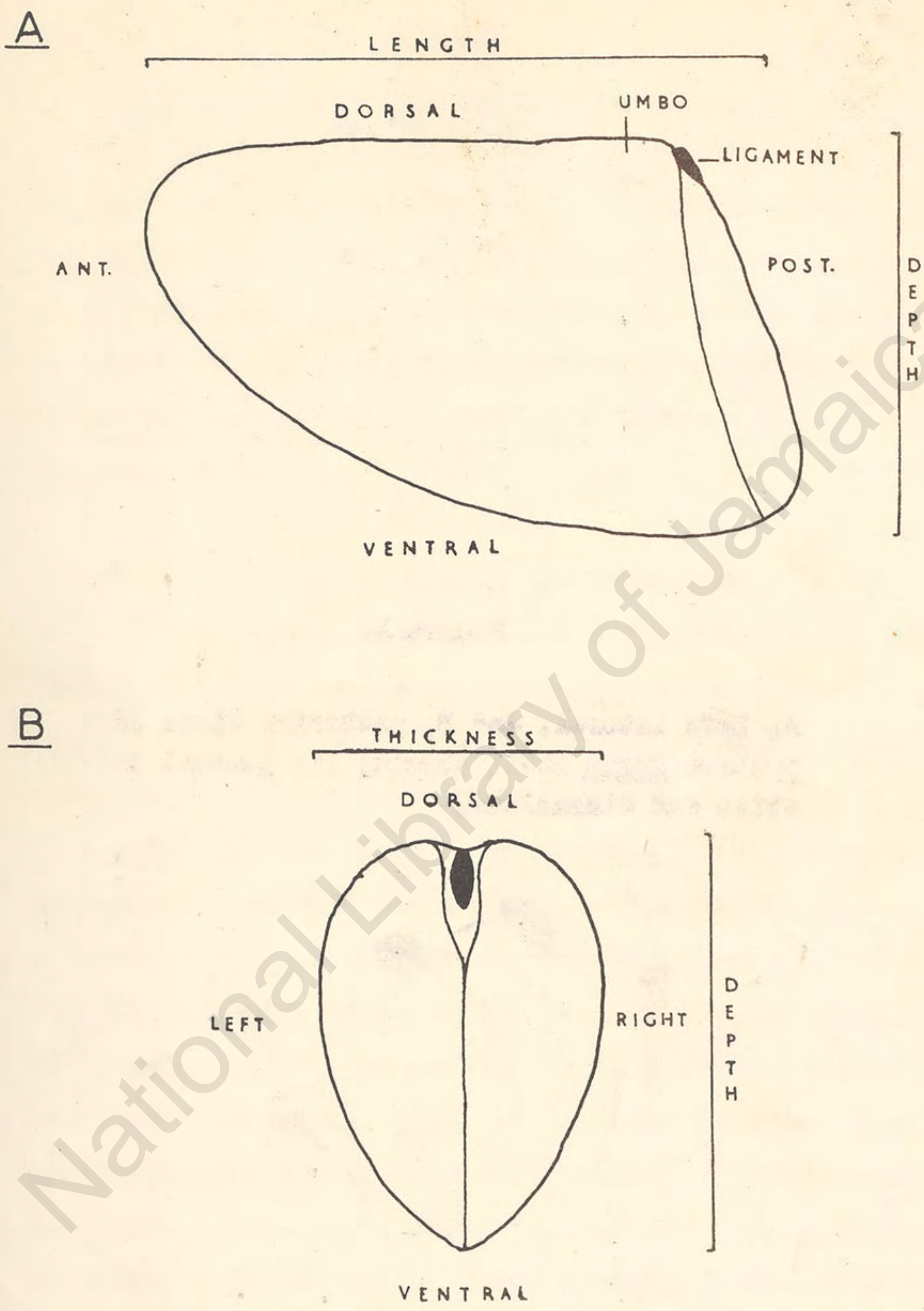
A
LENGTH
DORSAL
UMBO
LIGAMENT
ANT.
POST.
DEPTH
VENTRAL
B
THICKNESS
DORSAL
LEFT
RIGHT
DEPTH
VENTRAL

Figure 1

Donax occurs in nearly all seas, and may be said to be circumtropic to circumtemperate in distribution. In the Old World, *D. vittatus* (daCosta) occurs as far north as Scotland (Yonge, 1949a), while as many as eleven species are reported from Port Alfred in South Africa (Turton, 1951). In the New World, the northern limit is in the State of New York, U.S.A. where *D. fossor* (Say) occurs (Abbott, 1954); while the southern limit, although uncertain, is thought to be south of Brazil.

2. Review of the literature

The published literature on *Donax* may be divided into four groups of papers dealing respectively with its morphology, ecology, parasitology, and commercial exploitation.

A. Morphology: The morphology of *Donax* has not been studied extensively and only few authors have made significant contributions. In two papers, Graham (1934a & 1934b) described the structure of the cruciform muscle of *D.vittatus* (daCosta), and studied certain aspects of the anatomy of the clam in a consideration of the relationships of bivalves possessing the cruciform muscle. Atkins (1937) reported on the ciliary beat and currents on the gills of *D. vittatus* in a review of the ciliary mechanisms in lamellibranchs. Yonge (1949a) related the structure and functions of the siphons, gills, stomach, and cruciform muscle of *D. vittatus* in his work on the structure and adaptations of the Tellinacea, and it is this work which stands as the most authoritative account of the genus. Purchon (1960) described the stomach of D. faba (Gmelin) in an account of the types of stomachs found in the Eulamellibranchiata.

B. Ecology: One of the first notes on the ecology of Donax was by Orton (1929) who estimated that there were one hundred million dead D. vittatus on a three mile stretch of beach in England, but he did not say over what period of time they had died. Coe (1953) also reported a spectacular mortality of clams among a large population of D. gouldi (Dall) in 1938, and further noted that there had been seven resurgent populations since 1894. Other short references to the ecology of Donax were made by Haas (1940) who investigated the molluscs of Sanibel Island, Florida, and by Pearse, Humm, and Wharton (1942) who made an ecological study of the sand beaches at Beaufort, North Carolina. Until the 1950's, however, there were no attempts at any detailed account of the ecology of Donax. Coe (1955) was the first to pay individual attention to a single species and he published a series of observations on D. gouldi in California. He was followed by Loesch (1957) who made what was by far the most thorough study of any species. His account of D. variabilis roemeri (Philippi) and D. tumidus (Philippi) on the Texas coast represents the only real attempt at a critical analysis of the ecology of the clam. Subsequent studies have been made by Edgren (1959) who investigated D. variabilis (Say) on a Florida beach, and by Moment (1963) who demonstrated the protective variation in colour of D. variabilis.

The tidal migratory behaviour of *Donax* has received special attention. Mori (1938 & 1950) was the first to publish an account of the tidal migrations of any species of *Donax*, and his papers on the migrations of *D. semigranosis* (Dunker) on the coast of Japan led the way for more work on the subject. Hedgpeth (1953) reported information he had received from Burkenroad on the tidal migrations of a species of *Donax* on the coast of the Gulf of Mexico, and Jacobson (1955) observed the migrations of *D. fossor* (Say) at Rockaway Beach, New York, U.S.A.. Turner and Belding (1957) have made the most recent study of this habit of *Donax*, and their description for *D. variabilis* in North Carolina is now the most comprehensive account. Several books (Hedgpeth, 1957; Moore, 1958; Wilbur and Yonge, 1964) refer to the tidal migrations of *Donax* as an example of adaptive behaviour in intertidal animals.

C. *Parasitology*: The earliest papers mentioning *Donax* dealt primarily with the relations of certain larval trematodes to the host mollusc. Leidy (1879), Giard (1897a & b and 1907), Pelseneer (1896 & 1928), Chatton and Lwoff (1923), and Rees (1939) were among the leading authors on the parasites of *Donax*. This field of interest has continued to the present and the most recently published paper on the subject has been by Hopkins (1958). Cable (1956 & 1963) described the cercarial larva from *D. denticulatus*, and Loesch (1957) reported on the parasites of *D. variabilis* and *D. tumidus*.

D. *Commercial exploitation*: The commercial uses of

Donax have been reported by several authors. Weymouth (1920) listed it as one of the edible and highly favoured clams of California, and Coe (1953), Abbott (1954), Loesch (1957), and others also referred to some of the uses of the clam. Nayar (1955) investigated the life history of *D. cuneatus* (Linné) in India so as to determine the feasibility of developing a commercial fishery based on the clam.

3. Economic interest

Donax has been of primary interest to man as a source of food, and in Trinidad, for example, it has been estimated that it provided at least 60% of the meat diet of the early Indian tribes. Today its chief use is in the making of broth, and where there are large populations, the clams are often sold commercially. Rogers (1936) quotes the price of ten cents a quart for *D. laevigata* (Deshayes) in Southern California. Besides making broth, the clams may also be cooked with rice or may be parboiled and served with relish as a delicacy. In India, the meat is made into a paste and treated with condiments in the preparation of curries.

Donax has also been used for making liquor. Weymouth (1920) quotes the following extract from the Commissioner's report of the United States Commission of Fish and Fisheries, 1896:

"During 1895, favourable experiments having been made to utilise these clams for their liquor, a company was formed under the name of Pacific Coast Extract Company, and the business of putting up clam extract was begun. The extract is packed in glass and stone pint and quart packages and gallon jugs. The extract has met with a flattering reception, and encouraged the company to enlarge the business".

In Trinidad, D. striatus is served in beverages as "chip-chip cocktail" and fetches a high price.

The shell of Donax has many uses, the chief of which is the making of ornaments. Rogers regards Donax shells as among the most beautiful and as having the widest application of the shells of North America. It is used extensively in the preparation of shell flowers, bracelets, and necklaces. In the West Indies, these articles are highly favoured by tourists who may pay as much as $B.W.I.5 for one of these pieces. Rogers has reported having seen strings of Donax shells woven together as portieres sold at $30 in America.

Nayar (1955) mentions that in India, womenfolk gather the washed-up shells and use them for burning lime. In California, the shells are crushed and used by poultry dealers. Loesch (1957) reports that in Florida, cemented deposits of Donax shells are extensively mined, and the "Coquina rock" is used as building stones and for roads.

III. THE SPECIES OF DONAX IN THE WEST INDIES

1. Occurrence

The most recent check-list of molluscs in the West Indies (Warmke and Abbott, 1961) lists three species of Donax as occurring in this area:-

(1) D. denticulatus (Linné)[1]. The Common Caribbean Donax occurs from Cuba in the north to Brazil in the south, both on the Central and South American coast and on the Caribbean Islands. Smith (1945) reported it from the Florida Keys and Texas, but this has been refuted by Abbott who claims that it does not occur at all in the United States. This species grows to about 25 mm. in length.

(2) D. striatus (Linné)[1]. The Striate Donax has a more scattered distribution than D. denticulatus and has been reported from Cuba, Jamaica, and Trinidad by Aguayo and Jaume (1950). Warmke and Abbott say that it is uncommon in Puerto Rico. I have received a few specimens from British Honduras.

D. striatus grows to a larger size than D. denticulatus and may reach a length of 30 mm. It is found on beaches together with D. denticulatus although

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[1] D. denticulatus, D. striatus, and D. tumidus were originally known as D. denticulata, D. striata and D. tumida.

in most cases, in much fewer numbers.

(3) D. tumidus (Philippi)[1]. The Fat Little Donax is reported by Warmke and Abbott to occur in the Gulf of Mexico and the West Indies. Aguayo and Jaume claim a wider distribution with a northern limit at St. Augustine in Florida.

Unlike the first two species, D. tumidus is not always found at the water's edge. Loesch (1957) notes that in Texas, they occur in water from knee deep to waist deep in the winter; then during the spring and early summer they are at the water's edge. From the middle of summer through the winter, they are found only in water one to three feet deep, and possibly deeper.

The Fat Little Donax seldom grows more than 12 mm. in length.

Aguayo and Jaume list nine more species of Donax as occurring in Cuba. These are:

D. calamensis (Lamarck)
D. fossor (Say)
D. granifera (Deshayes)
D. incerata (Reeve)
D. pulchella (Hanley)
D. roemeri (Philippi)
D. rugosa (Linné)
D. texasiana (Philippi)
D. variabilis (Say)

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[1]See footnote on previous page.

These species are primarily North American and have their greatest abundance in the Southern United States. It is not surprising therefore that they do not extend further south in the Caribbean. Aguayo and Jaume in listing these species noted that as the genus needed some revision, it was possible that the actual number of species was quite less.

In the West Indies, Donax is known as cockle or cockrel in Jamaica, dice in Antigua, chip-chip in Trinidad, and coquina, the American name, in St. Vincent.

2. Availability for study

During the course of this study, most of the work was done in Jamaica although field trips were made to St. Kitts and Nevis, Antigua, Montserrat, Dominica, St. Lucia, Barbados, St. Vincent, The Grenadines, Grenada, and Trinidad to obtain additional data. In nearly all of these islands, D. denticulatus was common and readily available. D. striatus, however, was found only in Trinidad and Jamaica, and in the latter, it was unavailable for study for the greater part of the year due to its spasmodic occurrence in the easily accessible localities. D. tumidus was not found in any of the islands visited.

Because of the scarcity of D. striatus, and the absence of D. tumidus in these islands, the only species that could be studied in great detail was D. denticulatus. Wherever possible, however, comparative studies were made on D. striatus. As a result, this thesis is an account of a study of the Common Caribbean Donax, D. denticulatus, with comparative notes on the Striate Donax, D. striatus.

3. Description of species

The two species on which this study is based have not been previously described in detail, and this has resulted in some confusion in identification in some places. Thus in Jamaica, for example, small specimens of D. denticulatus have been mistaken for D. tumidus and D. variabilis, and D. striatus has been left unnamed despite its presence in The Jamaica Museum collections for several years.

The following is therefore a description of the characteristic features of the shell of the two species:

D. denticulatus

A. Shell markings: The diagnostic features in the identification of this species are based on shell markings (Figure 2). On the lateral surfaces of each valve are about 40 radial grooves which radiate from the top of the umbo near the position of the hinge (Figure 2A). Along each groove are many very minute pin-pointed teeth which, when viewed under the microscope, help to give a pimpled appearance. It is these pin-pointed teeth which give the species its name.

On the posterior slope of each valve are two curved ridges (Figure 2B). The outer ridge forms the margin between the lateral and posterior surfaces of the valve, while the inner ridge separates two distinct areas on the posterior slope. The outer area is characterised by having nine terraced grooves which are deeply sculptured. The inner

Figure 2

A, left lateral, and B, posterior views of the shell of <u>D. denticulatus</u>.

A	-	anterior end
DM	-	dorsal margin
H	-	position of hinge
L	-	ligament
WR	-	wavy ridges
PS	-	posterior slope
PVM	-	postero-ventral margin
VM	-	ventral margin
RG	-	radial groove
OR	-	outer ridge on posterior slope
IR	-	inner ridge on posterior slope
TG	-	terraced groove

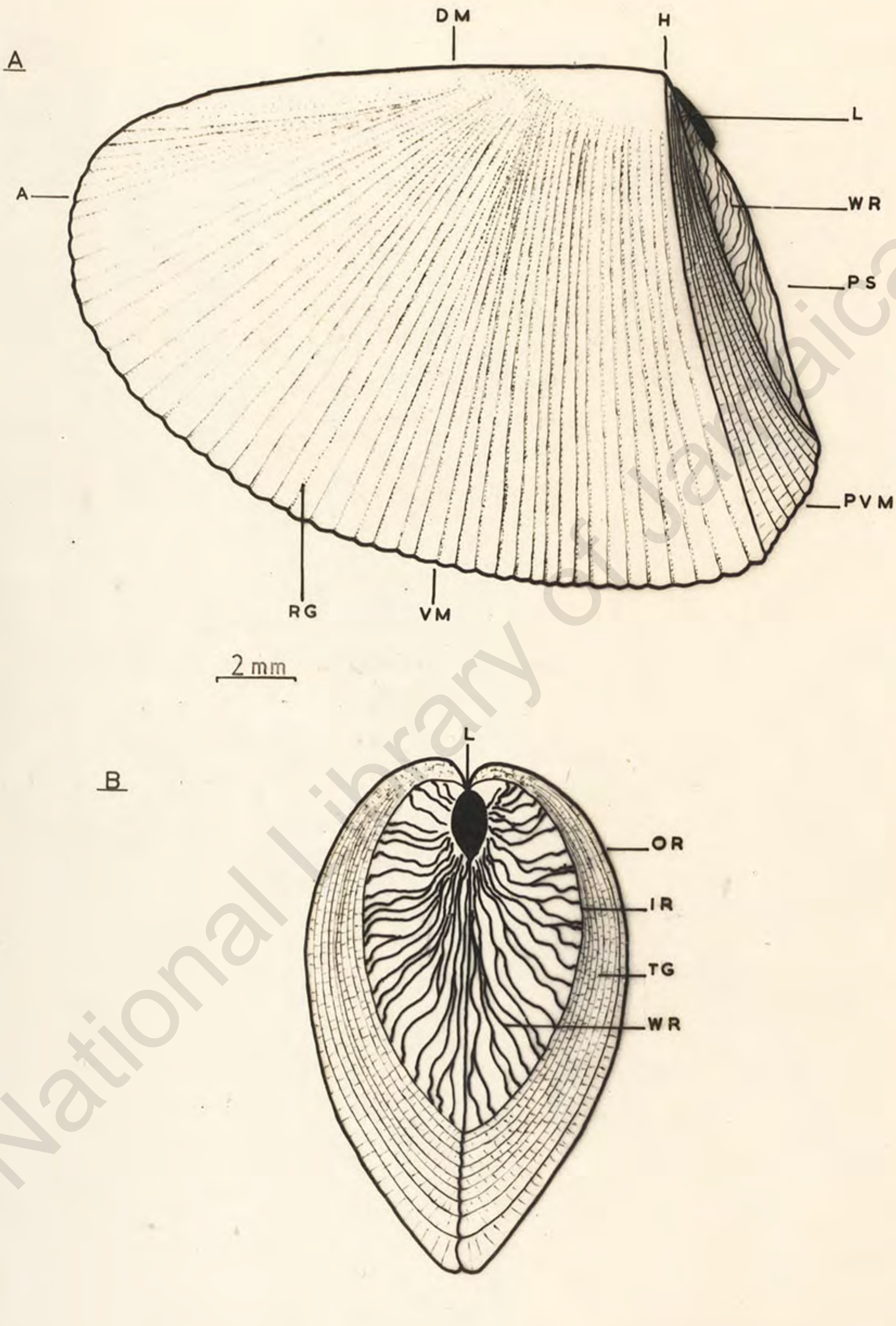

Figure 2

Figure 3

The depth on length (L:D) and thickness on length (L:T) curves for a sample of shells of *D. denticulatus*.

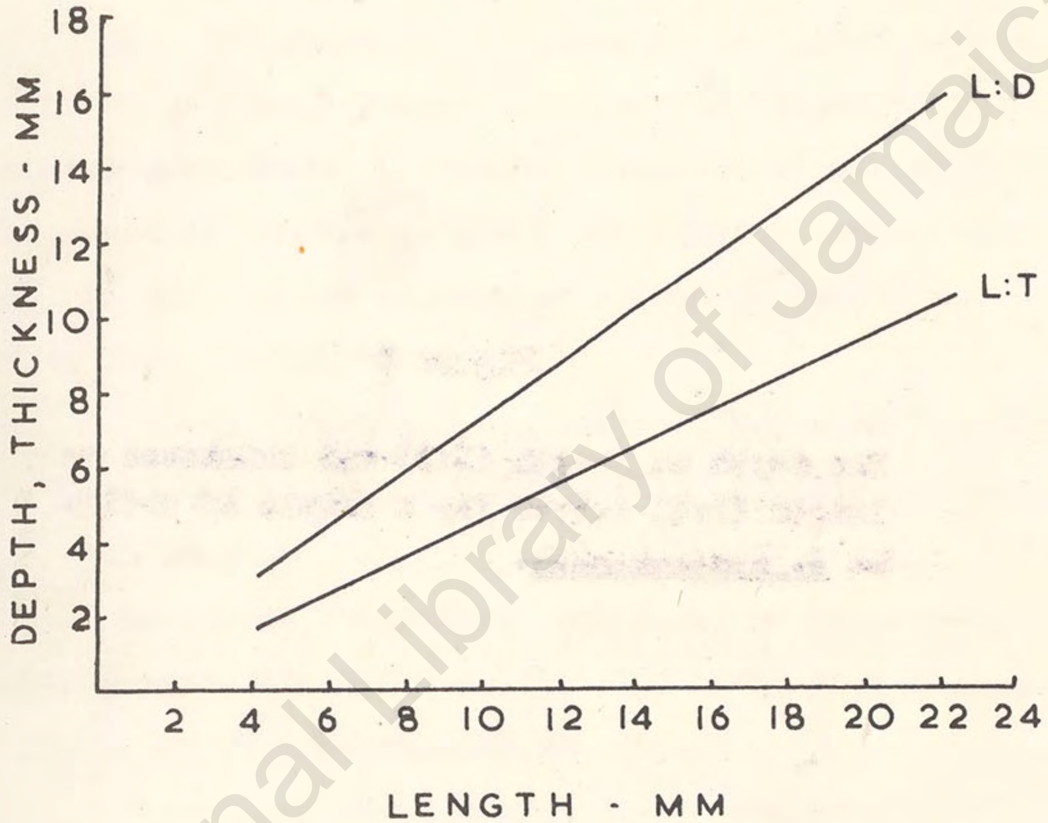
DEPTH, THICKNESS - MM
18
16
14
12
10
8
6
4
2
L:D
L:T
2 4 6 8 10 12 14 16 18 20 22 24
LENGTH - MM

Figure 3

area bears about 20 small rounded ridges which originate from a position near the ligament and radiate in a peculiar wavy direction. When the posterior slope is thus viewed with the naked eye, these ridges give the appearance of zigzag lines, and provide the most distinctive feature for a rapid identification of the species.

B. <u>Shape</u>: The shape of this species is fairly constant and provides useful length to depth and length to thickness ratios. Nearly a hundred specimens of all sizes were measured with Vernier Calipers for length, depth, and thickness, (Figure 1) and regression constants determined with the following results:

Length to depth: The slope of depth on length gave a regression constant of 0.732 with a significance value of more than 99.9%.

Length to thickness: The slope of thickness on length gave a regression constant of 0.462 with a significance value of more than 99.9%.

These results (Appendix I) are represented graphically in Figure 3.

The dorsal margin is almost perfectly straight and the hinge is situated four-fifths along the length of the shell from the anterior end. The posterior slope with its two ridges on each valve is convex, and between the outer and inner ridges on the midline, is a sharply angled postero-ventral margin. The ventral margin itself is gently curved and meets with the dorsal margin to form a rounded anterior end (See Figure 2A & B).

The two most distinctive features in this shape are the angled postero-ventral margin and the gently curved ventral margin.

C. <u>Colour</u>: This species is very beautiful and shows a variety of colours and patterns (Figure 4). The basic colours are white, cream, rust brown, light green, grey, light purple, and deep purple. Although the entire shell may have only one of these colours, it is more usual to have two or three, in which case, they have interesting patterns. The first and most frequent pattern is one in which the shell is basically white, but has radial stripes of brown or purple, either in pin stripes or broad rays. The second pattern consists of concentric bands of two or more colours, usually involving varying shades of purple and sometimes white, brown, or green. A third pattern, which is not very common, is one in which the shell is basically white but has a blotch of deep purple along the dorsal and posterior surfaces. Sometimes a mixture of these patterns occurs.

Except for white shells, the inside of the shell is usually a shade of purple throughout, and bears little or no resemblance to the colour or pattern on the outside.

<u>D. striatus</u>

A. <u>Shell markings</u>: Like <u>D. denticulatus</u>, the lateral surfaces of the valves of this species have about 40 radial grooves, but in this case, the grooves are smooth since they lack the teeth so characteristic of <u>D. denticulatus</u>.

Figure 4

The range and variety of (A) colours, and (B) patterns of shells of D. denticulatus.

A

B

Figure 4

The only diagnostic marking on the shell of D. striatus is on the posterior slope (Figure 5B).

The posterior surface of each valve has only one curved ridge, that separating the lateral and posterior surfaces, and there are between 20 and 25 grooves on each slope. Traversing these grooves in a radial direction are very many minute threads which originate from a position around the ligament. It is by these threads that the species is most reliably identified.

B. Shape: The shell of this species is quite variable in shape, especially among the adult clams. For this reason, it provides poor evidence on which to base an identification. Although there is some variation in the young clams, the dimensions are fairly constant, and reliable length to depth and length to thickness ratios may be obtained. On measuring more than fifty clams less than 20 mm. in length, the following results were obtained:

Length to depth: The slope of depth on length gave a regression constant of 0.697 with a significance value of more than 99.9%.

Length to thickness: The slope of thickness on length gave a regression constant of 0.442 with a significance value of more than 99.9%.

These results (Appendix II) are represented graphically in Figure 6.

A comparison of these curves with those for D. denticulatus shows that in length to depth, there is little difference, whereas in length to thickness,

Figure 5

A, left lateral, and B, posterior views of the shell of D. striatus.

A - anterior end
DM - dorsal margin
H - position of hinge
L - ligament
PS - posterior slope
RG - radial groove
AVM - antero-ventral margin
R - posterior ridge
G - groove
RT - radial threads

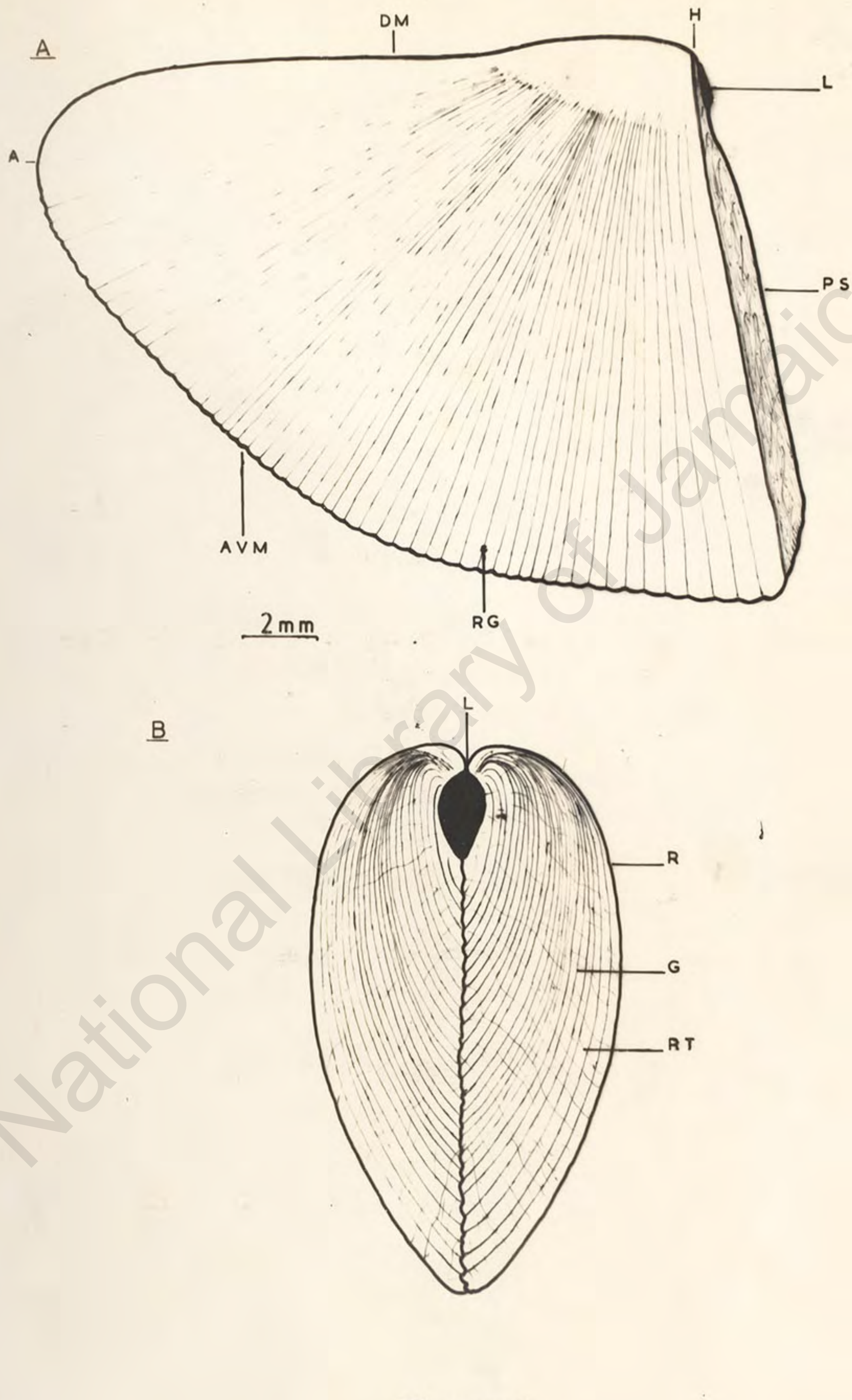

Figure 5

Figure 6

The depth on length (L:D) and thickness on length (L:T) curves for a sample of shells of D. striatus.

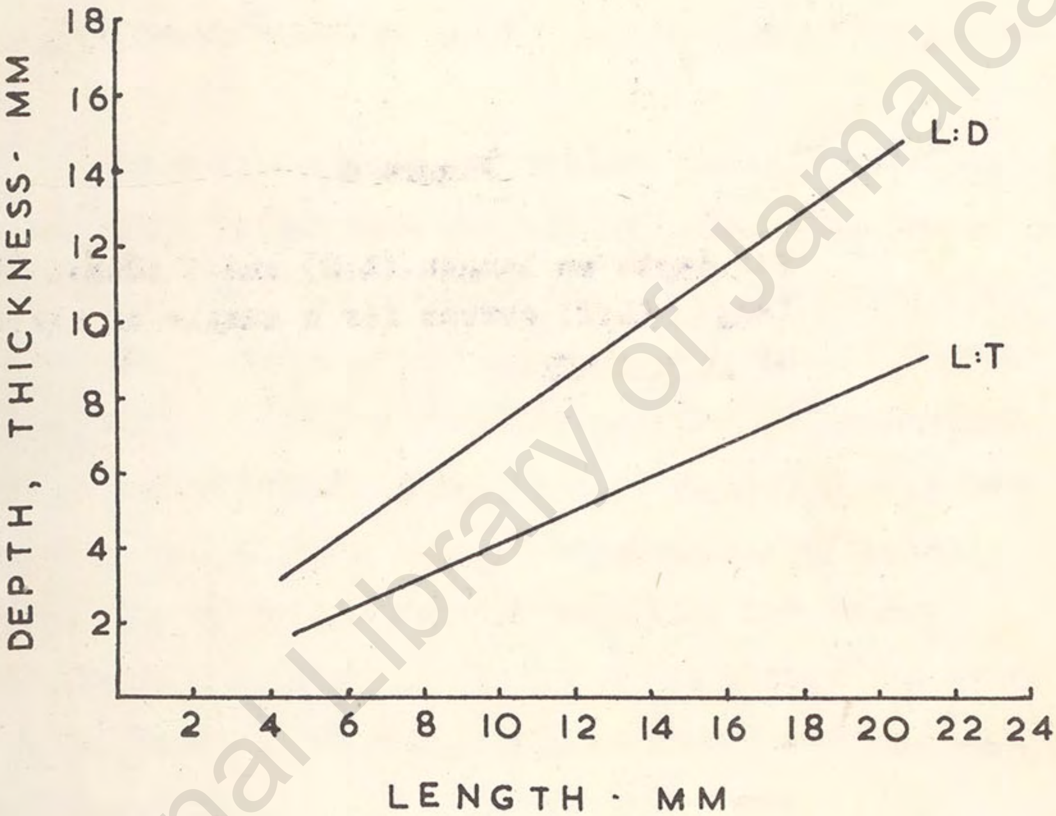
18
16
14
12
10
8
6
4
2
DEPTH, THICKNESS- MM
L:D
L:T
2
4
6
8
10
12
14
16
18
20
22
24
LENGTH · MM

Figure 6

<u>D. denticulatus</u> has an appreciably smaller ratio.

To illustrate the variation in shape among adult clams, the dimensions of two sets of clams from two different localities were measured. These were between 21 mm. and 30 mm. in length. The result (Appendix III) represented graphically in Figure 7A, shows that the length to depth ratio in one is much smaller than in the other.

The dorsal margin is straight in this species, and the hinge is situated four-fifths along the length of the shell from the anterior end. The posterior slope is also fairly straight and lacks a well defined postero-ventral margin. Warmke & Abbott describe the posterior slope as being flat to slightly concave, but I have seen several clams in which this slope is quite definitely convex. The ventral margin is variable, but in most clams, it is conspicuously angled about midway its length and meets with the dorsal margin to form a pointed anterior end. (Figure 5A).

C. <u>Colour</u>: <u>D. striatus</u> is not a brightly coloured species. The shells are either white or a pale shade of cream, pink, grey, or purple (Figure 8A). Most shells are predominantly of one colour and therefore lack the variety of patterns seen in <u>D. denticulatus</u>. In some, however, the monotony of colour is broken by concentric rings of varying shades of the same colour (Figure 8B). Only very rarely do shells have radial colour bands.

The inside of the shell may be white, pink, or a

Figure 7

A: The depth on length curves for samples of shells of <u>D. striatus</u> from two different localities.
B: Adult clams of <u>D. striatus</u> from two different localities showing the differences in shape and dimensions.

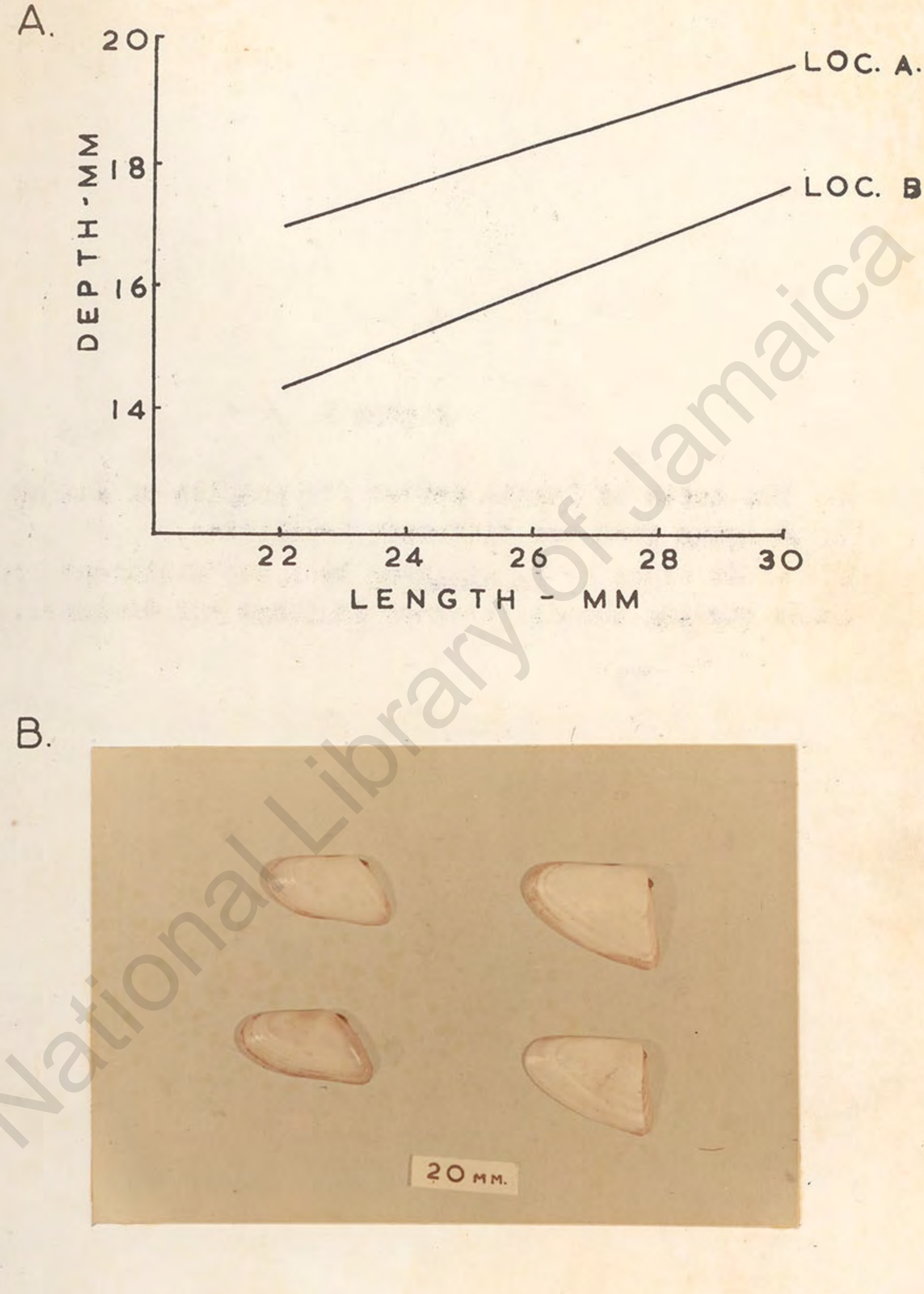

Figure 7

Figure 8

The range and variety of (A) colours, and (B) patterns of shells of <u>D. striatus</u>.

A

B

Figure 8

pale shade of purple.

An enumeration of the differences in the shells of D. denticulatus and D. striatus follows:

D. denticulatus	D. striatus
1. The radial grooves have minute pin-pointed teeth.	1. The radial grooves are smooth.
2. The posterior slope has two curved ridges on each valve which define two distinct areas.	2. The posterior slope has one curved ridge on each valve.
3. There are distinct wavy ridges on the posterior slope.	3. There are no wavy ridges on the posterior slope.
4. There are no radial threads on the posterior slope.	4. The posterior slope has several minute radial threads.
5. The posterior slope is always convex.	5. The posterior slope may be flat, concave, or convex.
6. There is a distinct angled postero-ventral margin.	6. There is no distinct postero-ventral margin.
7. The ventral margin is gently curved.	7. The ventral margin is angled.
8. The length to depth ratio is constant.	8. The length to depth ratio varies appreciably in adult clams.
9. Bright colours and a variety of patterns are common.	9. The colours are pale and there are no radial patterns.
10. The inside of the shell is usually a deep purple.	10. The inside of the shell is never a deep purple.