STUDIES ON THE ANATOMY OF SOME SOUTH AFRICAN MYTILIDAE (BIVALVIA) WITH NOTES ON THEIR ECOLOGY AND DISTRIBUTION.

by

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CONTENTS.

SUMMARY

The classification of the Mytilidae is dependent upon characters which are easily visible even in empty valves and is based on differences in the resilial ridge, the shape and sculpture of the shell and the number and position of the muscle impressions. However, these shell characters can be very misleading, so that the present trend in the study of this family is to obtain as much anatomical data as possible.

The anatomy of some South African Mytilidae is described in this thesis, ~~and~~ particularly ~~includes~~ the hinge teeth, muscle impressions, musculature, nervous innervation of the foot/byssus musculature and the alimentary canal. The species examined are *Perna perna* (Linnaeus) 1758, *Choromytilus meridionalis* (Krauss) 1848, *Aulacomya magellanica* (Chemnitz) 1785, *Septifer bilocularis* (Linnaeus) 1758, *Lamya capensis* (Krauss) 1848, *Musculus virgiliae* Barnard 1964, and *Semimytilus algosus* (Gould) 1850. The investigation has revealed that there is a single basic anatomical plan, which is only slightly modified in the different species.

1. Confirmatory evidence on the evolution of the Bivalvia is shown by the transitional heteromyarian condition of *A. magellanica*. Juvenile specimens are heteromyarian, while adults are monomyarian.

2. The orientation of the byssus retractor musculature is discussed in terms of the particular habitat occupied by the species, especially in relation to water movement and wave action. It is evident that while there may be differences in the positions of the scars on the shell valves, these may only be of functional importance.

3. It would seem that the orientation of the byssus muscles in relation to the resistance to predators is only of secondary importance.

4. Differences in the alimentary canal may involve both specific differences and the secondary effect of muscle position.

5. The anatomy of the oral contractor muscle, present only in <u>C.meridionalis</u>, and its function are described. It appears that this muscle acts as a ~~break~~ brake on the food intake especially in the presence of high concentrations of sand in suspension. It may therefore be one of the factors enabling <u>C.meridionalis</u> to take full ecological advantage of sandy niches.

The distribution of the species is presented and is examined in the light of the subdivision of the South African fauna into four sections, in relation to the hydrographic conditions.

1. The tropical Indo-Pacific species, *Septifer bilocularis* penetrates the South African east coast region to as far as Pt St Johns, and would appear to have a lower limiting distributional temperature of about 17°C. The presence of this species in Natal, confirms that this coast region is subtropical and has associations with the tropical Indo-west Pacific faunas.

2. *Lamya capensis* and *Musculus virgiliae*, two endemic estuarine species, are typical of the warm-temperate regions of the south coast, but extend northwards into the east coast region, so that these species are shared by both coastal regions.

3. *Aulacomya magellanica* and *Choromytilus meridionalis* are the typical species occurring on the cold west coast of South Africa. Since their upper limiting distributional temperature appears to be about 20°C, they are not confined to the west coast alone, but extend eastwards around Cape Point and onto the south coast. The circumpolar association of the South African fauna is exemplified by *A.magellanica*.

4. Although *Perna perna* is recorded from along the whole of the South African coast, it should not be regarded as a species which is common to all three of the coastal regions, but rather as a species common to the warmer waters of the coast. Its lower limiting distributional temperature appears to be about 13°C, but temperatures of less than this have been recorded.

5. There appear~~s~~ to be two areas of overlap between the cold water species, *C.meridionalis* and *A.magellanica*, and the typical warm water species, *P.perna*. These are at Swakopmund/ Luderitz, at the northern limit of the Benguela Current, and along the western end of the south coast region. The temperature in these regions of overlap varies between 13°C and 20°C.

6. Examination of the depth distribution of three species, and the temperatures at these depths, indicates that while temperature may be important in limiting distribution, other factors, such as substratum, may be equally limiting.

7. The effectiveness of Cape Point as a barrier between the cold water west coast fauna and the warm water south coast fauna is commented on.

The variation in size of *A.magellanica* with exposure to wave action is described. It is concluded that with a decrease in the effect of wave action, there is an increase in the size which specimens can attain.

I. INTRODUCTION

Due to reconsiderations of the taxonomy of the family Mytilidae (Lamy, 1936, 1937; Soot-Ryen, 1955) and subsequent revision of the South African genera and species by Barnard (1964), a preliminary investigation was undertaken as an Honours' project, to study the anatomy of three species. The species, Choromytilus meridionalis, Perna perna and Aulacomya magellanica, were formally regarded as belonging to a single genus Mytilus, but were separated into three distinct genera on the basis of shell sculpture, the nature of the resilial ridge and the position and number of the muscle scars (Barnard, 1964). Although this investigation was cursory, it revealed that there is evidence from the internal anatomy to substantiate the "splitting".

The present thesis re-examines that evidence and has been expanded to include:

(i) species of six genera, which were formally regarded as belonging to four genera i.e. Choromytilus meridionalis, Perna perna and Aulacomya magellanica formally all species of the genus Mytilus; Lamya capensis formally Modiola capensis; Musculus virgiliae previously confused with Modiola capensis, but now regarded as a new genus and species (Barnard, 1964); Septifer bilocularis of the genus Septifer.

(ii) a newly recorded genus from South Africa (Barnard, 1964), ~~which~~ that Soot-Ryen (1967; personal communication) suggests is identical with the South American species Semimytilus algosus.

Different positions of the muscle scars must mean that there are differences in the musculature and also possible differences in the structure and arrangement of the other organs. This then is the problem.

The internal anatomy of the South African Mytilidae is poorly known and the purpose of this paper is firstly to elucidate internal structure. Since "splitting" occurs when the knowledge of a family is insufficient, it is hoped that this study will provide further characters for a world revision, together with a basis for the interpretation of evolutionary changes within the family. It may be expected that the number of genera will be reduced.

While collecting the specimens, notes on their ecology and distribution were made. Preliminary work carried out in the Honour's project, on the function of the oral contractor muscle in C.meridionalis has been completed, and is now presented to show the functional importance of this particular muscle.

Although the oldest and probably the ancestoral bivalves e.g. Babinka, are known from the Upper Cambrian (Zeuner, 1958; Cox, 1960), mytiliform species have only been recorded from as far back as the Devonian (Soot-Ryen, 1955). However separation of the family Mytilidae (Devonian) from the related family Modiolopsidae (Ordovician to Devonian) has proved to be indistinct, so that the Mytilidae are considered to be a continuation of some branch of the Modiolopsidae. Cox (1937) holds that the mytilid ancestor was not typically mytiliform and probably resembled the Recent genera Isodala and Dacrydium.

The short synopsis of the characters of the Mytilidae given by Thiele (1934) has been expanded by Soot-Ryen (1955, p.3):

"Shell equivalve, generally very inequilateral with prosogyre umbones near the anterior end; ligament elongate, deep seated, generally with nymphae, the inner resilial part typically connected with the nymphae by a calcified white ridge. Shell showing three areas: (1) the anterior area, the lunule, more or less distinctly circumscribed, often with radiating sculpture and dysodont teeth on the inner margin; (2) the median part, generally glossy and rarely with radiating sculpture; and (3) the posterior part, often strongly sculptured or set off by a different color or by a keel. Shell ordinarily with the interior layer margaritaceous. Periostracum strong, sometimes with hair-like protuberances or with incrustations. Prodissoconch with provinculum, which persists in some smaller species. Mantle lobes united below the anal siphonal opening, branchial opening confluent with the pedal opening, posterior part of mantle edges often pigmented and furnished with papillae. Pallial line simple or with a shallow posterior concavity.

Anterior adductor muscle smaller than the posterior one, sometimes obsolete in adult shells. Anterior byssus retractor small, fastened before or behind the umbones. Posterior retractor is generally confluent with the posterior adductor. Foot finger-shaped with a ventral furrow, byssal gland behind the foot functional in most of the species. Gills filibranch; ventricle embracing the rectum, monoecious. Marine; a few species in brackish or fresh water."

It is desirable to present the characters of each of the genera, as given by Soot-Ryen (1955):

Genus PERNA Retzius 1788

Type-species *Perna magellanica* Retzius 1788

This genus is characterised by the pitted resilial ridge, the anterior position of the foot retractor, and the missing anterior adductor. The shell is more margaritaceous than the other *Mytilus*-like genera.

Genus CHOROMYTILUS Soot-Ryen 1952

Type-species *Mytilus chorus* Molina 1782

The resilial ridge, unlike *Perna*, is compact and the posterior byssus and foot retractors are continuous, though sometimes only narrowly connected. The anterior adductor is absent in adult specimens, but may be seen in young specimens. The byssus is very strong, branching from a central stem. The lunule is bent inwards, forming one central tooth in the right shell valve, corresponding to a groove in the left valve.

Genus AULACOMYA Mörch 1853

Type-species *Mytilus magellanicus* Chemnitz 1785

The outer form of the species is like other mytiliform species and is quite variable. There are usually strong radiating striae over most of the surface, which may be indistinct. The hinge in the left valve consists of a broadly folded and turned up tooth-like lunule, corresponding to a depression in the right one. The nymphae are strong anteriorly and the resilial ridge is compact. The anterior adductor may be present in young specimens but often obsolete or absent in adult forms. The anterior retractor is elongate behind the umbones; the posterior retractors are broadly united with the adductor.

Genus SEPTIFER Recluz 1848

Type-species *Mytilus bilocularis* Linné 1758

The species are mytiliform, with an anteriorly placed deck or septum for the anterior adductor. Marginal crenulations are present along the anterior and posterior ventral margins, and along the dorsal and posterior margins. The radial sculpture is not simply bifurcating, but usually consists of several separate lines arising from one radiating line; posterior part of mantle with small papillae. The posterior adductor embraces the retractors dorsally.

Genus MUSCULUS Röding 1798

Type-species *Mytilus discours* Linné 1767

This genus is characterised by the anterior adductor being placed anterior to the umbones and the posterior retractors being continuous and united with the posterior adductor. The shell is typically radially sculptured in the anterior and posterior part, without radiating sculpture in the middle. The valves are rather flat, without a distinct keel, but the postero-dorsal region is separated from the rest of the valve by a more or less pronounced furrow. The anterior retractor is like Modiolus, but the posterior retractors have a strong, elongated branch fastened along the dorsal margin and a single slender branch fastened above the posterior adductor.

Genus SEMIMYTILUS Soot-Ryen 1955

Type species Mytilus algosus Gould 1850

Shell mytiliform with nearly terminal umbones; lunule small and circumscribed by a fine line; anterior margin without teeth, slightly bent outward and usually constricted to form a rounded anterior margin. Anterior adductor present, posterior adductors and retractors continuous, anterior retractor fastened below the ligament behind the umbo, elongate, narrow, separated in the middle; resilial ridge compact. Pallial margin with groups of papillae.

The diagnosis of the genus Lamya is taken from Soot-Ryen (1958):

Genus LAMYA Soot-Ryen 1958

Type-species *Modiola capensis* Krauss 1848

Shell thin, modioliform, with broadly rounded lunule. Resilial ridge compact, ligament deep set, not visible dorsally, a few crenulations behind the ligament and an elongate, tooth-like callus beneath the umbo. Interior nacreous with darker colour markings. Anterior adductor large, posterior adductor relatively small and confluent with the narrow, band-like posterior retractors. Anterior retractor round, fastened in the umbonal cavity. Branchial opening with thickened mantle margins furnished with large, flat papillae placed vertically on the margin with smaller papillae in between. Gonads lateral in the mantle.

As can be seen, the classification of the family is dependent upon characters which are easily visible, even in empty valves i.e. differences in the resilial ridge, the shape and sculpture of the shell and the positioning of the muscle scars. However, disagreement exists as to which characters are significant.

Jukes-Browne (1905) considers that the position of the umbones and surface sculpturing are of secondary importance in the classification of the Mytilidae, while hinge characters and muscle impression position are of more value.

Wilson (1967; personal communication) is of the opinion that shell characters can be very misleading as taxonomic characters, and has pointed out (1966, p.6) that the musculature "may be convergent, as based on recent studies." He is therefore collecting as much anatomical data as possible, for the purposes of making a world-wide revision of the family. As has been mentioned above, it is hoped that this study will provide further characters of taxonomic significance for the world revision and form a basis for the interpretation of evolutionary changes within the family.

II. MATERIAL

The following species were examined during the course of this paper:

Choromytilus meridionalis (Krauss) 1848

Numerous specimens of both preserved and living material, from Pt Nolloth on the west coast to Plettenberg Bay on the south coast, were examined. Dissections were made on about 50 of these, and the drawings and descriptions are the composite results of these dissections. Empty valves in the collection of the South African Museum were also checked. The size of the specimens varied between 30 mms and 100 mms. Juvenile specimens (8 mms - 40mms) were examined.

Perna perna (Linn.) 1758

About 200 specimens were examined, and detailed dissections were done on about 50 of these, including 12 large specimens from Mossamedes (85 mms to 140 mms total length), and 10 small specimens from Inhaca Is (55 mms average total length). The remaining specimens were collected from various localities between ~~ranged from~~ Llandudno, on the Cape Peninsula west coast, to Uvongo, on the Natal east coast. Their size varied between 40 mms and 90 mms (total length). Both living and preserved material, and also juveniles were examined.

Aulacomya magellanica (Chemnitz) 1785

2255 specimens were collected at the Breakwater in Table Bay and were measured; about 20 of these were dissected. About

30 other specimens, living and preserved, were also dissected. These specimens varied in size between 30 mms and 100 mms (total length), and came from west coast localities (Kommetjie to St Helena Bay). Juvenile material from the Breakwater was also examined.

Septifer bilocularis (Linn.) 1758

Preserved material from Santa Carolina Is, Mozambique (35 mms to 55 mms total length) and the Natal coast (30 mms average total length) was examined. About 15 specimens were dissected in detail. Empty valves in the South African Museum collection were also examined.

Lamya capensis (Krauss) 1848

Preserved and living material from the Knysna Lagoon (15 mms to 30 mms total length) was examined. Detailed dissections were made on about 30 of these. A single, preserved, 'giant' specimen (total length 62 mms), taken at Still Bay, was also dissected. Unfortunately further material of these 'giant' specimens was not obtained (c.f. Soot-Ryen, 1958). Empty valves in the South African Museum collection were examined.

Musculus virgiliae Barnard 1964

Material was collected in the Knysna Lagoon and in the Keurbooms River. Specimens varied in size between 15 mms and 30 mms (total length). About 20 of these were dissected in detail. Empty valves were also examined.

Semimytilus algosus (Gould) 1850

Only preserved material was available. This was collected at Cape Cross, South West Africa, and varied in size from 10 mms to 25 mms (total length). Of the 14 specimens available, 8 were dissected. Empty valves sent to Soot-Ryen were compared with specimens of *S.algosus* from the west coast of South America and found to be identical.

III. DISTRIBUTION

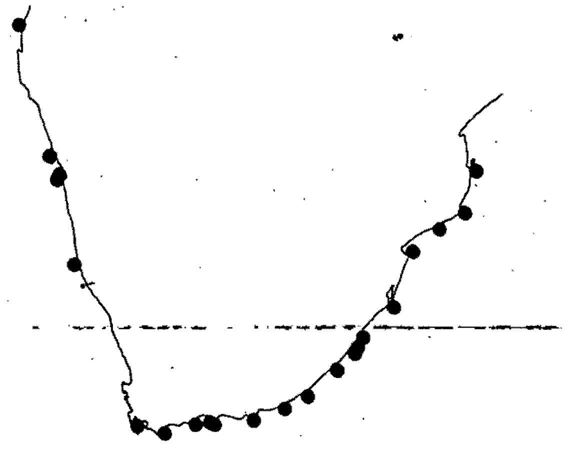
During the period January, 1966 to March, 1967, collecting trips were made between Hondeklip Bay and Pt Elizabeth. One species, *Septifer bilocularis*, was obtained from Santa Carolina Island, Mozambique, and the Natal coast. Numerous specimens were collected in South West Africa and Angola by Dr. M.L.Penrith (South African Museum), during an intertidal fish survey.

The work done on the ecology of intertidal rocks around the South African coast by the Zoology Department of the University of Cape Town, under Professor T.A. ~~Stevenson~~ Stephenson, during the period 1931 - 1940, forms the basis of comparison for any group of intertidal animals. During the course of this survey, eight localities between Pt Nolloth and Durban were studied in detail, while observations were made at thirty-one other localities, from north of Pt Nolloth to Umpangazi. Unpublished records of this Department have also been made available to the author.

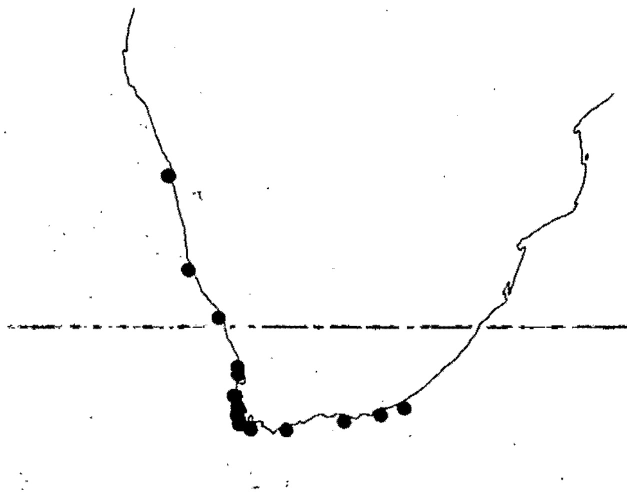
Figures 1 and 2 summarise the distribution of the species dealt with in this paper.

FIGURE 1

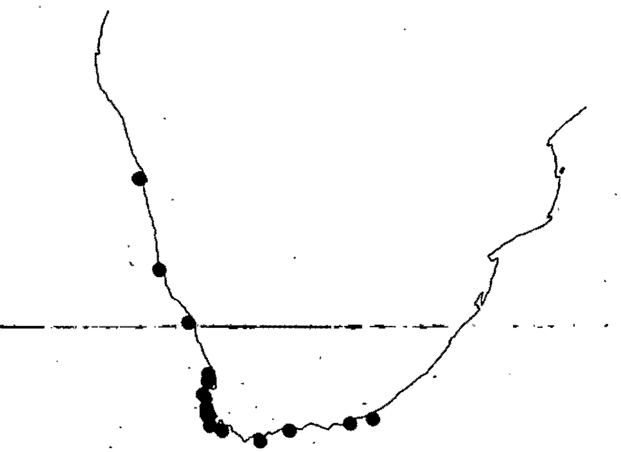
Perna perna (Linnaeus), *Choromytilus meridionalis* (Krauss), *Aulacomya magellanica* (Chemnitz), *Lamya capensis* (Krauss), *Musculus virgiliae* Barnard, *Septifer bilocularis* (Linnaeus) and *Semimytilus algosus* (Gould). Distribution from various sources.



P. perna

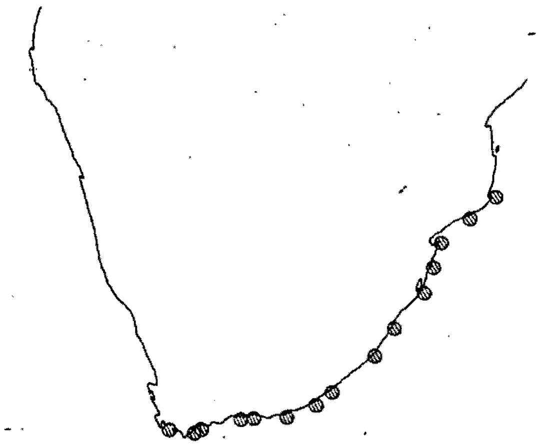


C.meridionalis



A. magellanica

S. bilocularis



L. capensis

M. virgiliae

Discussion on Distribution

Although accessory factors, such as phosphate and nitrate concentrations, may play a part in the distribution of intertidal animals (Ekman, 1953), ~~Stevenson~~ Stephenson (1939) regarded that the important factor was that of temperature. Temperature seems to be one of the limiting factors in the distribution of mytilids, although this group of molluscs has a wide tolerance range. Henderson (1929) has found that the upper lethal temperature for *Mytilus edulis* is 40.8°C, while the lower lethal temperature is below 0°C (Dodgson, 1928; Kanwisher, 1955). However, it seems that the duration of the particular temperature is the basic criterion, since Bruce (1926) has shown that *M.edulis* cannot live for more than 1 hour at 30°C. Also, severe winters have resulted in the mass mortality of mussel populations. Day (1967; personal communication) informs me that on the North Carolina coast, *M.edulis* is present in winter (winter temperature 9°C), but die in summer (summer temperature 27 -°C). Hence Hutchings (1947) and Stubbings (1954) have reported that the southern limit of *M.edulis* coincides with the 27°C isotherm, while the northern limit partly coincides with the 10°C isotherm.

Salinity seems to be of little importance; although marine mytilids cannot tolerate fresh water, some are able to live in water in which the salinity is greatly reduced. Motwani (1955) has shown that the lower limit for *M.edulis* lies between

12.65 ‰ and 15.00 ‰ and Dodgson (1920) that the upper limit is at 62.0 ‰.

On the basis of the survey work on the South African intertidal fauna and flora, ~~Stevenson~~ Stephenson (1944) divided the coast into three main regions, whose limits were found to lie in areas of overlap, rather than at particular topographical boundries. These regions were:

(a) The west coast, from Pt Nolloth (or north of Pt Nolloth) to Cape Point; that part of the coast influenced by the cold Benguela Current.

(b) the south coast, from Cape Agulhas to Pt Elizabeth

(c) the east coast, from the Bashee River mouth to Umpangazi (or north of Umpangazi); that part of the coast influenced by the warm Agulhas Current.

and the overlaps:

(i) the western overlap, from Cape Point to Cape Agulhas

(ii) the eastern overlap, from Pt Elizabeth to the Bashee River mouth.

The cold Benguela Current runs in a north-westerly direction along the west coast of South Africa and South West Africa, and is the result of upwelling of cold water (9° - 11°C) (Clowes, 1950) from a depth of 200 - 300 metres (Currie and Hart, 1960). As the water moves away from the coast, it is warmed by solar radiation, so that the temperatures are usually lowest inshore (Gilchrist, 1902; Buys, 1957). The shore temperatures

Table 1: Surface temperatures of sea water for localities on the South African coast (after Isaac, 1937 (a))

Locality	Mean annual temp (°C)	Max. temp (°C), month	Min. temp (°C), month
Walvis Bay	16.1	18.4 (Jan)	13.4 (July)
Saldanha Bay	14.8	18.2 (Feb)	11.8 (July)
Cape Town Pier	12.8	13.6 (Jan, Apr, Dec)	12.4 (Sept)
Muizenberg	16.6	19.6 (Dec)	13.2 (June)
Simon's Bay	15.3	18.4 (Jan)	13.4 (July)
Hermanus	14.6	17.1 (Jan)	13.4 (Mar, July, Sept)
Danger Point	15.6	17.1 (Jan)	14.5 (July, Aug, Sept)
Cape Agulhas	17.7	20.9 (Jan)	13.9 (July)
Struys Bay	17.4	20.9 (Feb)	13.8 (July)
Knysna Heads	16.8	19.9 (Feb)	13.5 (Aug)
Cape St Francis	17.3	19.7 (Jan)	14.8 (Sept)
Bird Island	18.2	20.9 (Jan)	15.9 (Aug)
East London	17.6	19.2 (Jan)	15.7 (Sept)
Pt St Johns	19.3	21.0 (Jan)	16.8 (July)
Durban	21.8	24.7 (Feb)	19.3 (Aug)

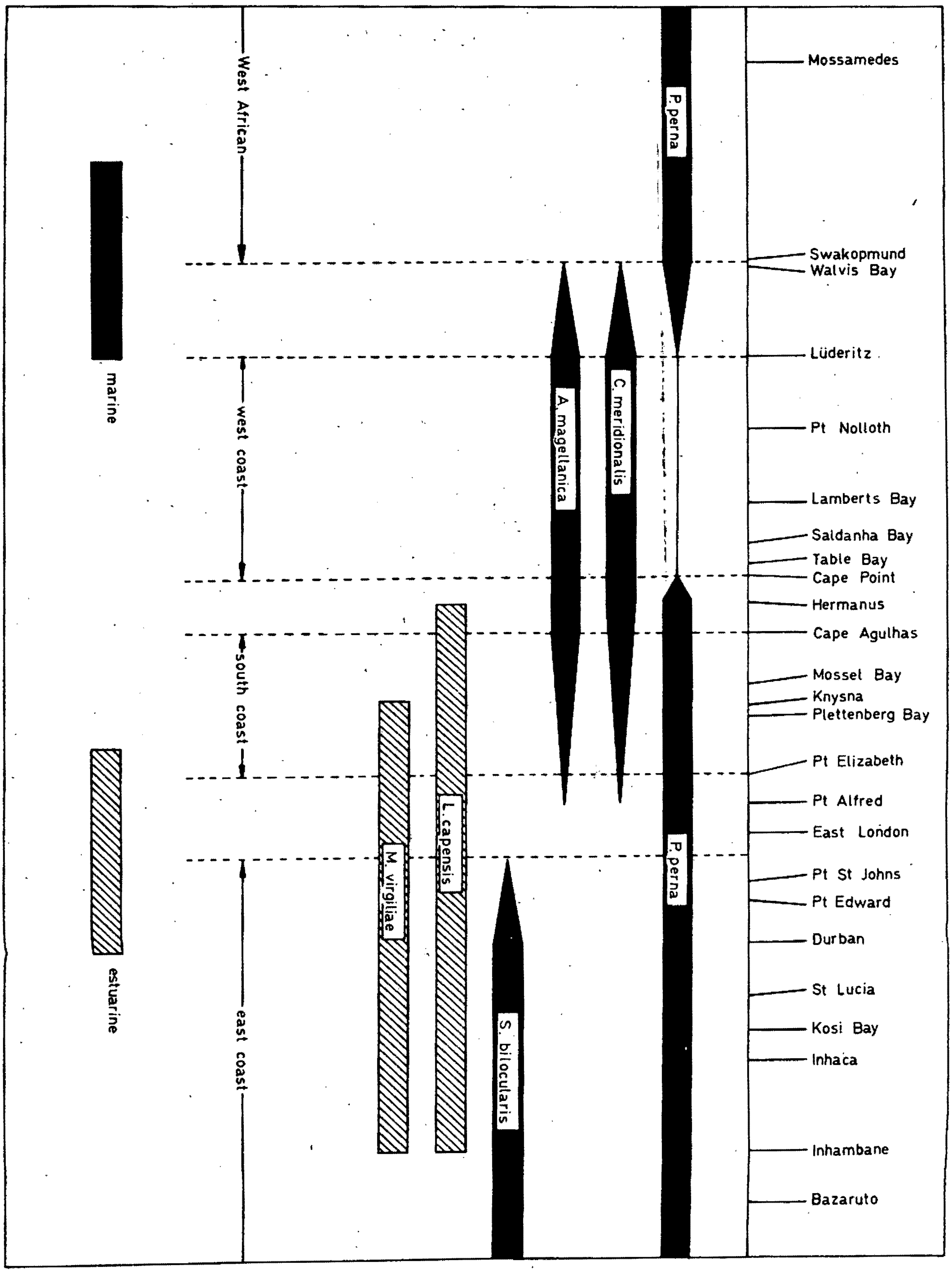
vary between 10°C and 16°C from Cape Point to Walvis Bay (Table 1).

Stephenson ~~Stevenson~~ *et al* (1936) have pointed out the similarity in temperature at Table Bay and Walvis Bay (Table 1), which is evidence that the effect of the Benguela Current is still felt in the tropics of the west coast. Higher summer temperatures at Walvis Bay can be accounted for by insolation. There is a slight fall off in temperature northwards from Cape Point (Isaac, 1937 (b)), and a minimal region in the area Hondeklip Bay to Pt Nolloth. Saldanha Bay experiences unusually high temperatures in summer (Table 1), and should not be regarded as typically west coast (Stephenson ~~Stevenson~~, 1939).

The Agulhas Current, which flows southwards along the east coasts of Mozambique and South Africa, is characterised by its high temperature and low salinity. This current may or may not be strengthened by the Mozambique Current (Menaché, 1961). The Agulhas Current flows as a bore inshore, but between Pt St Johns and East London, it moves off-shore, with a resulting decrease in shore temperature (Table 1). From East London to Pt Elizabeth, the effect of the Agulhas Current is still felt, the temperatures rarely dropping below 15°C, while temperatures of more than 20°C are experienced (Table 1). Colder temperatures may be experienced due to local upwelling (Mallory, 1961), especially in the Pt Elizabeth to Mossel Bay region. In the vacinity of Cape Agulhas, the current is deflected to the south and south-east (Orren, 1963). The lower temperatures experienced

FIGURE 2

Distribution of Mytilidae around the southern African coast, showing the division into east coast (warm water), south coast, west coast (cold water) and West African (warm water) regions.


Mossamedes
Swakopmund
Walvis Bay
Lüderitz
Pt Nolloth
Lamberts Bay
Saldanha Bay
Table Bay
Cape Point
Hermanus
Cape Agulhas
Mossel Bay
Knysna
Plettenberg Bay
Pt Elizabeth
Pt Alfred
East London
Pt St Johns
Pt Edward
Durban
St Lucia
Kosi Bay
Inhaca
Inhambane
Bazaruto
West African
west coast
south coast
east coast
marine
estuarine
P. perna
A. magellanica
C. meridionalis
L. capensis
M. virgiliae
S. bilocularis

at Hermanus and Danger Point are probably the result of local upwelling. Higher temperatures are found in False Bay (Table 1), where the hydrographic conditions are more complex, and warm water tends to pile up at the north-eastern corner of the Bay (Atkins, 1965).

The distribution of the species dealt with in this paper is summarised in figures 1 and 2.

On the basis of his subdivision of the intertidal region of the South African coast, Stephenson (1948) recognised that the fauna could be divided into four 'sections': the subtropical population of Natal; the warm-temperate fauna of the south coast; the cold-temperate population of the west coast. Each of these sections comprised endemic forms and species which it shared with adjacent faunal sections. The fourth consisted of a few species which occurred around the whole of the South African coast.

It must be pointed out that only three of the species examined in this paper are endemic to the southern African coast; Swakopmund and Inhambane being taken as the limits. The species are *Choromytilus meridionalis*, *Lamya capensis* and *Musculus virgiliae*.

Perna perna occurs on the Atlantic coast of South America (Soot-Ryen, 1955), where it is associated with the warm water of the Brazil Current. The species has been recorded from North and West Africa (Algeria, Senegal, Dakar, Gambia, Angola : Lamy, 1936; Ghana : Bassindale, 1961), and this West African warm-water population extends southwards along the African coast to Lüderitz (fig 2). *P.perna* is also known from the Red Sea and Aden (Lamy, 1936), and this East African warm-water population extends southwards along the east coast of Africa to ~~approximately~~ Cape Point. The species has been recorded west of Cape Point, along that part of the coast influenced by the cold Benguela Current, at Platboompunt, Yzerfontein and Saldanha Bay (University of Cape Town). I have taken five specimens (60 mms average total length) at Llandudno, although this species was not recorded here by Stevenson. However the specimens are occasional, isolated and usually occur high up the shore, in the upper Balanoid zone.

The largest specimens were taken at Swakopmund, while specimens further north at Mossamedes and those from the South African east coast were ~~far~~ smaller by comparison. It is suggested that optimum conditions for growth are afforded by the warm South Equatorial Water and the plankton-rich Benguela Water.

Although *P.perna* is recorded from along the whole of the southern African coast, it has an interrupted ~~isolated~~ distribution along the west coast, as has been pointed out above. It should therefore not be regarded as a species which is common to all three of the coast regions, but rather as a species common to the warmer waters of the coast. This is further supported by the fact that a gradation is seen along the south coast. At Plettenberg Bay, towards the eastern limit of the south coast, *P.perna* greatly outnumbers *C.meridionalis* and *A.magellanica*, while in False Bay, specimens of *C.meridionalis* and *A.magellanica* outnumber those of *P.perna*.

Choromytilus meridionalis is a cold water species, with its western limit at Walvis Bay (fig 2). Although Lamy (1936) gives Beira as the eastern limit, and Bartsch (1915) has recorded the species from Natal, no reliance can be placed on these records. Macnae and Kalk (1958) and Boshoff (1967) have never recorded *C.meridionalis* from Inhaca Island, and the University of Cape Town has never found the species alive east of the Breede River mouth. However Krauss (1848) has given Elim (Bredasdorp District) as a locality, and I have found the species in abundance at Plettenberg Bay (Look-out Beach rocks). Barnard (1964) suggests that Pt Alfred is the extreme easterly limit.

Known also from the Straits of Magellan, Falkland Is and Kerguelen (Barnard, 1964), *Aulacomya magellanica* has a similar distribution to *C.meridionalis*, with a western limit at Swakopmund/Walvis Bay and an eastern limit at Pt Alfred (fig 2). The species has been recorded once from Natal (Sowerby, 1892), but has never been found in this region by the University of Cape Town.

While *P.perna* can be regarded as the typical species from warm waters, *C.meridionalis* and *A.magellanica* are the typical species occurring on the west coast.

However, *C.meridionalis*, the endemic species of the west coast, is not confined to that region alone, but extends eastwards around Cape Point and onto the south coast region. As has been pointed out above, there is a decrease in numbers eastwards from Cape Point.

A similar situation is found with *A.magellanica*. It is typically west coast, but extends onto the south coast. Its presence in the Falkland Is and Kerguelen, lends support to Ekman's (1953) idea of the circumpolar association of the South African fauna.

It is interesting to note the existence of an overlap area along the region of the coast between Swakopmund and Lüderitz. This overlap separates the cold-water west coast species from the tropical West African species. The overlap is short and coincides with the northern limit of the Benguela Current.

Septifer bilocularis, which has been recorded from Japan, Manilla, New Caledonia, Molacca, Seychelles, Zanzibar and Madagascar (Lamy, 1936), penetrates the South African coast region, to as far as Pt St Johns (fig 2). Although a single living specimen has been taken at Pt Elizabeth, it is unlikely that the species extends as far south as this.

The occurrence of *S.bilocularis* on the Mozambique and

Natal coasts, endorses Stephenson's ~~Stevenson's~~ statement (1948) that the fauna of the east coast is subtropical, and that it has associations with the tropical Indo-west Pacific faunas. The southerly limit of this species corresponds with Stephenson ~~Stevenson's~~ limit of the east coast.

The two estuarine species, *Lamya capensis* and *Musculus virgiliae*, are of east coast/south coast, warm water distribution. *M.virgiliae* extends from the Great Brak River in the south, to Lagoa Poelela, near Inhambane in Mozambique, in the north. *L.capensis* has its southern limit at Hermanus. Although Bartsch (1915) has recorded the species from False Bay, and the University of Cape Town have obtained it in dredge samples from False Bay, transportation of the species from some other locality seems the likely explanation, since the species is estuarine and has never been found at the Muizenberg Vlei estuary. It has been recorded as far north as Lagoa Poelela.

L.capensis and *M.virgiliae*, both endemic species, are therefore present on both the south and east coasts. These species may be regarded as temperate forms from the south coast, which extend onto the east coast i.e. the species are shared by both coastal regions (c.f. Stephenson ~~Stevenson~~, 1948).

It would seem therefore, that temperature plays an important part in the distribution of the South African mytilids, and comparison of Table 1 with figure 2 would suggest that *P.perna* has a lower limiting temperature of about 13°C, while

Table 2: The maximum depths (metres) and temperatures (°C) at those depths at which species have been obtained by dredging operations of the University of Cape Town.

Species	Region	Depth	Temp (°C)	
		(metres)	Max	Min
Perna perna	south coast	38	16.0	10.2
	False Bay	44	16.0	14.1
	west coast	INTERTIDAL ONLY		
Aulacomya magellanica	south coast	INTERTIDAL ONLY		
	False Bay	56	14.6	13.1
	west coast	62	8.9	
	S.W.A.	35	16.7	
Choromytilus meridionalis	south coast	INTERTIDAL ONLY		
	False Bay	42	15.8	13.0
	west coast	141	8.7	8.4
	S.W.A.	40	13.8	

C.meridionalis and *A.magellanica* have an upper limiting temperature of about 20°C. The regions of overlap are in those localities with a temperature range between 13°C and 20°C. The tropical species, *S.bilocularis*, would seem to have a lower limiting distributional temperature of about 17°C. As yet, no experiments have been carried out to determine the average lethal temperatures of the South African species.

Certain species have been obtained during experimental dredging, carried out by the Zoology Department of the University of Cape Town. Table 2 represents the maximum depths at which these species were encountered. The maximum and minimum temperatures at those depths are also shown, but in some cases, these consist of a single recording only.

Two points of interest arise from this: firstly, the shore range of the three species is more extensive than previously thought. Morgans (1958) has recorded maximum depths of 0.5 metres (below the datum line) for *P.perna* and 5.0 metres for *A.magellanica* in False Bay. Table 2 shows that both *P.perna* and *A.magellanica* can live at much greater depths, since they have been taken at 44 metres and 62 metres respectively. It would appear that the depth range for *C.meridionalis* is even greater, as the species has been taken at 141 metres.

Secondly, a minimum temperature of 10.2°C is recorded for *P.perna*, which is well below the proposed limiting distributional temperature of 13°C.

These facts indicate that while temperature may be important, other factors, such as the nature of the substratum, may be equally limiting on distribution.

~~Stevensen~~ Stephenson (1948), in his final assessment of the South African region, suggests that Cape Point marks an important (? temperature) barrier between west coast and east/south coast populations. In the light of the above discussion, some doubt is cast on this statement and the effectiveness of such a barrier, for *A.magellanica* and *C.meridionalis*, both typically west coast species, extend around Cape Point and occur over the whole south coast region (fig 2). Further *P.perna* can and does occur on the west coast.

Semimytilus algosus has only been recorded in South West Africa from one locality, at Cape Cross, which falls within the latitudinal distributional belt of the species on the west coast of South America (Soot-Ryen, 1955 : fig 16).

IV. GROSS ANATOMY

A. Hinge Teeth

Dentition of the shells in the Mytilidae is variable (Jukes-Browne, 1905), since the dysodont teeth arise as terminations of the internal ribs. The cardinal teeth are small or obsolete. The teeth are covered by the periostracum (White, 1937), which is continuous dorsally from one valve to the other, and are so arranged that the teeth of one valve fit into the sockets of the other.

According to Trueman (1964), the hinge teeth, or denticulations, are not pivotal structures, but a mechanism which ensures the correct alignment of the valves, when the shell is opened or closed. He points out that their functional morphology is unknown. However the structure of the region in front of the umbo, and the hinge teeth, are of taxonomic value in some Mytilidae. This applies especially in modioliform species, and both Soot-Ryen (1955) and Barnard (1964) have used these characters for the purposes of classification. Barnard (1964) has given descriptions and some figures for the South African Mytilidae, but for the sake of completeness, they are again figured and described in this paper.

P.perna, C.meridionalis and A.magellanica

In these typically mytiliform species, the structure of the hinge teeth is simple but variable. In *P.perna* and

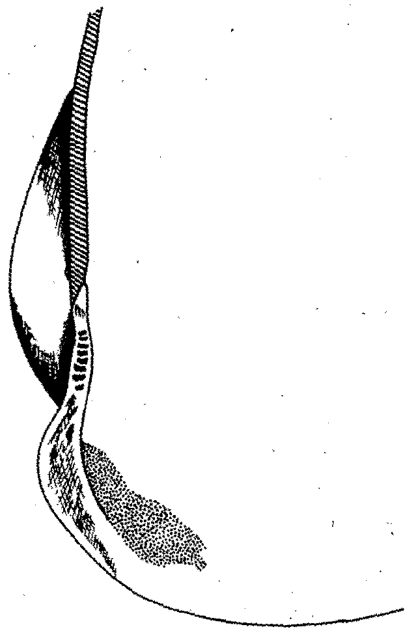
<u>FIGURE 3</u>

The anterior region of the right shell valve, showing the hinge teeth and the muscle scars (stippled).

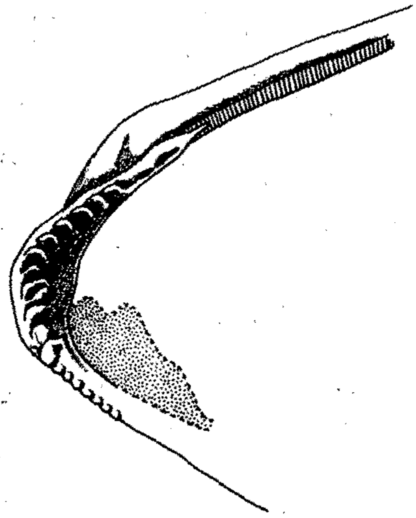
A. *Lamya capensis*

B. *Musculus virgiliae*

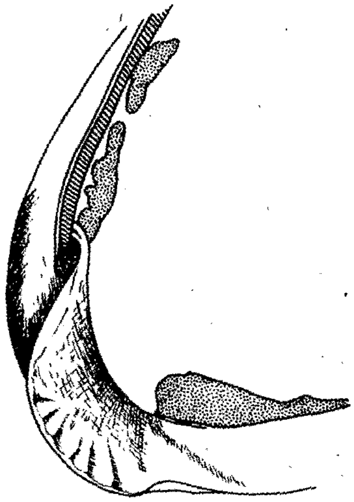
C. *Semimytilus algosus*



A



B



C

C.meridionalis, there are two teeth in the left valve and one in the right, or vise versa. In C.meridionalis, there are occasionally two teeth in each valve. The teeth are less complex in A.magellanica, where a tooth-like projection in the one valve fits into a groove in the other.

S.algosus (fig 3 C)

The anterior region of the shell protrudes slightly in front and there are no teeth.

S.bilocularis

There is an anteriorly-placed septum in each of the valves, the margin of which may be evenly curved, or may have a slight notch. The anteriorly placed umbones are strongly twisted, with the lunule bent inwards. This is furnished with a number of radiating furrows, forming the teeth. The number of teeth is variable in each valve.

L.capensis (fig 3 A)

The anterior region of the shell is expanded in front of the umbo, but is without teeth. There is a slight denticulate callus below the umbo.

M.virgiliae (fig 3 B)

The anterior margin of the shell is expanded in front of the umbo and possesses teeth. Barnard (1964) states that the number varies from 6 to 8, but specimens have been examined in which the number is 12. Some of the teeth are larger than others, but there is no definite plan to this. The teeth in the one valve fit into the depressions between the teeth in the other.

B. Muscle Impressions

The impressions, or scars, on the inner surfaces of the shell valves are caused by the insertions of the adductor, pedal retractor and byssus retractor muscles. In these regions, the external epithelium of the mantle undergoes differentiation (Franc, 1960), to bring about attachment by the secretion of hypostracum and by the specialisation of epithelial fibres, which form linking tissue between the muscular fibres and the hypostracum (Brück, 1914).

In some species, the impressions are smooth and can only be recognised by a difference in colour, but in others, the impressions become pitted and crenulate, so that their surface texture is markedly different from the rest of the inner surface of the valve. The scars usually occur as slight depressions in the valves, due to the absence of a nacreous layer in those areas, but in some species, notably S.bilocularis, the shell is thicker and somewhat elevated in the scar regions.

1. Anterior adductor muscle impression

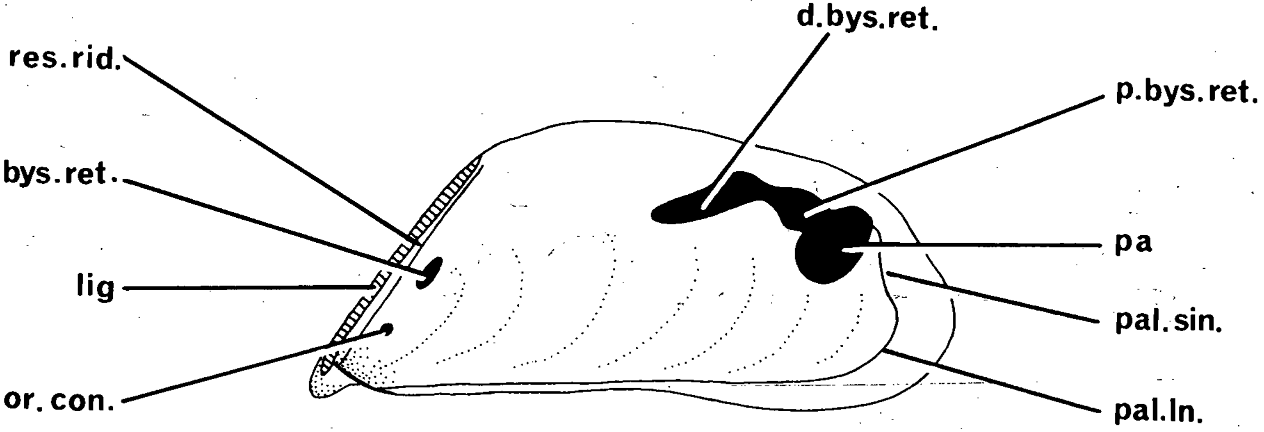
C.meridionalis and P.perna

Although this is stated as probably being present in

FIGURE 4

The left shell valve of *C.meridionalis* (upper) and *P.perna* (lower) showing the positions of the muscle impressions.

res. rid. - resilial ridge; lig - ligament; pal. sin. - pallial sinus; pal. ln. - pallial line; a. bys. ret. - anterior byssus retractor muscle impression; d. bys. ret. - dorsal byssus retractor muscle impression; p. bys. ret. - posterior byssus retractor muscle impression; or. con. - oral contractor muscle impression; pa - posterior adductor.


d.bys.ret.
res.rid.
p.bys.ret.
a.bys.ret.
pa
lig
pal.sin.
or.con.
pal.ln.

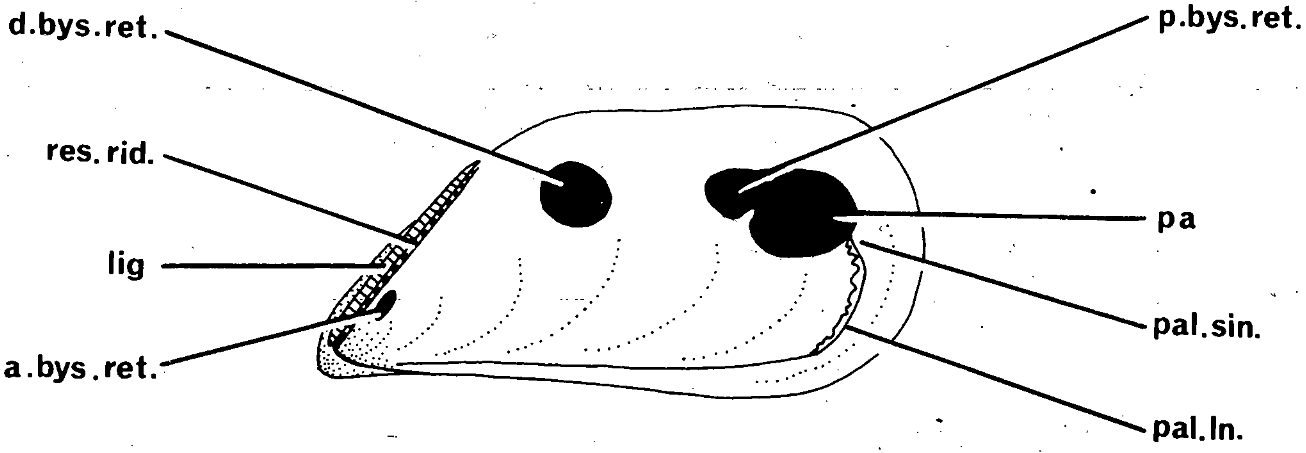

d.bys.ret.
p.bys.ret.
res.rid.
pa
lig
pal.sin.
a.bys.ret.
pal.ln.

FIGURE 5

The left shell valve of *A.magellanica*, showing the position of the muscle impressions, and the position of the anterior adductor scar, present in juvenile specimens.

lig. - ligement; res. rid. - resilial ridge; pal. ln. - pallial line; a a - anterior adductor; p a - posterior adductor; a. bys. ret. - anterior byssus retractor muscle impression; d. bys. ret. - dorsal byssus retractor muscle impression; p. bys. ret. - posterior byssus retractor muscle impression.

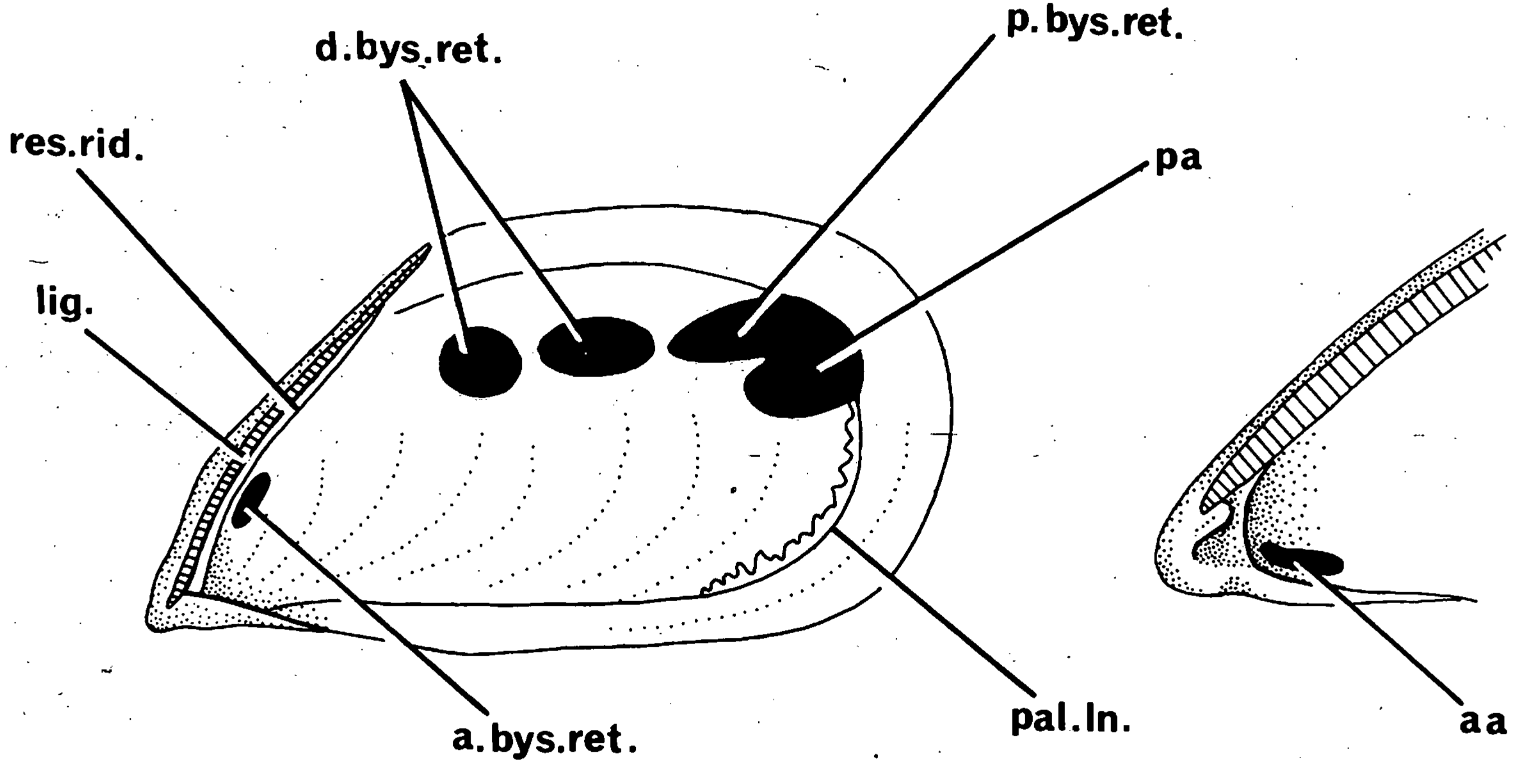
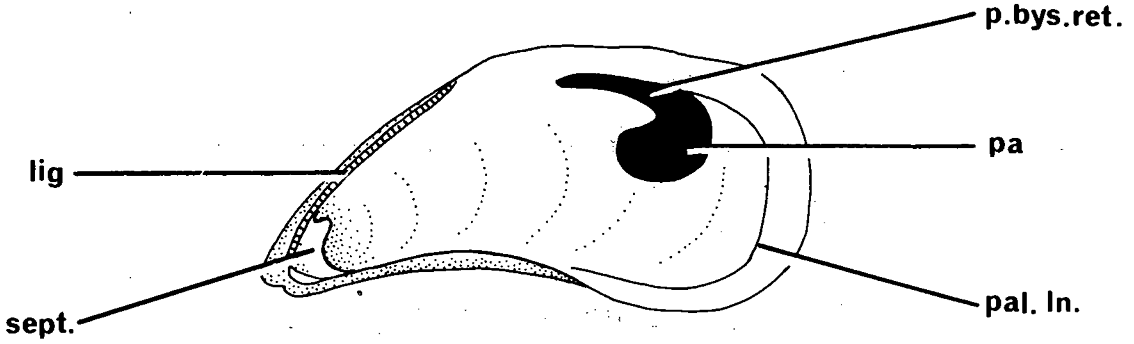

d.bys.ret.
p. bys.ret.
res.rid.
pa
lig.
a. bys.ret.
pal.ln.
aa

FIGURE 6

The left shell valve of S.bilocularis (upper) and S.algosus (lower) showing the position of the muscle impressions.

lig - ligament; sept. - septum; pal. sin. - pallial sinus; pal. ln. - pallial line; a a - anterior adductor; p a - posterior adductor; a. bys. ret. - anterior byssus retractor muscle impression; p. bys. ret. - posterior byssus retractor muscle impression.


p.bys.ret.
pa
lig
sept.
pal. ln.

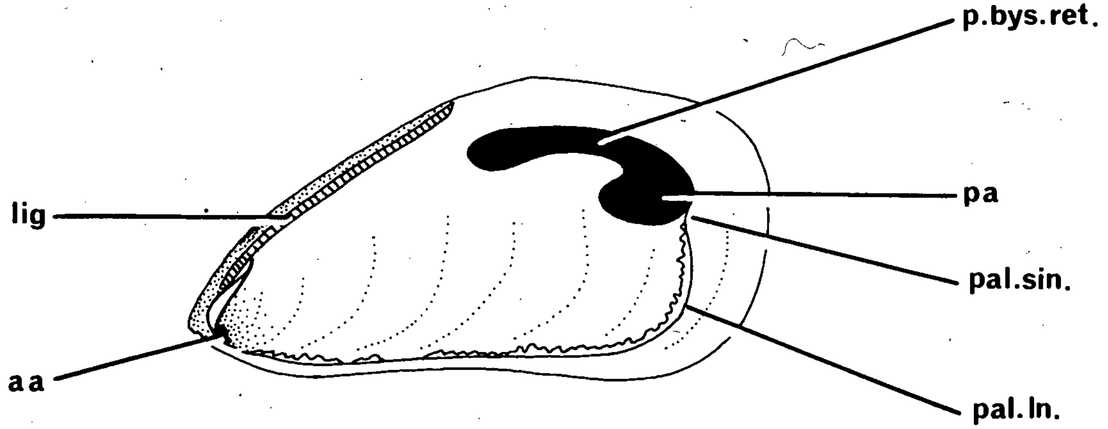

p.bys.ret.
pa
lig
pal.sin.
aa
pal.ln.

FIGURE 7

The left shell valve of *L.capensis*, showing the positions of the muscle impressions.

u - umbo; pal. sin. - pallial sinus; pal. ln. - pallial line;

a a - anterior adductor; p a - posterior adductor;

a. bys. ret. - anterior byssus retractor muscle impression;

p. bys. ret. - posterior byssus retractor muscle impression.

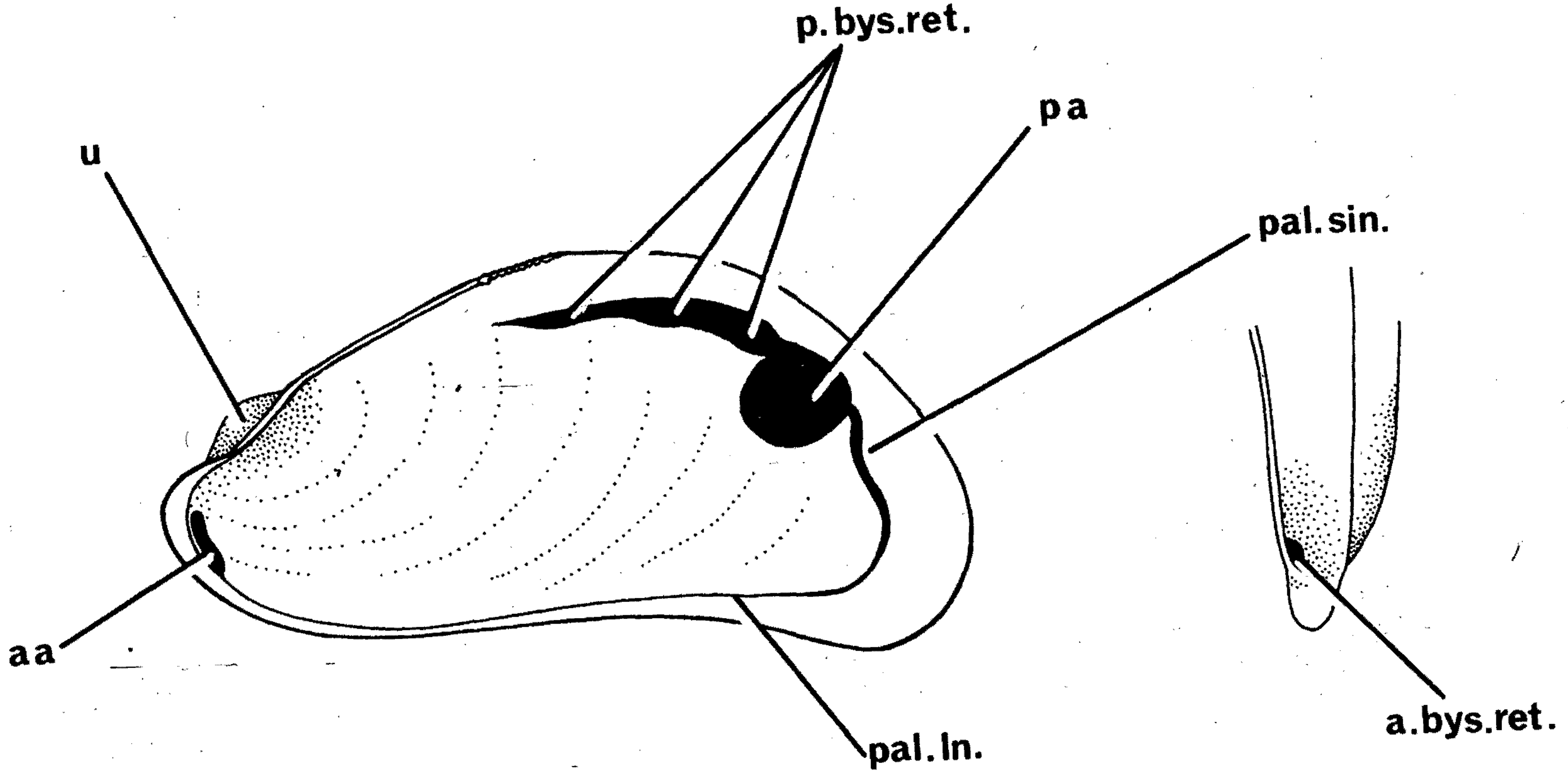
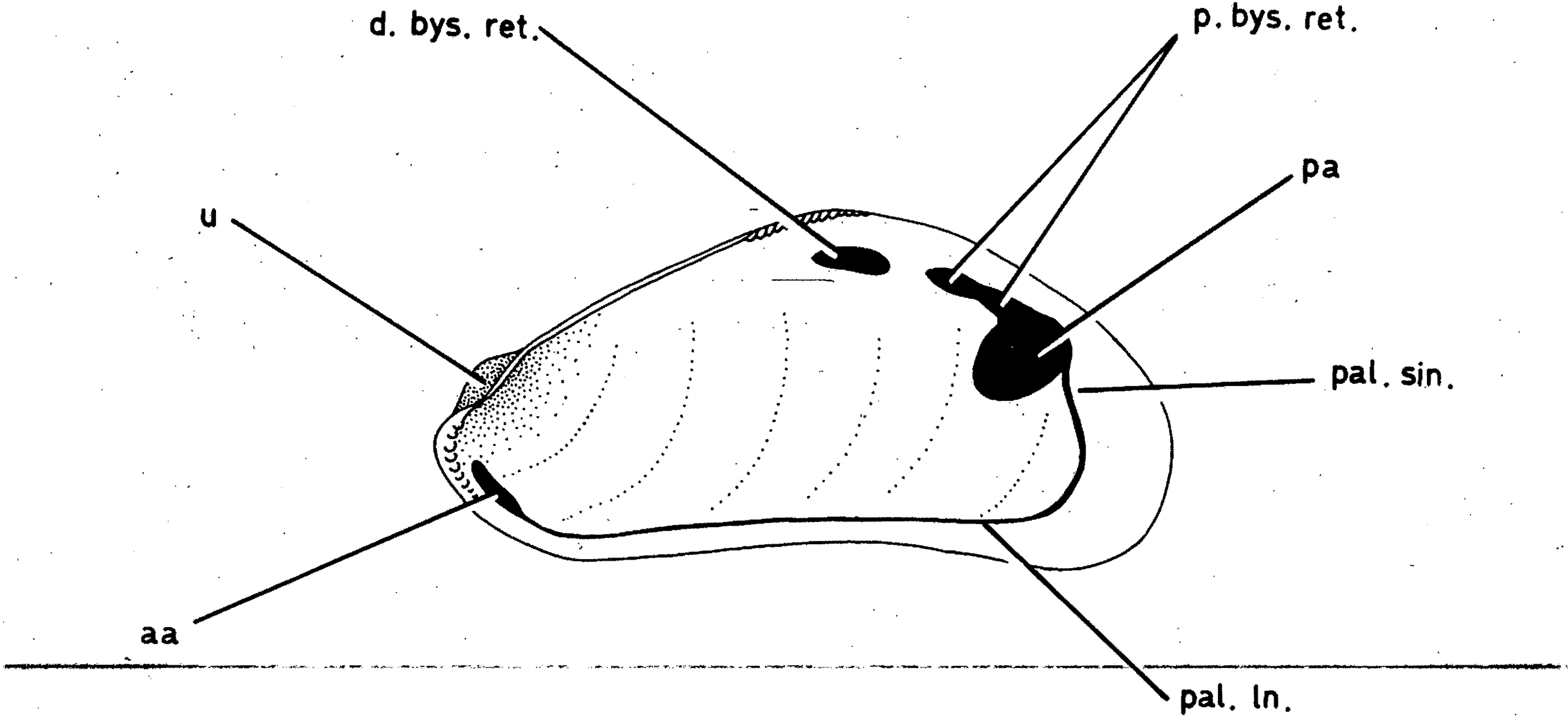

p. bys.ret.
u
p a
pal. sin.
a a
pal. ln.
a.bys.ret.

FIGURE 8

The left shell valve of *M.virgiliae*, showing the positions of the muscle impressions.

u - umbo; pal. ln. pallial line; pal. sin. - pallial sinus; a a - anterior adductor; p a - posterior adductor; d. bys. ret. - dorsal byssus retractor muscle impression; p. bys. ret. - posterior byssus retractor muscle impression.


d. bys. ret.
p. bys. ret.
pa
u
pal. sin.
aa
pal. ln.

juvenile specimens of C.meridionalis (Barnard, 1964), the anterior adductor muscle impression was found to be absent in several hundreds of specimens examined. The scar was also absent from all stages of P.perna.

A.magellanica (fig 5)

The scar is found in juvenile specimens of A.magellanica, where it occurs as an oval scar at the anterior ventral margin of the shell, just behind the terminal umbo. Its longest axis is antero-posteriorly directed. The anterior adductor muscle impression is absent in all adult specimens.

S.algosus (fig 6)

A similar position for the anterior adductor scar occurs in S.algosus. The scar is situated at the anterior ventral margin of the shell valve, but it is more circular than that of A.magellanica.

L.capensis and M.virgilisae (fig 7 & 8)

The scar in these two species is situated in front of the subterminal umbo, about midway between the umbo and the ventral margin in L.capensis, but nearer the ventral margin in M.virgilisae. The scar is oval in shape, with its greatest axis in an almost dorso-ventral direction.

S.bilocularis (fig 6)

The anterior adductor muscle has no impression on the shell valve in S.bilocularis, for the muscle is reduced (Pelseneer, 1911) and does not insert on the shell itself. It inserts on the anteriorly placed deck or septum. The septum is not unlike the thick elevated adductor scar of Hormomya (Soot-Ryen, 1955). Specimens occur in which the margin of the septum is evenly curved, others in which there is a slight notch (Barnard, 1964).

2. Anterior byssus retractor muscle impression

L.capensis and M.virgiliae (fig 7 & 8)

In the species with a subterminal umbo (L.capensis and M.virgiliae), the anterior byssus retractor muscle impression is situated at the apex of the umbo. The scar is circular in shape. In species with a terminal umbo, the scar is always found behind the umbo and adjacent to the resilial ridge.

C.meridionalis (fig 4)

The impression is oval and occurs at the side of the ligament, at a point about two-fifths to one-third the length of the ligament from its anterior end. The distance of the scar from the ligament is about equal to the shortest axis of the scar i.e. its width, although the distance may often be less than this. The impression is oval (length:width - 2:1), but in some specimens it may be almost circular (length:width - 1.5:1).

P.perna (fig 4)

The shape of the impression in juvenile specimens of

P.perna is the same as in *C.meridionalis*, but in larger specimens the scar tends to become more elongate, ~~so that~~ until the length:width ratio is about 3:1. The scar is more anteriorly placed than in *C.meridionalis*, occurring at a point one-fifth to one-third the length of the ligament from its anterior end. The distance of the scar from the ligament is never more than the width of the scar, but it may be less.

A.magellanica (fig 5)

The scar in *A.magellanica* is very elongate (length:width - 4:1), and the scar is situated at a point about one-fifth the length of the ligament from its anterior end. Its distance from the ligament is the same as in *P.perna*.

S.algosus (fig 6)

In this species, the scar is unique, for it consists of two separate scars situated behind the umbo at a point about one-quarter the length of the ligament from its anterior end. Both scars are elongate oval; anterior scar length:width - 3:1; posterior scar length:width - 2:1. The distance of the anterior scar from the ligament is slightly greater than the width of the scar, but the distance of the posterior scar is equal to, or slightly less than, the width of the scar.

S.bilocularis (fig 6)

The shape of the scar is similar to ~~the shape in~~ that of *C.meridionalis* (length:width - 2:1), but in *S.bilocularis*, it occurs about half the length of the ligament from its anterior end, or slightly less. Its distance from the ligament is equal to its width.

3. Oral contractor muscle impression.

The impression was noted by Krauss (1848), who failed to find the associated muscle in preserved specimens, but ~~which~~ it has been subsequently proved by Swart (1926) to be the area of insertion of the oral contractor muscle. The impression is only present in *C.meridionalis* and is not mentioned in Soot-Ryen's (1952) description for the genus *Choromytilus*. It may therefore be a specific character for *C.meridionalis* alone.

However, Soot-Ryen (1955) has shown that two South American genera have a small scar, similarly placed between the anterior adductor and the anterior byssus retractor muscle impressions. These genera are *Mytella* Soot-Ryen 1955 (see Soot-Ryen, 1955 : figs 35, 36, 37) and *Arcuatula* (Jousseaume) Lamy 1919 (see Soot-Ryen, 1955 : fig 46). According to Soot-Ryen (1955), these small scars are derived in two different ways. The scar in *Arcuatula* is caused by a small ventral branch of the anterior byssus retractor muscle, while the scar in *Mytella* (p. 52) "seems to be made by a thickening of the mantle and not by a branch of the anterior retractor."

In *C.meridionalis* (fig 4), the oral contractor muscle impression is circular and much smaller than that of the anterior byssus retractor muscle. The oral contractor muscle scar is situated more anteriorly than the anterior byssus retractor scar, about half-way between that scar and the ventral margin. Its distance from the ligament is about twice the diameter of the scar and so is further from it than the scar of the anterior byssus retractor.

4. Posterior adductor muscle impression

Except in *S.bilocularis*, the impression has a similar situation in all the species examined. It is the largest and most conspicuous of the muscle scars, and marks the area for insertion of the posterior adductor muscle. The scar varies in shape, from circular to oval, the longest axis of the oval scar being directed towards the umbo. The scar is situated opposite the midpoint of the posterior border of the valve, or slightly more dorsally (figs 4, 5, 6, 7, 8), with its outer edge concurrent with the pallial line. It occurs immediately above the pallial sinus, when the sinus is present.

In *S.bilocularis* (fig 6), the posterior adductor muscle scar is situated in a similar position, at the postero-dorsal region of the shell valve, but the circular scar is elongated on its antero-dorsal side. This portion of the scar lies directly above the posterior byssus retractor scar, embracing it above, but the distinction between the two scars can be easily made. This anteriorly directing portion of the scar runs about half the length of the byssus retractor scar.

5. Posterior and dorsal byssus retractor muscle impression

C.meridionalis (fig 4)

The posterior byssus retractor muscle impression is situated anteriorly to the posterior adductor scar, with which it is confluent. The shape of this impression varies from circular to oval, with its longest axis parallel to the ventral pallial line. The dorsal byssus retractor scar occurs in a line opposite the posterior end of the ligament and parallel to the dorsal edge of the shell. This scar is usually continuous with, and narrowly connected to that of, the posterior byssus retractor (fig 4). Some specimens have two completely separate scars. The pedal retractor does not leave a separate scar.

P.perna (fig 4)

The posterior retractor scar is confluent with, and situated anteriorly to, the posterior adductor scar, at its antero-dorsal end. The dorsal byssus retractor scar is situated in a line opposite the posterior end of the ligament. Unlike C.meridionalis, the dorsal and posterior byssus retractor scars are always well separated from each other.

A.magellanica (fig 5)

The posterior byssus retractor scar is situated anteriorly to, but is not usually confluent with, the posterior adductor scar. There are a series of smaller scars situated in a line, as in C.meridionalis, of which the largest is the most anterior. The number of scars varies up to five separate scars, but there are never less than two. In this case, the two scars are quite separate.

S.bilocularis (fig 6)

The dorsal and posterior retractor muscle form a single continuous scar in S.bilocularis. The scar is well developed and runs from the groove in the posterior adductor scar (caused by the forward projection of that scar), parallel to the dorsal margin of the shell and in a line opposite the posterior end of the ligament. The scar can be easily distinguished from the anteriorly directing portion of the posterior adductor scar, by a difference in shell texture. The posterior adductor scar seems to have a more open system of folds and crenulations, and there is a narrow nacreous shelf between the adductor and retractor scars. In smaller specimens the scar exists as a slight depression in the shell, due to the lack of secretion of a nacreous layer, but in the larger specimens obtained from Santa Carolina Island, Mozambique, the posterior retractor scar is elevated above the level of the shell valve, due to a thickening of the shell in this region.

L.capensis (fig 7)

Confusion exists in Barnard's (1964) figures 8e, f, g. Firstly his nomenclature for the musculature is obsolete; his anterior pedal retractor (a.r.p.) should read anterior byssus retractor; his posterior pedal retractor (p.r.p.) is simply the pedal retractor; and his anterior byssus retractor corresponds to a ~~non-existent and~~ separate dorsal byssus retractor muscle impression which is not present in *L.capensis*. Secondly, he states that the scar in *L.capensis* is continuous with the posterior adductor, yet his drawings of the musculature (fig 8f, g) show that there are well separated dorsal and posterior byssus retractor muscles. Because of the nature of his muscle p.r.p., it is suspected that the figures 8f and 8g are those of *M.virgiliae* (see section on Musculature).

The scar of the dorsal/posterior byssus retractor muscles is continuous with that of the posterior adductor. It runs forwards, parallel with the dorsal margin of the shell, to about the posterior two-thirds of the hinge. Here it narrows. The single scar does not have a regular outline, but is expanded in several regions along its length (usually 3 or more), marking the insertions of the major branches of the muscles.

M.virgiliae (fig 8)

The posterior byssus retractor scar (corresponding to Barnard's (1964) p.ret.by. in fig 8d) is continuous with that of the posterior adductor, and usually consists of 2 scars situated close against the posterior adductor scar. The dorsal retractor scar (Barnard's p.retr.ped. in fig 8d) is situated anteriorly to the posterior retractor scars, but does not extend forwards under the ligament. Comparatively, it is somewhat larger than the other retractor scars and is sometimes seen to be divided into two separate scars.

S.algosus (fig 6)

The posterior retractor muscle impression is continuous with the posterior adductor scar. The scar runs anteriorly and parallel to the dorsal margin, as far as and below the hind end of the ligament. The anterior one-third of the scar is expanded and is about one and a half times wider than the rest of the scar.

C. Pallial line

The nature and extent of the pallial line are more or less the same in all the species examined. In C.meridionalis, P.perna, L.capensis, S.algosus and M.virgiliae, there is a slight depression in the line under the posterior adductor muscle scar, the pallial sinus. The sinus is well developed in C.meridionalis, L.capensis, S.algosus and M.virgiliae, but is smaller in P.perna. It is absent in A.magellanica and S.bilocularis.

The pallial line extends from the depression under the hinge teeth (or the groove in the valve at this point), along the ventral, posterior and postero-dorsal regions of the shell, to terminate at the posterior adductor scar. In some species, the pallial line is continued dorsally and terminates at a point about one-fifth to four-fifths the length of the ligament from its posterior end. Along the postero-dorsal and posterior edges, the pallial margin is about twice the width of the margin on the ventral edge.

D. Musculature

The muscles in each of the genera were studied, with the exception of the pallial muscles and the anterior and posterior adductor muscles.

The muscles of the mantle edge, or pallial muscles, are similar in all species of the Mytilidae (Sabatier, 1877; List, 1902). The muscle band consists of small, white fibres, which insert on the shell at the pallial line, and run into the free edge of the mantle. The fibres may be well separated from one another (Field, 1922) or may anastomose (Sabatier, 1877). They run perpendicularly to the edge of the shell, except in the region dorsal and anterior to the posterior adductor (White, 1937) and to the anterior adductor (Pelseneer, 1911), where they slope obliquely to the outer edge of the mantle. The muscles are well developed in the posterior region, where the mantle fold is thicker (Field, 1922). Here the muscle fibres run into the anal siphon. Sabatier (1877) holds that these fibres are equivalent to the siphonal muscles of siphonates.

The pallial muscles are innervated by two pairs of pallial nerves, of which the anterior pair originate at the cerebral ganglia, while the posterior pair originate at the visceral ganglia. The pallial nerves meet in the mantle edge, forming a nerve ring between the cerebral and visceral ganglia. The pallial nerves give off finer branches to the muscular fibres along their course.

The anterior and posterior adductor muscles are inserted on the shell valves in the areas of their respective scars, and run transversally between the two shell valves. In some species, the anterior adductor is smaller than the posterior adductor (heteromyarian condition), while in others the anterior adductor is absent (monomyarian condition). As has been shown above, juvenile specimens of A.magellanica are heteromyarian~~s~~, while adults are typically monomyarian. The posterior adductor is more or less cylindrical in shape and consists of numerous muscle bundles. Owing to the convexity of the shell, the bundles of the anterior portion of the posterior adductor are longer than those of the posterior portion.

S.bilocularis is unusual in that the anterior adductor is reduced and inserts on the septum of each shell valve rather than on the shell itself. Also, the posterior adductor surrounds the posterior retractors of the byssus from behind, so that a shelf of muscle is formed above the retractors (Pelseneer, 1911 : fig 6, pl. VI). This condition is also found in Meleagrina, Malleus and Isognomum (Pelseneer, 1911).

List (1902) has noted that in some mytilids, the posterior adductor seems to be composed of two differently coloured fibres. This is particularly noticeable in S.bilocularis. Bowden (1958) has reviewed the histological work on muscle structure, and it seems that the histological division is correlated with a functional one (Hoyle, 1964).

Contraction of the adductor muscles closes the shell, and it has been established (Dall, 1889; Trueman, 1964) that a tension is produced in the ligament. This tension opens the valves, when the adductors relax. However, it would seem that the mechanism is more complex in the different genera (Trueman, 1953, 1954; Chapman & Newell, 1956; Yonge, 1955, 1958).

Because of the nature of the musculature in the Protobranchia (Brück, 1914), several workers have confused the nomenclature of the retractor muscles in the Mytilidae (Sabatier, 1877; Winton, 1937; Barnard, 1964). For example, Barnard (1964) figures "anterior and posterior foot retractors" in Brachidontes variablis, M.virgiliae and L.capensis (figs 8a, d, e, f, g), yet Pelseneer (1911) has pointed out that in heteromyarians (Mytilidae) and some monomyarians, the anterior foot retractor muscles, present in protobranchs disappears, and the posterior foot retractor becomes more medially placed. It is then known as the foot or pedal retractor. Purdie (1887) and not Fletcher (van Nieuwenhoven, 1947) was the first to recognise the difference between the pedal musculature and the byssal musculature. This has been confirmed by List (1902), and White (1937) has pointed out (p.77) that "the pedal and byssal muscles are completely separate from each other and after removal of the connective tissue, it is possible to remove the foot entire without disturbing the byssus."

A general scheme for the position and orientation of the byssal muscles is given below after Purdie (1887):

The muscles of the byssus (all known as retractors)
a system independent of the adductors and of that of the
form ~~an independent muscular system to that of the valves~~
foot proper (foot retractors)
~~(adductors) and to that of the foot proper (foot retractors)~~.
Apart from
~~Excluding~~ the adductors, the byssus retractors make up the ~~great~~ bulk of the internal musculature. They consist of three pairs:

(a) the anterior byssus retractor muscles, which originate at the byssus and pass forwards between the foot retractors, diverging as they do so, to insert on the shell at their appropriate muscle scars.

(b) the dorsal retractors (Swart, 1926), or middle retractors (Purdie, 1887), which originate at the byssus and run dorsally (sometimes postero-dorsally) to insert on the shell at the dorsal retractor muscle scars.

(c) the posterior byssus retractor muscles, which run from the byssus in a postero-dorsal direction to insert on the shell at their appropriate scars.

The byssus is therefore situated at the apex of three muscular V's; the anterior V (anterior byssus retractors) is nearly horizontal; the dorsal V (dorsal byssus retractors) is nearly upright; and the posterior V (posterior byssus retractors) rests on the posterior adductor muscle.

In some species, the dorsal and posterior retractor muscles cannot be distinguished from one another, and in such ~~this~~ cases, I have called all the muscles the posterior byssus retractor muscles. There are therefore two groups:

(a) with separate dorsal and posterior byssus retractor muscles: *P.perna*, *M.virgiliae* and in some specimens of *A.magellanica* and *C.meridionalis*.

(b) without a separate dorsal byssus retractor muscle: *L.capensis*, *S.algosus*, *S.bilocularis* and usually *A.magellanica* and *C.meridionalis*.

P.perna (figs 9, 10)

(i) *anterior byssus retractor muscles*.

The anterior byssus retractor muscles (*M.retractor byssi anterior* of List (1902)), consist of a pair of muscles which originate on the anterior and outer lateral edges of

FIGURE 9

The origin of the byssus retractor muscles at the byssus in

P.perna

bys.thds - byssus threads; bys.lam. - byssus lamina; a. bys. ret. - anterior byssus retractor muscle; d. bys. ret. - dorsal byssus retractor muscle; p. bys. ret. - posterior byssus retractor muscle.

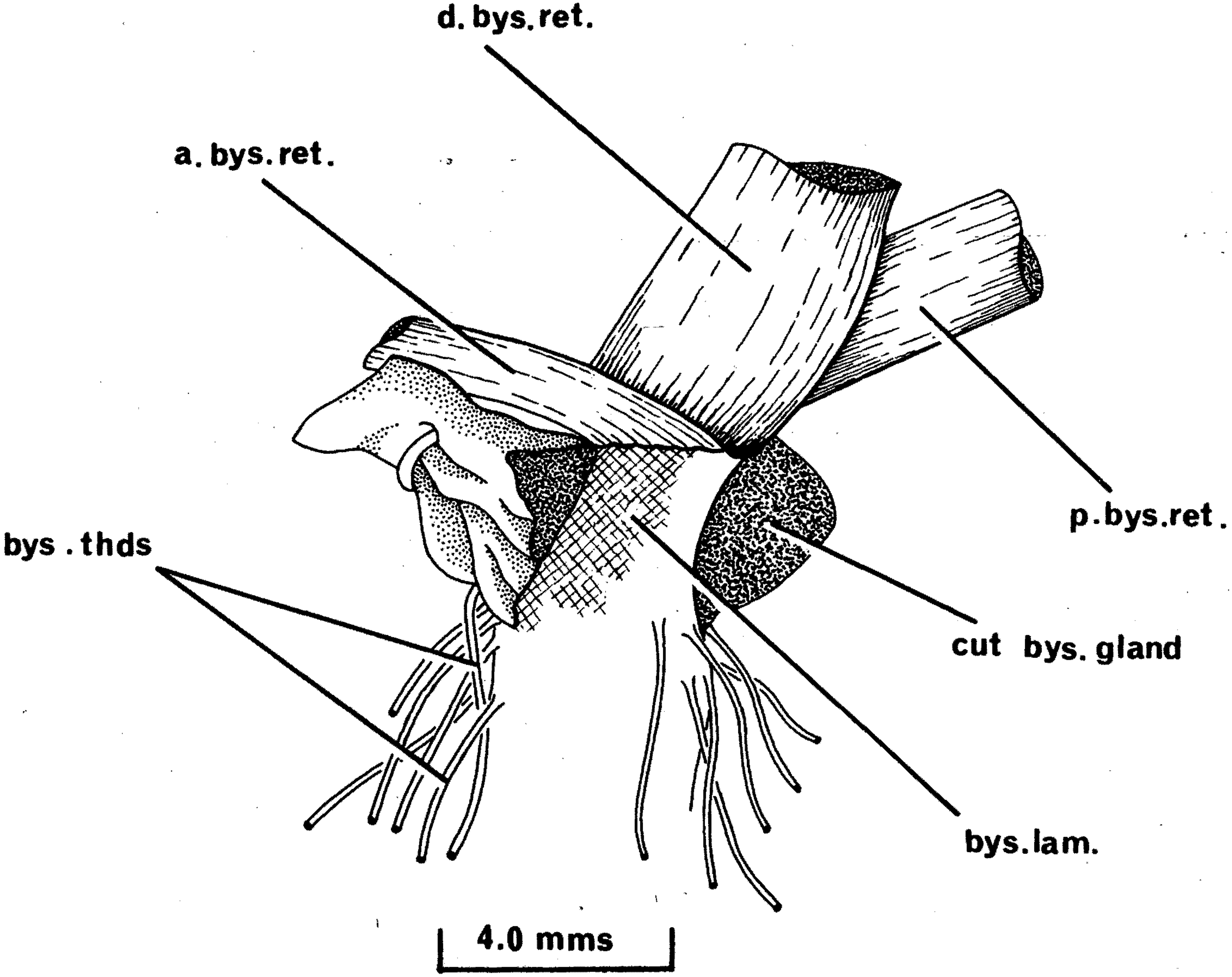
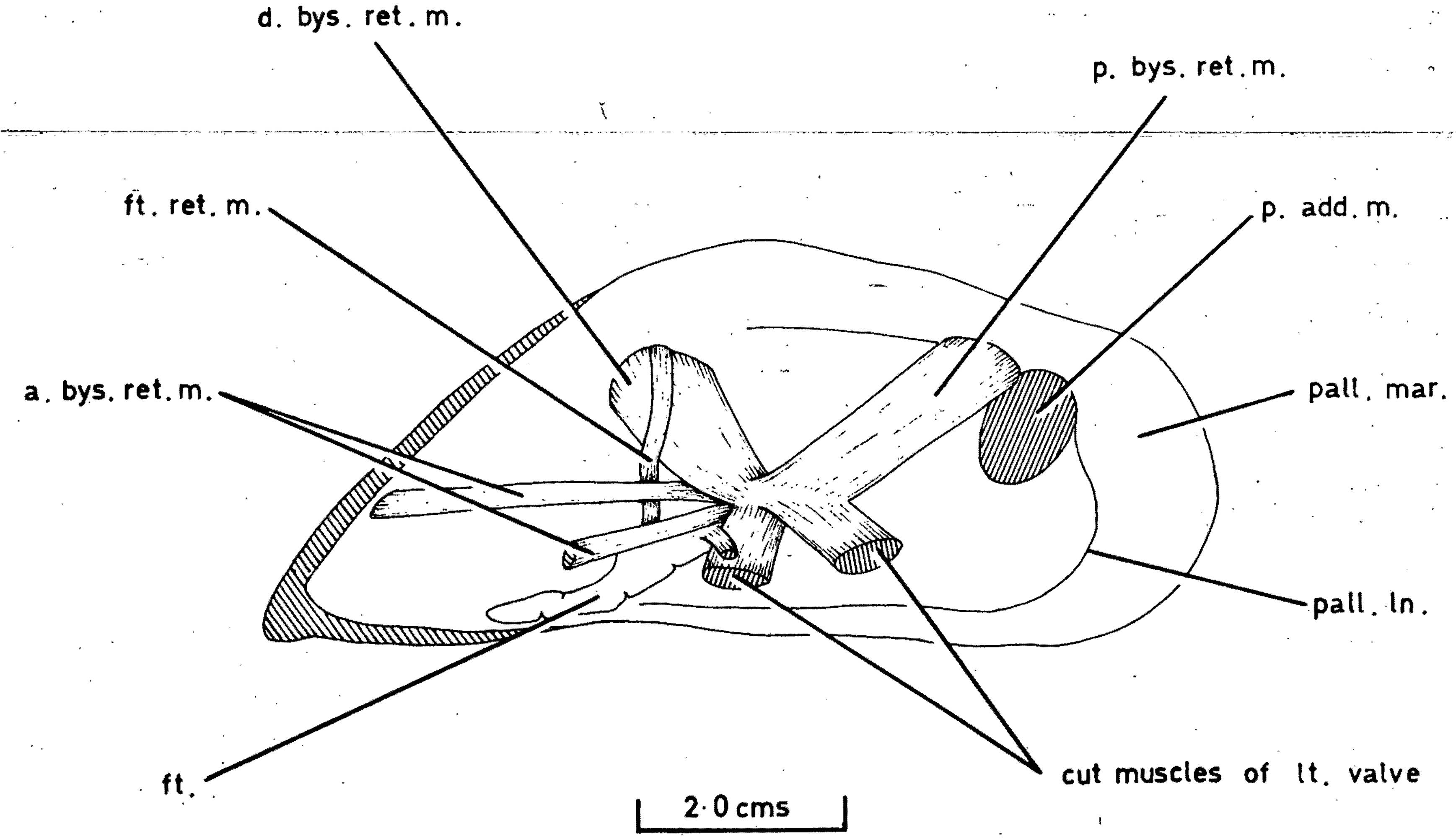

d. bys. ret.
a. bys. ret.
p. bys. ret.
bys . thds
cut bys. gland
bys. lam.
4.0 mms

FIGURE 10

The orientation of the byssus and pedal musculature of *P.perna* from the left side.

ft. - foot; pall. ln. - pallial line; pall. mar. - pallial margin; p. add. m. - posterior adductor muscle; ft. ret. m. - foot retractor muscle; a. bys. ret. m. - anterior byssus retractor muscle; d. bys. ret. m. - dorsal byssus retractor muscle; p. bys. ret. m. - posterior byssus retractor muscle.


d. bys. ret. m.
p. bys. ret. m.
ft. ret. m.
p. add. m.
a. bys. ret. m.
pall. mar.
pall. ln.
ft.
cut muscles of lt. valve
2·0 cms

the byssus organ, and which overlay the points of origin of the dorsal and posterior byssus retractor muscles (fig 9). The paired anterior retractors leave their origin, pass between the foot retractors and run in an antero-dorsal direction, separating as they do so, to insert on the shell at the region of the anterior byssus retractor muscle scars. At a point just anterior to the cerebral ganglia, and more dorsal to them, the muscles pass through the mantle to their points of insertion. The muscles are white in colour and eliptical in cross-section, their greatest axis being in a dorso-ventral plane.

(ii) dorsal byssus retractor muscles (fig 10)

Although the dorsal byssus retractor muscles arise in close conjunction with the posterior byssus retractors, their points of origin may be seen to lie on the dorsal side of the byssus organ, between the points of origin of the anterior retractors and the posterior retractors (fig 9). The muscle consists of a single main bundle, which is dorso-ventrally flattened. It runs from the byssus in a slightly postero-dorsal direction on each side, and inserts at the dorsal byssus retractor muscle impression. At their points of insertion, the dorsal retractors are circular in cross-section. The general shape of the dorsal byssus retractor muscle can be depicted as an inverted cone, the apex of which is directed onto the byssus apparatus.

(iii) posterior byssus retractor muscles (fig 10)

The paired posterior byssus retractor muscles are somewhat dorso-ventrally flattened, and have their origin at the posterior and postero-dorsal region of the byssus apparatus (fig 9). Their origin is more medial to the overlaying dorsal and anterior byssus retractors. The posterior retractors pass backwards in a postero-dorsal direction and insert on the shell at a point adjacent and anterior to the posterior adductor muscle. The muscle arises as a single muscle mass, although separate muscle bundles can be distinguished near the insertion. The number of muscle bundles varies in different specimens, but it is usually similar on both sides of the animal.

C.meridionalis (fig 11)

(i) anterior byssus retractor muscles (fig 11)

The paired anterior byssus retractor muscles have similar origins and run in a similar direction as in *P.perna*. They insert on the shell about one-third the length of the ligament from its anterior end. The muscles are cylindrical in shape, with their greatest axis in a dorso-ventral direction.

(ii) dorsal byssus retractor muscles (fig 11)

Dorsal byssus retractors are usually not distinguishable,

FIGURE 11

The orientation of the byssus and pedal musculature of *C.meridionalis*, as seen from the left side.

ft. - foot; pall. ln. - pallial line; pall. mar. - pallial margin; p. add. m. - posterior adductor muscle; ft. ret. m. - foot retractor muscle; a. bys. ret. m. - anterior byssus retractor muscle; p. bys. ret. m. - posterior byssus retractor muscle.

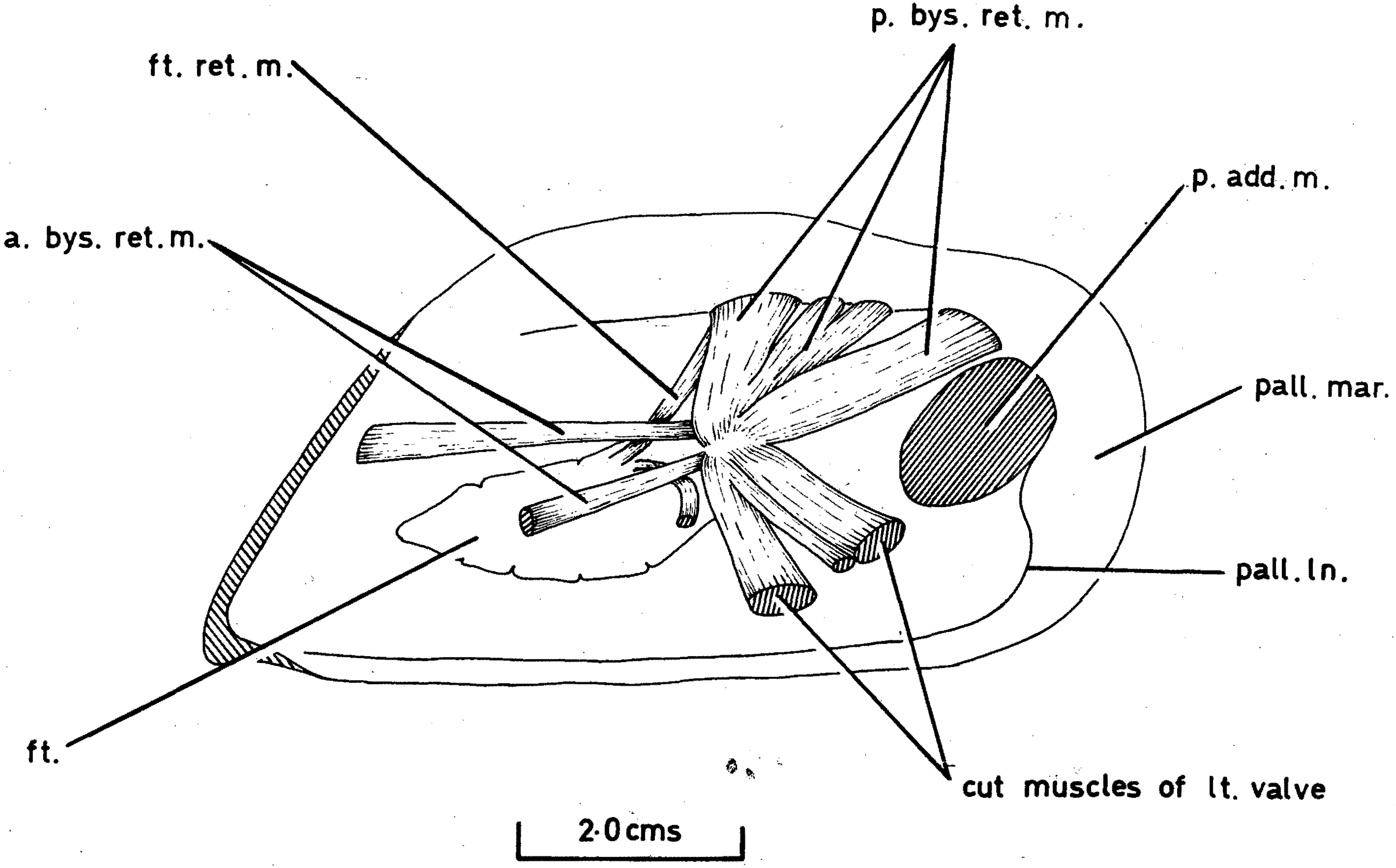

p. bys. ret. m.
ft. ret. m.
p. add. m.
a. bys. ret. m.
pall. mar.
pall. ln.
ft.
cut muscles of lt. valve
2·0 cms

FIGURE 12

The orientation of the byssus and pedal musculature of *A.magellanica*, as seen from the left side.

ft. - foot; bys. thds. - byssus threads; pall. ln. - pallial line; pall. sin. - pallial sinus; pall. mar. - pallial margin; p. add. m. - posterior adductor muscle; ft. ret. m. - foot retractor muscle; a. bys. ret. m. - anterior byssus retractor muscle; p. bys. ret. m. - posterior byssus retractor muscle.

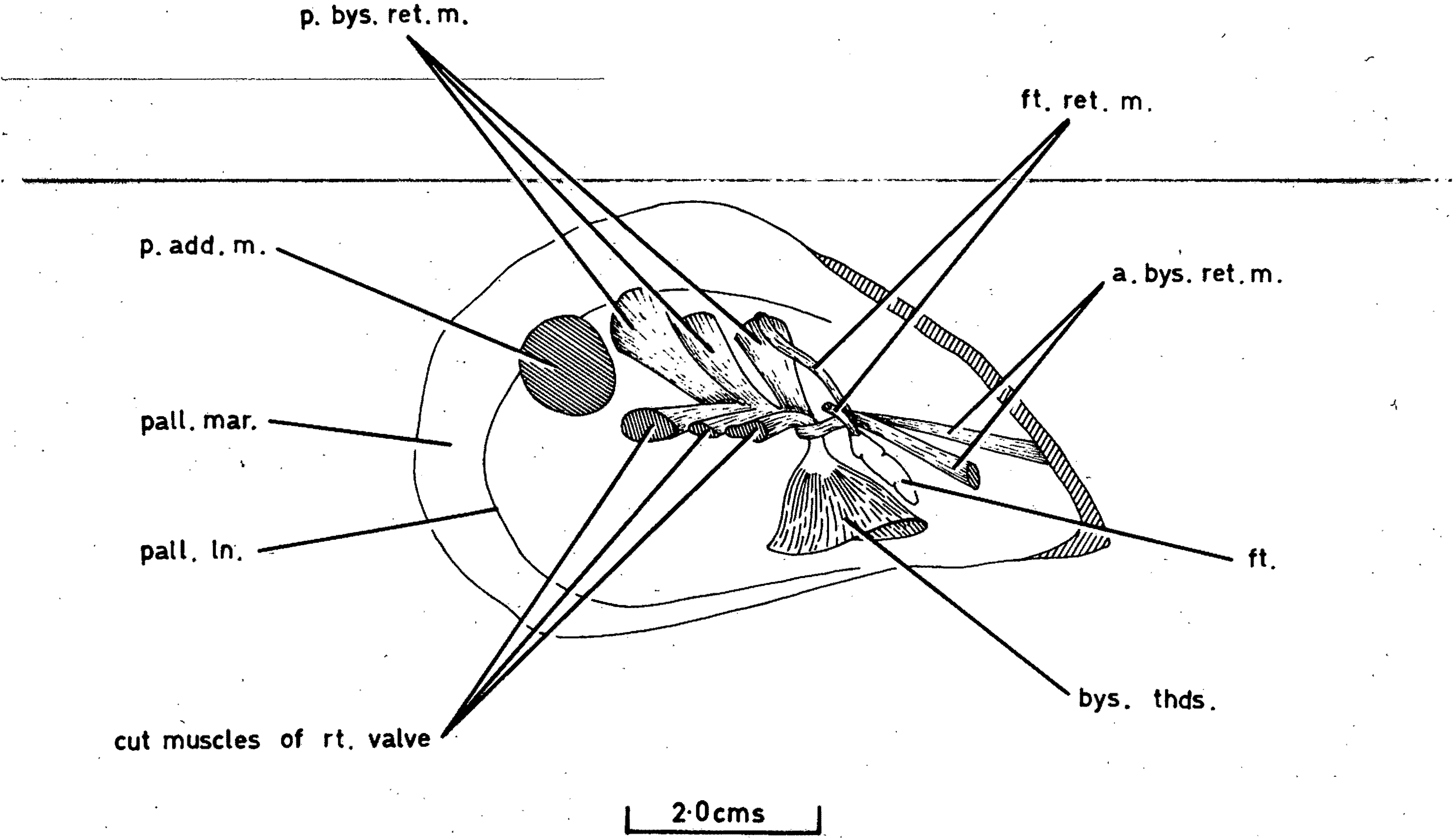
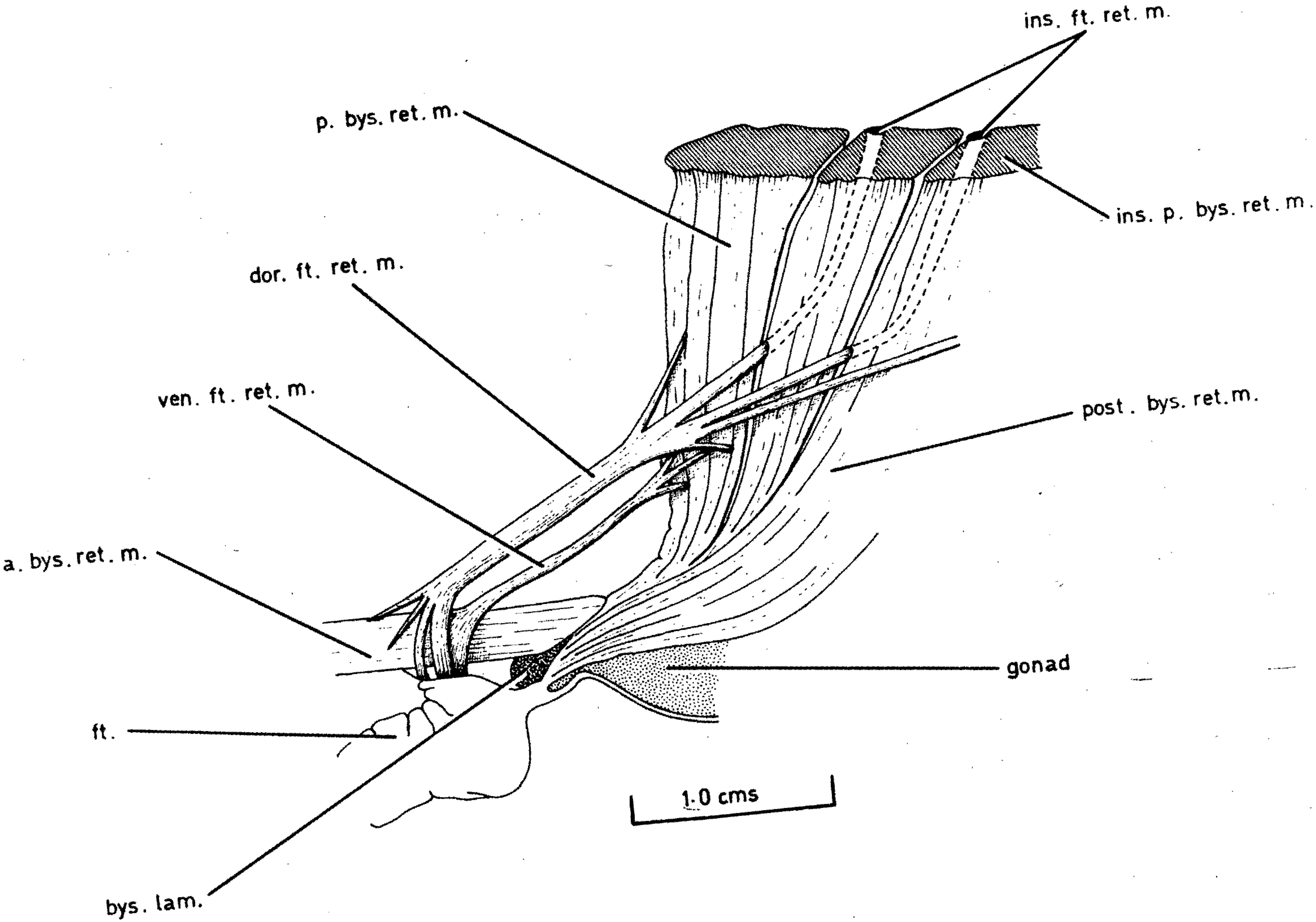

p. bys. ret. m.
ft. ret. m.
p. add. m.
a. bys. ret. m.
pall. mar.
pall. ln.
ft.
bys. thds.
cut muscles of rt. valve
2·0cms

FIGURE 13

The muscles of the left shell valve of S.bilocularis, showing especially the dual nature of the foot retractor muscle.

bys. lam. - byssus lamina; ft. - foot; dor. ft. ret. m. - dorsal foot retractor muscle; ven. ft. ret. m. - ventral foot retractor muscle; a. bys. ret. m. - anterior byssus retractor muscle; p. bys. ret. m. - posterior byssus retractor muscle; ins. ft. ret. m. - insertion of the foot retractor muscle; ins. p. bys. ret. m. - insertion of the posterior byssus retractor muscle.


ins. ft. ret. m.
p. bys. ret. m.
ins. p. bys. ret. m.
dor. ft. ret. m.
ven. ft. ret. m.
post. bys. ret. m.
a. bys. ret. m.
gonad
ft.
1·0 cms
bys. lam.

and the muscle bundles simply run from their origin at the byssus to insert on the shell at a scar, which is continuous with the posterior retractor scar. In some cases, 2 or 3 muscle bundles are well separated from the main muscle mass, and are termed dorsal byssus retractors.

(iii) posterior byssus retractor muscles (fig 11)

The posterior byssus retractor muscles consist of a single muscle bundle on each side; their origin and insertion is similar to *P.perna*. The muscles are dorso-ventrally flattened.

A.magellanica (fig 12)

The anterior byssus retractor muscles run as in *P.perna*, but their insertion on the valve differs in being more forwardly placed than in *P.perna*. The muscle originates as a loop on the lateral and posterior surfaces of the byssus apparatus (fig 12) and runs anteriorly between the pedal retractors. The posterior byssus retractor muscles run from the mid-line of the byssus in a postero-dorsal direction and insert anteriorly to the posterior adductor. When dorsal byssus retractor muscles are distinguishable, they consist of 2 - 5 separate bundles of muscles, running postero-dorsally and inserting on the shell in a series of scars in a line opposite the end of the ligament and anteriorly to the posterior retractor muscle.

S.bilocularis (fig 13)

(i) *anterior byssus retractor muscles*

These muscles have their origin on the antero-lateral and anterior regions of the byssus apparatus. In *S.bilocularis*, the muscle runs antero-ventrally on each side, to insert on the shell at scars situated about half-way along the ligament. The muscles pass through the mantle just above and ~~more anteriorly~~ a little in front of to the cerebral ganglia. At their origin, the muscles are circular in cross-section, but towards their insertion, they become laterally flattened.

(ii) *posterior byssus retractor muscles* (fig 13)

Since dorsal retractor muscles cannot be distinguised, all the muscles are termed posterior byssus retractors.

These muscles consist of a single group of muscles, composed of many bundles, which have their origins on the posterior and postero-dorsal regions of the byssus gland. Their postero-dorsal origin is somewhat more medial to the origin of the anterior byssus retractors, which overlay them laterally at this point. The muscle bundles pass dorsally and posteriorly, and insert on the valves at their impressions (fig 6A) The most posterior of the bundles lies against the oval part of the posterior adductor (in the crux), and they are ~~shelved~~ covered

FIGURE 14

The musculature of the left valve of S.algosus, showing the division of the anterior byssus retractor muscle into two branches.

ft. - foot; bys. - byssus; a. bys. ret. m. - anterior byssus retractor muscle; p. bys. ret. m. - posterior byssus retractor muscle; ft. ret. m. - foot retractor muscle.

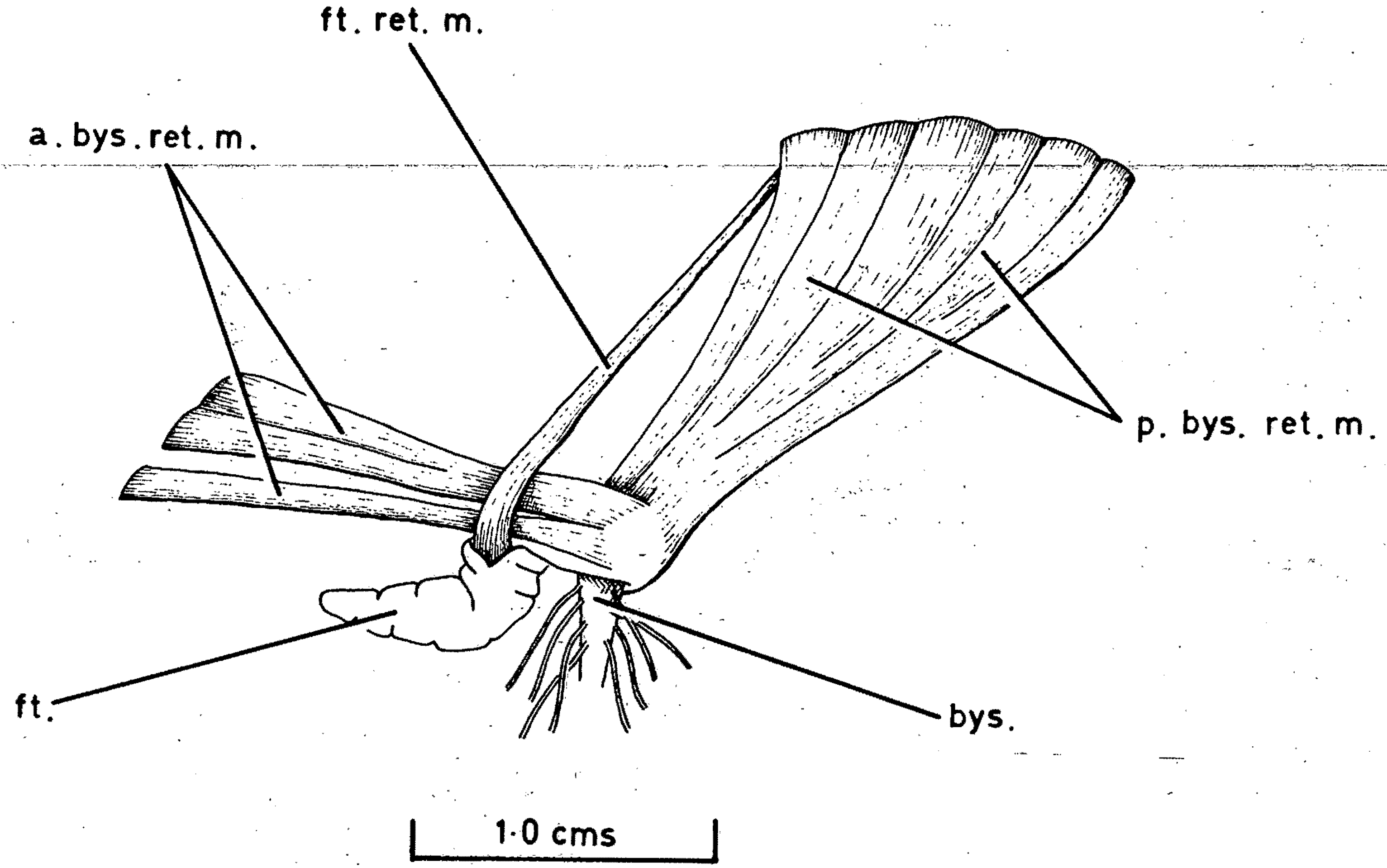

ft. ret. m.
a. bys. ret. m.
p. bys. ret. m.
ft.
bys.
1·0 cms

FIGURE 15

The musculature of the left shell valve of *M. virgilias*, showing the separate dorsal and posterior byssus retractor muscles and the anteriorly directing branch of the foot retractor muscle.

ft. - foot; bys. - byssus; ft. ret. m. - foot retractor muscle; a. bys. ret. m. - anterior byssus retractor muscle; d. bys. ret. m. - dorsal byssus retractor muscle; p. bys. ret. m. - posterior byssus retractor muscle.

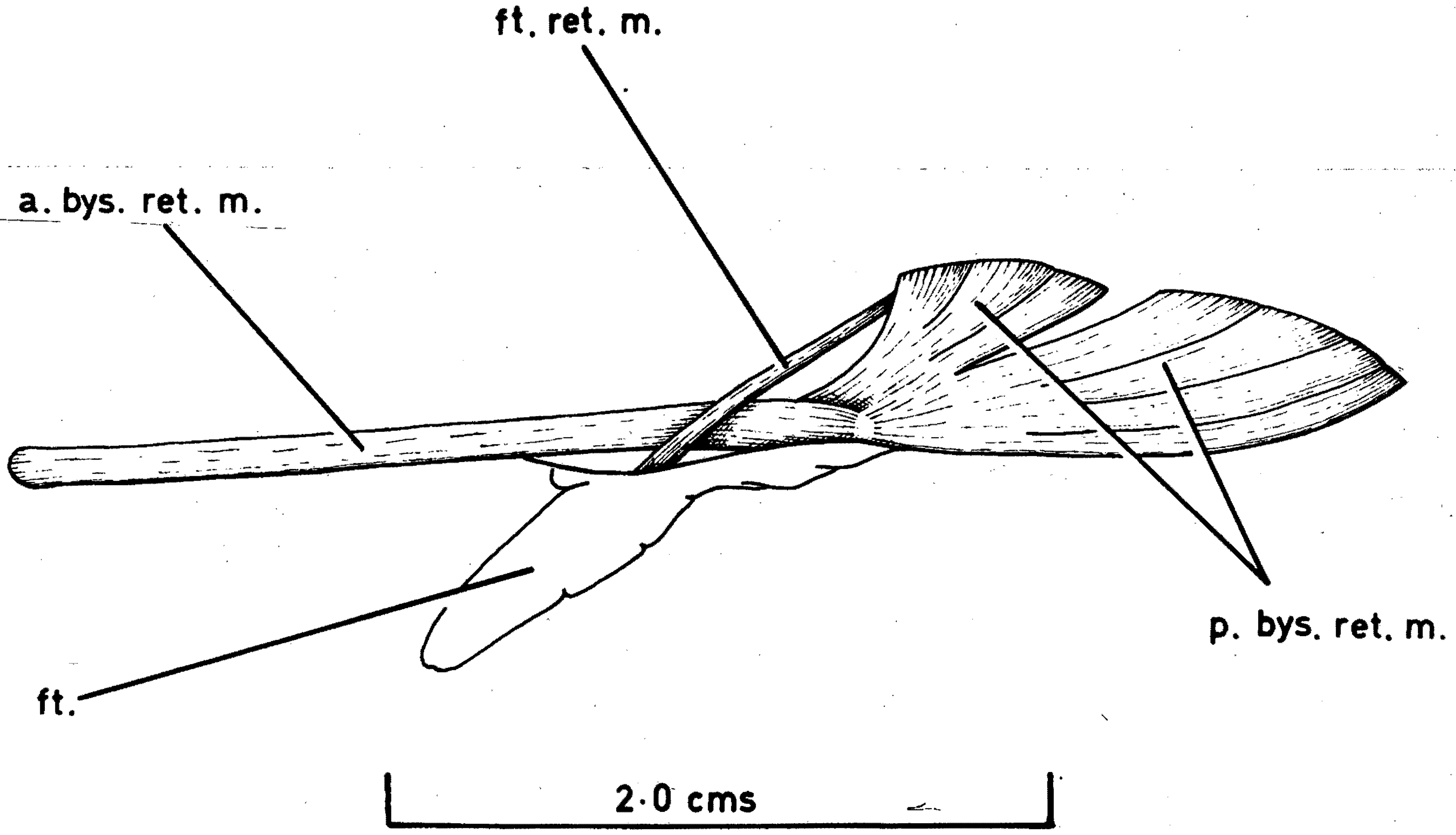
FIGURE 16

The musculature of the left shell valve of L.capensis.

ft. - foot; ft. ret. m. - foot retractor muscle;

a. bys. ret. m. - anterior byssus retractor muscle;

p.bys. ret. m. - posterior byssus retractor muscle.


ft. ret. m.
a. bys. ret. m.
p. bys. ret. m.
ft.
2·0 cms

dorsally by the protrusion of the adductor (see above).

S.algosus (fig 14)

(i) *anterior byssus retractor muscles* (fig 14)

S.algosus is unusual in that there are two anterior byssus retractor muscles on each side. These muscles insert at two separate scars on each shell valve, just behind the umbones, and at a point about one-quarter the length of the ligament from its anterior end. The anterior retractor muscles on each side, have their origin as a single muscle mass, situated on the anterior and antero-lateral sides of the byssus organ, and they run antero-dorsally. A short distance from their origin, the single muscle mass splits into two distinct muscle~~s~~ bundles. The dorsal bundle is by far the largest and sometimes shows signs of splitting into bundles itself. However, there are always only two scars on each of the shell valves.

(ii) *posterior byssus retractor muscles* (fig 14)

There is no separate dorsal byssus retractor muscle. The posterior retractors consist of 4 - 8 bundles of muscular tissue, inserting on the shell in a line parallel to the dorsal side of the shell and opposite the posterior end of the ligament. The most posterior of the bundles inserts on the shell adjacent to, and anterior to, the insertion of the posterior adductor. Because of the mode of the insertion of the pedal retractor, the most anterior bundle is expanded at its insertion. The origin of the posterior retractors is on the dorsal, lateral and posterior surfaces of the byssus organ.

M.virgiliae (fig 15)

(i) *anterior byssus retractor muscles* (fig 15)

This consists of a single muscle bundle on each side, having the same origin on the byssus apparatus as *P.perna*, and inserting on the shell valves as circular scars in each umbo.

(ii) *dorsal byssus retractor muscles* (fig 15)

The dorsal byssus retractors are usually split into two muscle bundles on each side; they run from the origin on the byssus organ and insert on the shell valves at their appropriate scars (fig 8).

(iii) *posterior byssus retractor muscles* (fig 15)

These muscles have their origins on the posterior, lateral and medial surfaces of the byssus organ. They run postero-dorsally and insert on the shell, anterior to the posterior adductor muscle. As with the dorsal retractor, the posterior retractor is split into two bundles.

L.capensis (fig 16)

(i) anterior byssus retractor muscles (fig 16)

A single muscle in each valve, running from the byssus to the shell, as in M.virgilise.

(ii) posterior byssus retractor muscles (fig 16)

There is no separate dorsal retractor muscle. The posterior byssus retractor muscles consist of 4 - 7 bundles of muscle, originating at the byssus and running postero-dorsally to insert on the shell at a scar, which is continuous with that of the posterior adductor muscle.

Pedal Musculature

The pedal muscles are connected with the movements of the foot alone, and except at their points of insertion on the shell valves, are entirely separate from the byssal muscles, to which they are joined by connective tissue. The pedal musculature consists of two groups of muscles:

(a) the intrinsic muscles of the foot - a thin layer of circular muscle fibres lying under the epithelium of the foot (Field, 1922 : figs 144, 145). Towards the tip of the foot, these muscle fibres become obliquely arranged, to form a coarse network. Contraction of the circular fibres results in an increase in pressure on the blood-filled cavity of the foot, and with subsequent relaxation of the foot retractor muscles, extension of the foot takes place.

(b) the extrinsic muscles of the foot - these are the foot or pedal retractor muscles; the M. retractor pedis of List (1902). They have their origin in the foot and run as longitudinal fibres in a dorsal direction to insert on the shell valves. Contraction of these muscles results in retraction of the foot.

The pedal musculature described in this paper is that of the foot retractors.

P.perna (fig 10)

The insertion of the foot retractor is at the mid-point of the dorsal side of the scar of the dorsal byssus retractor muscle. From its insertion on the shell, the foot retractor muscle runs along the dorsal surface of the dorsal byssus retractor muscle, in an antero-ventral direction. At a point about one-third the length of the dorsal retractor, the foot retractor runs around the anterior surface of the byssus retractor and separates from it. It continues antero-ventrally and traverses the anterior byssus retractor muscle externally, before running into the foot on both sides. At its insertion, the foot retractor is circular in cross-section, but before entering the foot, and where it crosses over the anterior byssus retractor, it becomes laterally flattened. This flat sheet of muscle enters the foot and runs along the dorsal and lateral sides of that organ.

C.meridionalis (fig 11)

The ~~point of~~ insertion of the foot retractor muscle is on the ventral surface of the most anterior scar of the posterior retractor muscles, or in those specimens with a dorsal retractor, on the ventral side of the dorsal retractor scar. It elongates the scar antero-ventrally. From its insertion on the shell valves, the foot retractor runs antero-ventrally on each side of the visceral mass, as a single muscle bundle on each side. This bundle becomes laterally compressed as it traverses the anterior byssus retractor and enters the foot.

A.magellanica (fig 12)

The ~~point of~~ insertion of the foot retractor muscle in this species is on the dorsal side of the most anterior scar of the posterior byssus retractor muscle. The foot retractor runs as in *P.perna*; it also traverses the anterior byssus retractor externally and runs into the foot.

S.bilocularis (fig 13)

The muscle has its origin along the upper dorsal side of the foot. The foot retractor is not well developed in this species. On emerging from the foot, the separate muscle fibres, which in some specimens are arranged into two bundles while in others remain as a single sheet or fascia of fibres, pass dorsally and externally across the anterior byssus retractor muscles. They then run postero-dorsally and at points about one-third the length of the posterior byssus retractor, divide into smaller bundles, which penetrate the different muscle bundles of the posterior byssus retractor. These smaller bundles pass through the posterior retractor bundles (fig 13) and run onto the inner medial side of those bundles. They insert on the shell valve along the dorsal side of the posterior byssus retractor muscle impression at several ~~points~~ scars. There are no distinct scars for the insertion of the foot retractors. In cases where two foot retractors are present on each side, the more dorsal one is the largest, while the smaller ventral one seems to have its insertion on the outer lateral sides of the posterior byssus retractor muscle itself.

S.algosus (fig 14)

The foot retractor originates along the dorsal side of the foot, from which it emerges, and runs postero-dorsally. It is quite separate from the posterior byssus retractor muscle. It inserts on the shell on the anterior dorsal side of the posterior byssus retractor scar.

M.virgiliae (fig 15)

The insertion of the foot retractor muscle is on the antero-dorsal edge of the dorsal byssus retractor muscle scar. From its insertion, the muscle immediately runs around to the anterior edge of the dorsal retractor and separates from it.

It continues antero-ventrally and becomes laterally flattened as it does so. It traverses the anterior byssus retractor muscle externally, but here it divides into two muscle bundles:

(a) a small anteriorly directing bundle - this consists of a few muscle fibres only, which seperate from the main portion of the foot retractor at a point opposite the dorsal edge of the anterior byssus retractor. It runs anteriorly for a short distance on the lateral sides of the anterior byssus retractor, and has its origin on the lateral and ventral sides of this muscle, a short distance in front of the pedal ganglion.

(b) the main bundle - this crosses over the anterior byssus retractor muscle and dives into the foot. It has its origin along the dorsal and lateral sides of the foot.

<u>L.capensis</u> (fig 16)

The foot retractor has its insertion on the dorsal side of the most anterior scar of the posterior byssus retractor muscle. It runs along the inner dorsal surface of the posterior retractor, in an anterior direction, before turning antero-ventrally and running into the foot, as in <u>P.perna</u>. The muscle does not branch.

E. Innervation of the Foot/byssus Musculature

Dissections were performed under a binocular microscope on both living and preserved material. The descriptions and drawings are the composite results of not less than ten full dissections for each species. The nerves of specimens preserved in formalin were easiest to follow, but were brittle. Tracing of the finer nerves was done with the aid of microdissectors, manufactured by Singer Instruments. Vital staining with methylene blue was tried (Alexandrowicz, 1932), but was found to be unsatisfactory due to poor penetration. Because of the expense, the osmic acid method given by List (1902) was not used.

Considerable confusion exists as to the correct terminology of the nerves which arise at the pedal ganglia and which innervate the muscles of the foot, the muscles of the byssus and the byssus itself. Purdie (1887), Field (1922) and Takahashi (1960) have used an English terminology, while List (1902) has preferred the classical nomenclature. For his work on <u>Anodonta</u>, Splittstösser (1912) has called all the nerves <u>N.pedalis</u>, and has distinguished them further by the use of numerals. The nomenclature in this paper follows Purdie (1887), Field (1922) and White (1937) where possible.

The pedal ganglia lie on the dorsal surface of the anterior byssus retractor muscles, just anterior to the point where the foot retractors pass laterally over the anterior byssus retractor muscles. The ganglia are egg-shaped and are usually coloured orange-yellow in unpreserved material. The ganglia appear to have fused into a single mass, but a median furrow indicates the dual nature of this mass. The apices of each ganglion point anteriorly and slightly laterally, and are connected to the cerebral ganglia by the cerebro-pedal connectives. These connectives run anteriorly, along the dorsal surface of each anterior byssus retractor muscle for a short distance, before crossing laterally and obliquely to the ventral side of these muscles, to unite with the cerebral ganglia. The cerebro-pedal and cerebro-visceral connectives are separate in all the species, except L.capensis, in which the two are joined to form on each side, a short single common connective, which emerges from the posterior end of the cerebral ganglion.

C.meridionalis is peculiar in that the cerebro-pedal connective passes straight backwards from the cerebral ganglion, runs through the anterior byssus retractor muscle, splitting it in two, and emerges from the dorsal side of that muscle (figs 19, 20) to terminate at the pedal ganglion.

Although List (1902) and White (1937) figure only three pairs of nerves, besides the cerebro-pedal connectives, the present study has shown that four pairs of nerves leave the pedal ganglia. This is in agreement with Purdie (1887), Field (1922) and Takahashi (1960).

FIGURE 17

The left pedal ganglion and associated nerves of *P.perna*, showing the innervation of the foot retractor and byssus retractor muscles and the byssus.

ft. - foot; a. bys. ret. m. - anterior byssus retractor muscle; d. bys. ret. m. - dorsal byssus retractor muscle; c.p.c. - cerebro-pedal connective; a. bys. ret. n. - anterior byssus retractor nerve; s. ft. ret. n. - superficial foot retractor nerve; ft. ret. m. - foot retractor muscle; p.g. - pedal ganglion; p.n. - pedal nerve; bys. gl. - byssus gland; bys. n. - byssus nerve; v. bys. ret. n. - ventral byssus retractor nerve.

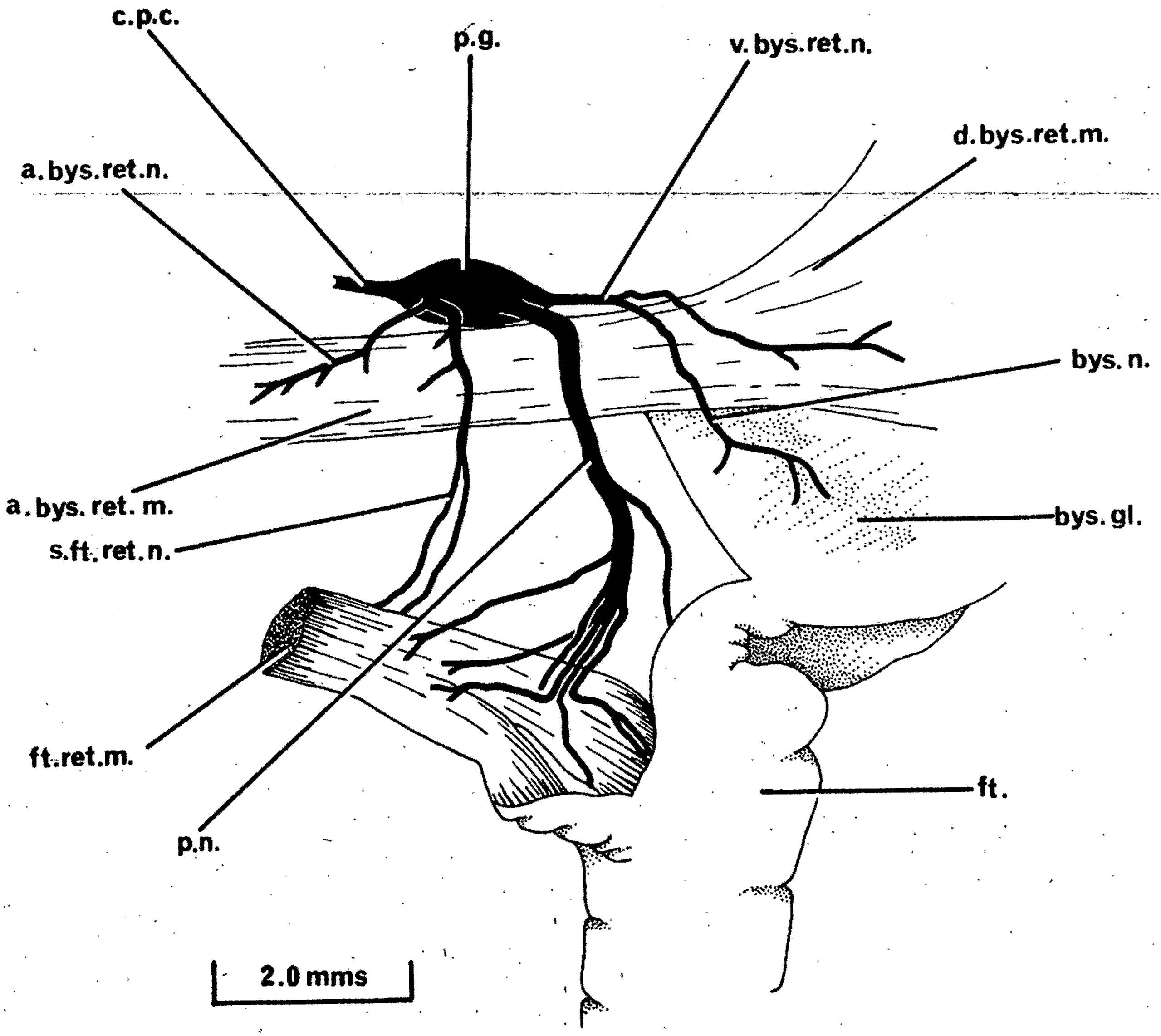

c.p.c.
p.g.
v. bys.ret.n.
d.bys.ret.m.
a. bys.ret.n.
bys. n.
a. bys. ret. m.
bys. gl.
s.ft. ret. n.
ft.ret.m.
ft.
p.n.
2.0 mms

FIGURE 18

The pedal ganglion and dorsal nerves of *P.perna*, showing the innervation of the dorsal and posterior byssus retractor muscles.

p.g. - pedal ganglion; c.p.c. - cerebo-pedal connective; p.n. - pedal nerve; d. bys. ret. n. - dorsal byssus retractor nerve; d. bys. ret. m. - dorsal byssus retractor muscle; p. bys. ret. m. - posterior byssus retractor muscle.

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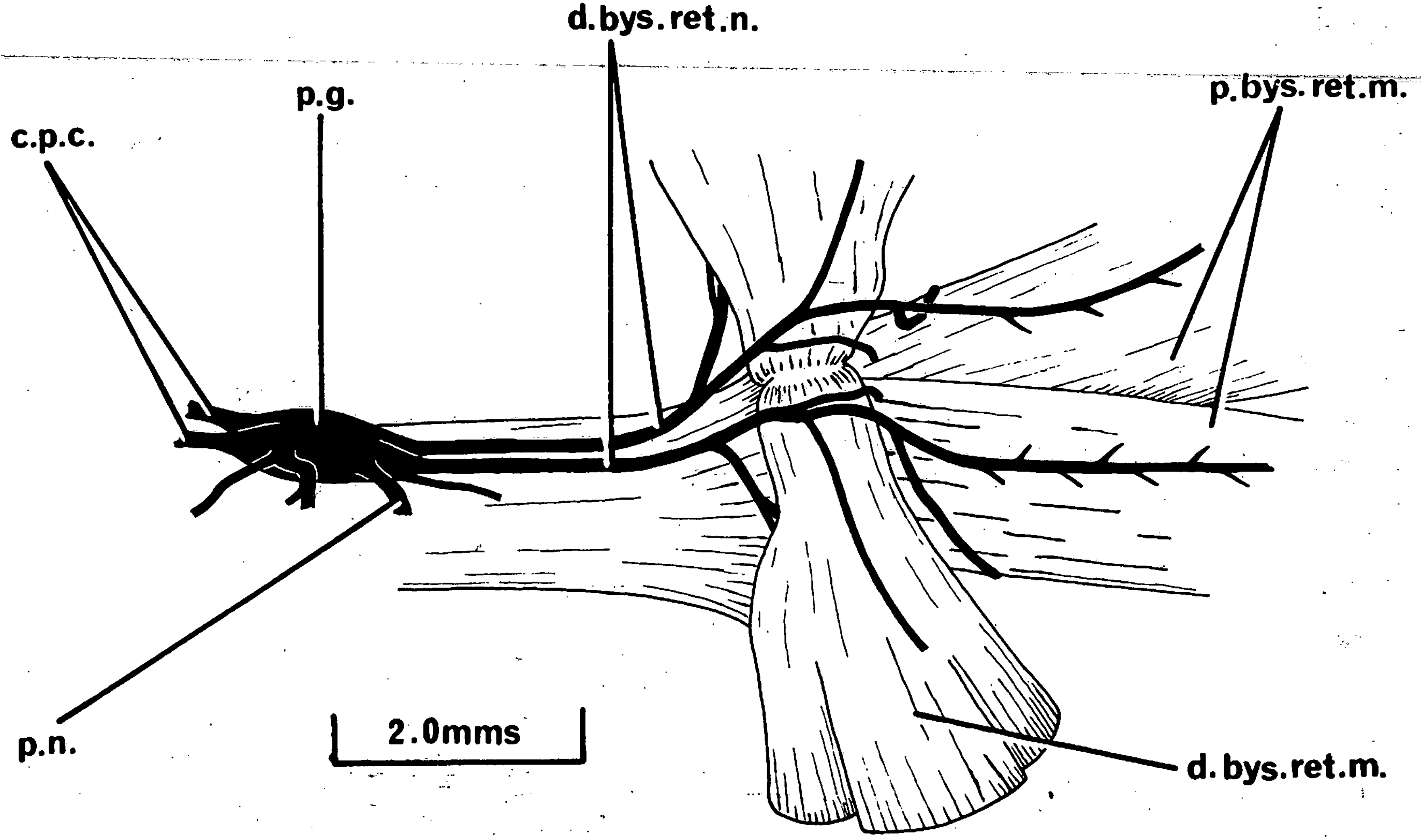

d.bys.ret.n.
p.g.
p.bys.ret.m.
c.p.c.
p.n.
2.0mms
d.bys.ret.m.

FIGURE 19

The pedal ganglion of <u>C.meridionalis</u> seen from the left side and showing the innervation of the anterior byssus retractor muscle and foot retractor muscle. The outer limb of the anterior byssus retractor muscle has been cut away.

p.g. - pedal ganglion; c.p.c. - cerebro-pedal connective; inner limb ARBM - inner limb of the anterior byssus retractor muscle; a. bys. ret. n. - anterior byssus retractor nerve; ft. ret. m. - foot retractor muscle; ft. - foot; p.n. - pedal nerve; outer limb ARBM - outer limb of the anterior byssus retractor muscle.

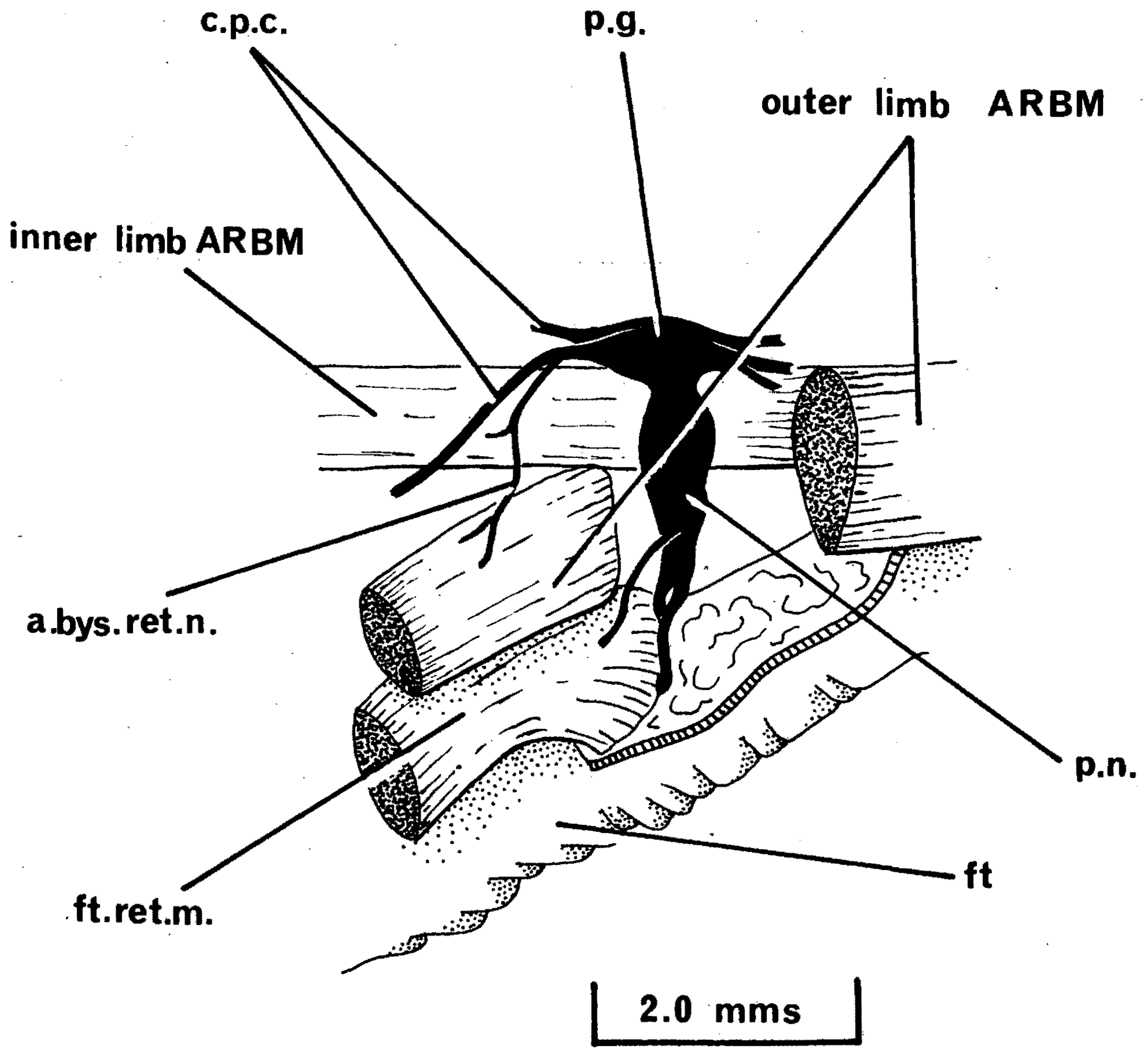
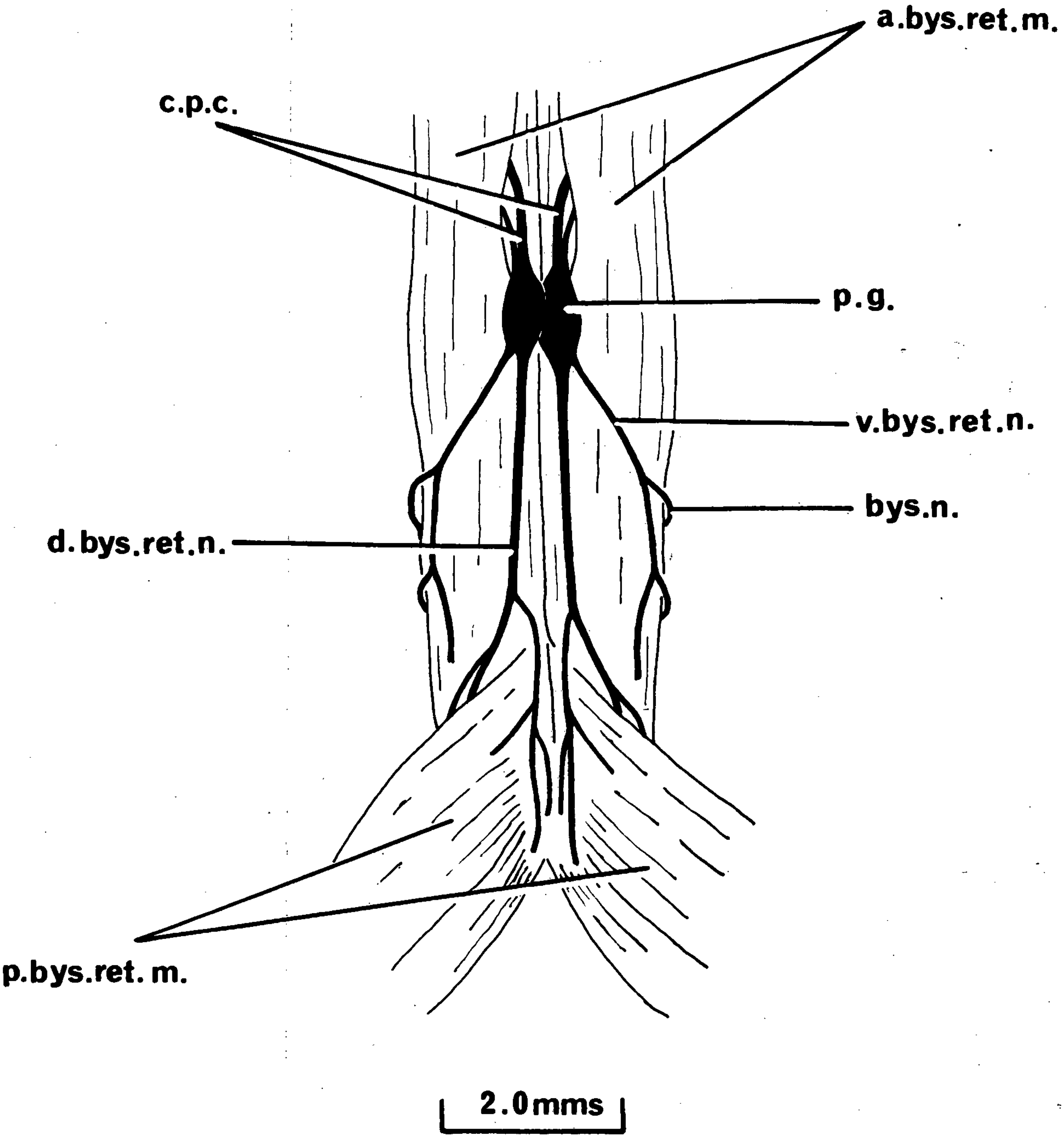

c.p.c.
p.g.
outer limb ARBM
inner limb ARBM
a.bys.ret.n.
p.n.
ft.ret.m.
ft
2.0 mms

FIGURE 20

A dorsal view of the pedal ganglion of *C.meridionalis* in situ, with the foot retractor muscles removed. The passage of the cerebro-pedal connective through the anterior byssus retractor muscle is shown.

c.p.c. - cerebro-pedal connective; d. bys. ret. n. - dorsal byssus retractor nerve; p. bys. ret. m. - posterior byssus retractor muscle; v. bys. ret. n. - ventral byssus retractor nerve; p.g. - pedal ganglion; a. bys. ret. m. - anterior byssus retractor muscle.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p.bys.ret.m.
2.0mms

FIGURE 21

The left pedal ganglion of A.magellanica and associated nerves. The foot retractor muscle has been pulled antero-ventrally.

p.g. - pedal ganglion; a. bys. ret. n. - anterior byssus retractor nerve; c.p.c. - cerebro-pedal connective; p.n. - pedal nerve; ft. ret. m. - foot retractor muscle; ft. - foot; bys. - byssus; by. n. 1 - byssus nerve 1; by. n. 2 - byssus nerve 2; p. bys. ret. m. - posterior byssus retractor muscle; v. bys. ret. n. - ventral byssus retractor nerve; a. bys. ret. m. - anterior byssus retractor muscle.

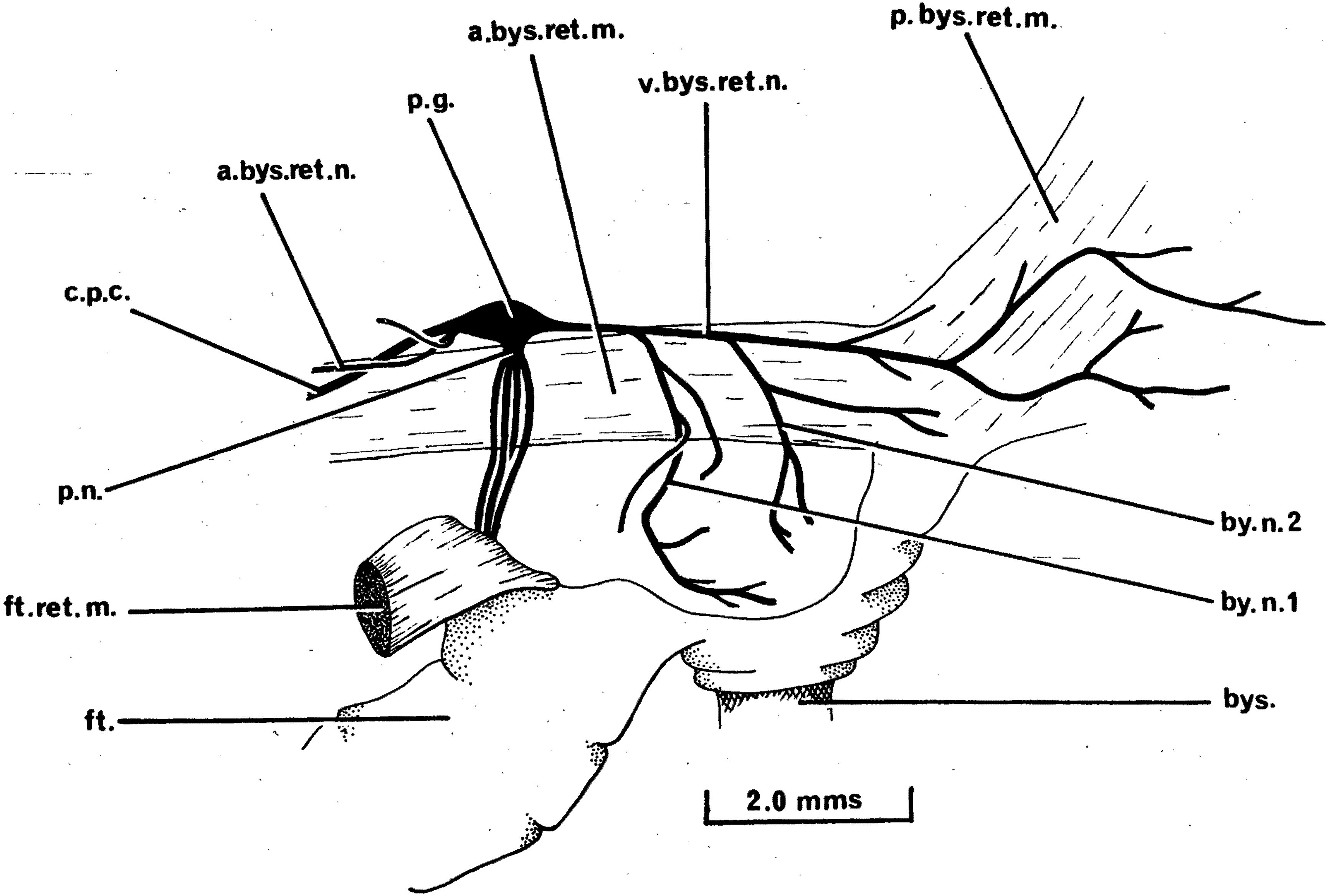
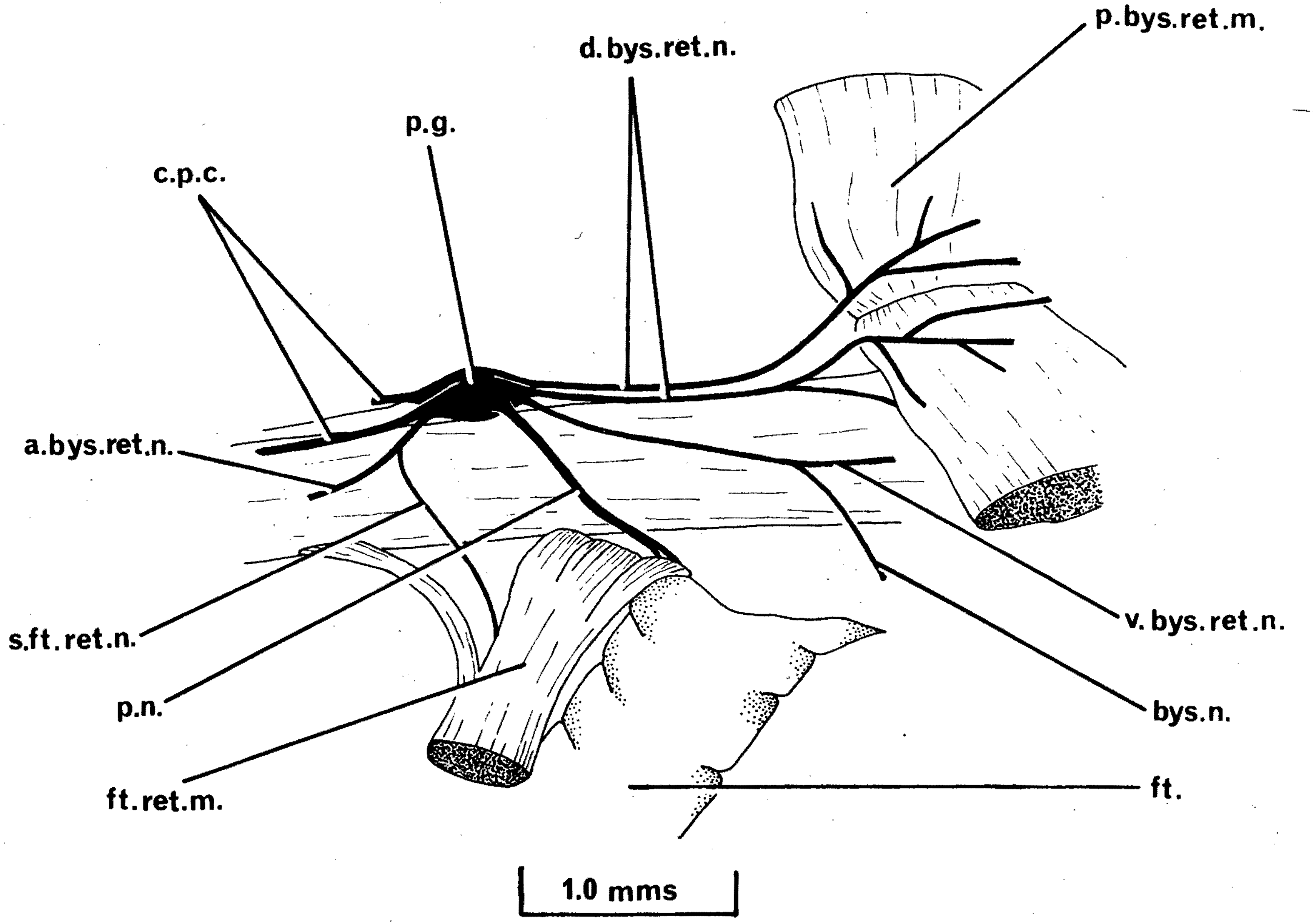

a.bys.ret.m.
p. bys.ret.m.
v.bys.ret.n.
p.g.
a.bys.ret.n.
c.p.c.
p.n.
by.n.2
by.n.1
ft.ret.m.
bys.
ft.
2.0 mms

FIGURE 22

The left pedal ganglion of *M.virgiliae* and associated nerves. The foot retractor muscle has been pulled antero-ventrally.

p.g. - pedal ganglion; c.p.c. - cerebro-pedal connective; a. bys. ret. m. - anterior byssus retractor muscle; s. ft. ret. n. - superficial foot retractor nerve; a. bys. ret. n. - anterior byssus retractor nerve; p.n. - pedal nerve; ft. ret. m. - foot retractor muscle; ft. - foot; bys. n. - byssus nerve; v. bys. ret. n. - ventral byssus retractor nerve; p. bys. ret. m. - posterior byssus retractor muscle; d. bys. ret. n. - dorsal byssus retractor nerve.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d.bys.ret.n.
p.g.
c.p.c.
a.bys.ret.n.
s.ft.ret.n.
p.n.
ft.ret.m.
v.bys.ret.n.
bys.n.
ft.
1.0 mms

FIGURE 23

The left pedal ganglion of *S.bilocularis* and associated nerves. The foot retractor muscle has been pulled antero-ventrally.

p.g. - pedal ganglion; c.p.c. - cerebo-pedal connective; a. bys. ret. m. - anterior byssus retractor muscle; a. bys. ret. n. - anterior byssus retractor nerve; p.n. - pedal nerve; ft. ret. m. - foot retractor muscle; ft. - foot; bys. - byssus; bys. n. - byssus nerve; v. bys. ret. n. - ventral byssus retractor nerve; p. bys. ret. m. - posterior byssus retractor muscle; d. bys. ret. n. - dorsal byssus retractor nerve.

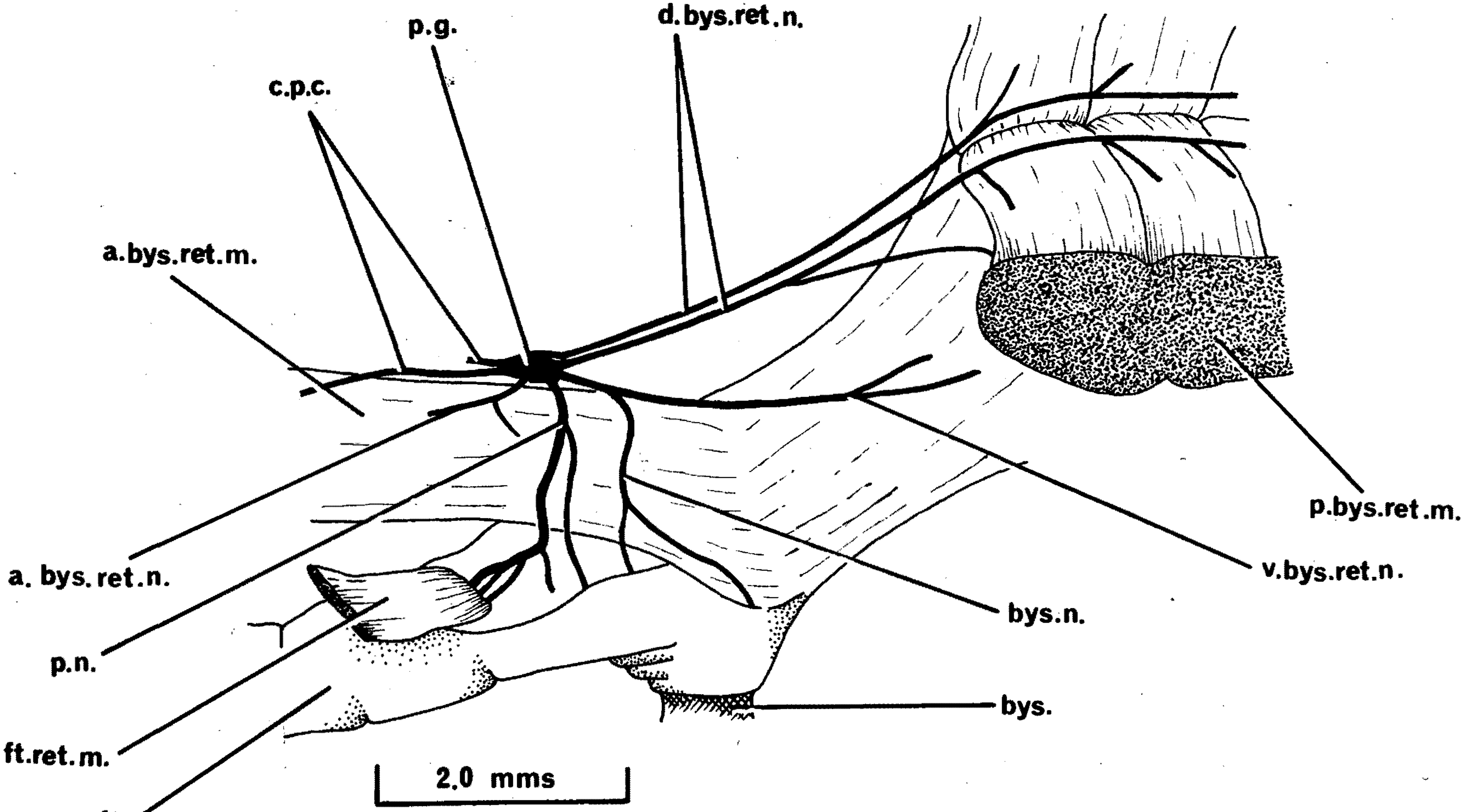
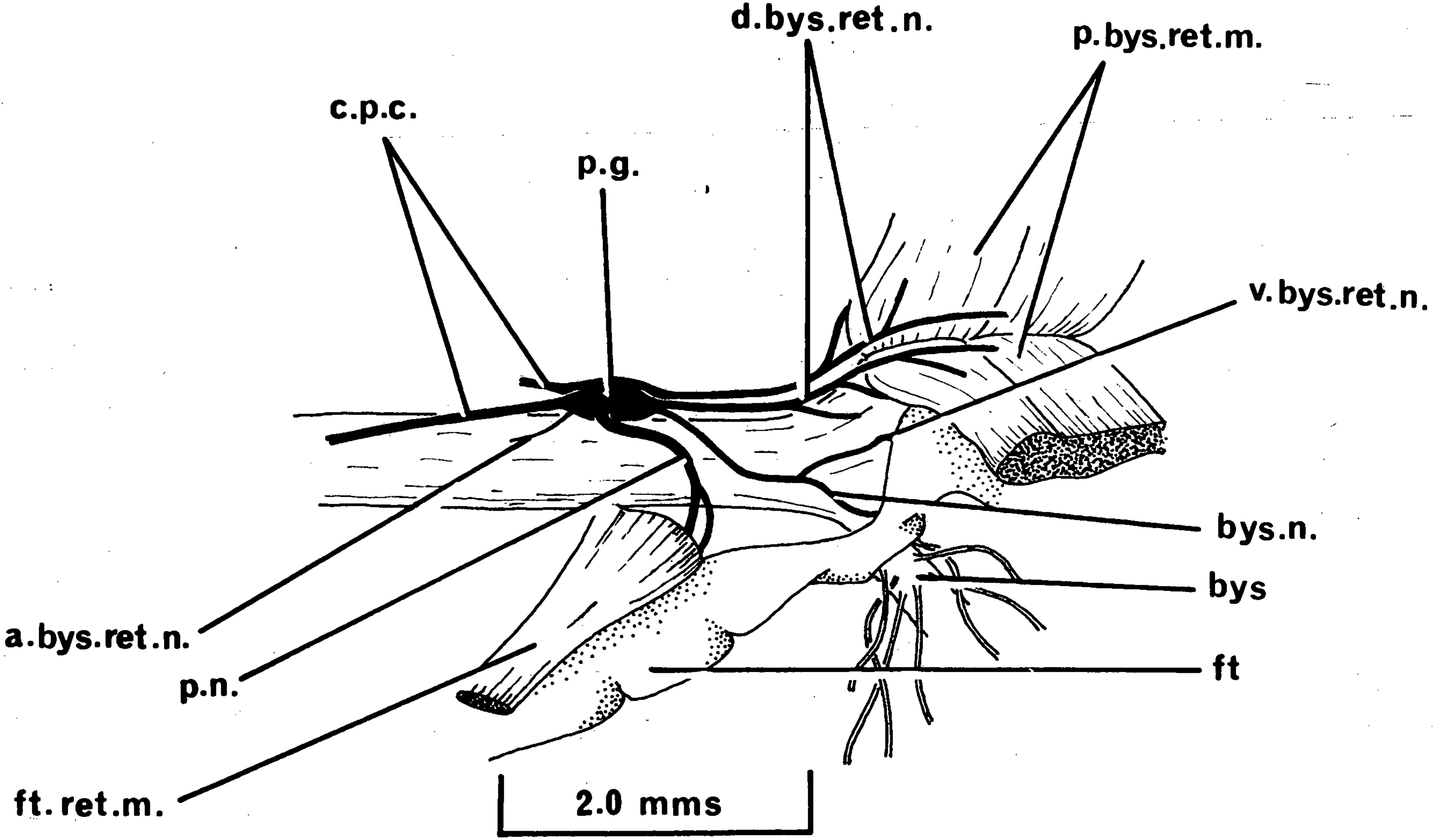

p.g.
d.bys.ret.n.
c.p.c.
a.bys.ret.m.
a. bys. ret.n.
p.n.
ft.ret.m.
ft
p.bys.ret.m.
v.bys.ret.n.
bys.n.
bys.
2,0 mms

FIGURE 24

The left pedal ganglion of *L. capensis* and associated nerves. The foot retractor muscle has been pulled antero-ventrally.

p.g. - pedal ganglion; c.p.c. - cerebo-pedal connective; a. bys. ret. n. - anterior byssus retractor nerve; p.n. - pedal nerve; ft. ret. m. - foot retractor muscle; ft. - foot; bys. - byssus; bys.n. - byssus nerve; v. bys. ret. n. - ventral byssus retractor nerve; p. bys ret. m. - posterior byssus retractor muscle; d. bys. ret. n. - dorsal byssus retractor nerve.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p.n.
ft.ret.m.
2.0 mms

(a) anterior byssus retractor nerve

Although un-named in *Mytilus latus*, Purdie (1887, p. 38) has described it as ".... a small nerve that becomes lost in the retractors of the foot." List (1902) gives no counterpart for this nerve in *Mytilus galloprovincialis*, but it may be represented by his *N.visceralis* in part. However, the *N.visceralis* proper should arise from the cerebro-visceral connective (White, 1937 : fig 30) and not from the cerebro-pedal connective, as figured by List (1902 : fig 17). Van Nieuwenhoven (1947) states that the nerves which innervate the anterior byssus retractor muscles in *Mytilus edulis* arise from the posterior surface of the pedal ganglion, but Takahashi (1960) has shown, by both dissection and electrical stimulation, that this statement is erroneous, and that in *M.edulis*, the anterior byssus retractor nerve consists of fine fibres originating in the pedal ganglion via branches of the cerebro-pedal connective. This arrangement (Takahashi, 1960 : fig 2) was not found in any of the species examined in this paper.

The anterior byssus retractor nerve (figs 17 - 24) arises as a single root on the anterior lateral edge of the pedal ganglion. In *P.perna* (fig 17) and *S.bilocularis* (fig 23) this root is well separated from the cerebro-pedal connective, but in *M.virgilise* (fig 22), *C.meridionalis* (fig 19), *L.capensis* (fig 24) and *A.magellanica* (fig 21), the anterior byssus retractor nerve arises almost at the ~~point where~~ junction of the cerebro-pedal connective ~~joins~~ with the pedal ganglion. As will be seen, there are slight modifications to this.

In *P.perna*, the nerve divides into two branches almost immediately (fig 17). The thinner and more anteriorly directing branch is the anterior byssus retractor nerve. This runs superficially along the outer lateral surface of the anterior byssus retractor muscle, giving off small side branches as it does so. The thicker of the two nerves, which I have termed the superficial foot retractor nerve, runs posteriorly and horizontally along the ganglion for a short distance (fig 17), before turning laterally outwards and running over the anterior byssus retractor muscle. It gives off a small branch, anteriorly directed, which dives deeply between the muscle bundles of the anterior retractor muscle. The main portion of the nerve continues in a lateral direction, until it reaches the foot retractor muscle, where it branches into two approximately equal nerves (fig 17), which run anteriorly around the muscle and come to lie on its outer lateral surface. Both nerves continue dorsally towards the point of insertion of the foot retractor muscle.

In *S.bilocularis* (fig 23), the anterior byssus retractor nerve is very fine. It runs antero-ventrally in an oblique direction, across the anterior byssus retractor muscle, as in *P.perna*, towards the point of insertion of this muscle on the shell. A short distance from the ganglion, the nerve gives off a fine branch, corresponding in position to the superficial foot retractor nerve in *P.perna*. It was not possible to follow this nerve, because it was too fine.

A similar situation in found in *M.virgiliae* (fig 22), where the anterior byssus retractor nerve follows the usual course, and the fine lateral branch, the superficial foot retractor nerve, passes laterally outwards between the two bundles of the foot retractor muscle. This nerve continues dorsally along the outer lateral surface of the foot retractor muscle. Unlike the nerve in *P.perna*, the superficial foot retractor nerve does not branch.

In *A.magellanica* (fig 21), a modification of the above plan is found. Here, the anterior byssus retractor nerve first gives off a fine branch, which runs latero-dorsally through the digestive gland (? superficial foot retractor nerve), while the main portion of the nerve crosses dorsally over the cerebro-pedal connective, and runs parallel with this connective along the dorsal side of the anterior byssus retractor muscle. However, when the cerebro-pedal connective crosses to the ventral side of the anterior retractor muscle, the anterior byssus retractor nerve continues along the mid-line of the dorsal side of the muscle to its insertion on the shell (fig 21). No nerve was found which corresponded to the superficial foot retractor nerve.

A superficial foot retractor nerve was also absent in

C.meridionalis (fig 19). In this species, the anterior byssus retractor nerve arises on the ventral surface of the cerebro-pedal connective, at its junction with the pedal ganglion. *C.meridionalis* is peculiar in that the anterior byssus retractor muscle is split into two bundles, by the passage of the cerebro-pedal connective. The anterior byssus retractor nerve follows the course of the cerebro-pedal connective through the anterior retractor muscle, and gives off small side branch nerves, which innervate the two muscular bundles.

The anterior byssus retractor nerve in *L.capensis* (fig 24) has its origin on the ventral surface of the pedal ganglion, as in *C.meridionalis*. It is a very fine nerve, seen only by lifting the ganglionic mass away from the muscles. It follows the general plan, by running obliquely across the anterior byssus retractor muscle, in an anterior direction, as in *P.perna*.

(b) *pedal nerve*

This is the most easily distinguishable of the nerves which arise from the pedal ganglion. It has been termed the *N.pedalis* by List (1902). In all species except *L.capensis*, the point of origin of this nerve is on the postero-lateral outer edge of the ganglion, at its region of greatest curvature. In *L.capensis* (fig 24), the origin is somewhat more anteriorly placed, at about the mid-point of the outer lateral edge of the ganglion.

In P.perna and L.capensis (figs 17, 24), the nerve runs posteriorly for a short distance, before turning laterally outwards to run over the anterior byssus retractor muscle, in a ventral direction. But in S.bilocularis, C.meridionalis and M.virgiliae (figs 23, 19, 22), directly on leaving the pedal ganglion, the pedal nerve runs obliquely over the anterior byssus retractor muscle. In A.magellanica (fig 21), its course is almost directly ventral, and a very short distance from the ganglion, the pedal nerve divides into a number of smaller, approximately-equally sized branches (usually 4), which run laterally over the anterior byssus retractor muscle and penetrate the foot along the inner side of the foot retractor muscle.

In all the other species examined, the pedal nerve runs over the anterior byssus retractor muscle as a single nerve. On entering the foot, the pedal nerve gives off a smaller posterior branch, which dives into the byssus gland. The pedal nerve continues into the foot with the foot retractor muscle, as in A.magellanica, and splits up into numerous smaller and approximately equally-sized nerves. These run dorsally and ventrally along the inner side of the foot retractor muscle (figs 17 - 24).

(c) ventral byssus retractor nerve

This nerve is termed the N.retractorum byssi (Np_1) by List (1902), but in accordance with Field (1922) and

White (1937), is called the ventral byssus retractor nerve in this paper. Purdie (1887) maintains that this is the byssal nerve, but in all cases, I have derrived the byssal nerve from the ventral byssus retractor nerve. The nerve follows the same general plan in all the species examined, so that the description for _P.perna_, given below, suffices as a general description.

The ventral byssus retractor nerve arises as a small root, at the posterior end of the pedal ganglion, between the pedal nerve and the dorsal byssus retractor nerve. It runs posteriorly along the dorsal surface of the anterior byssus retractor muscle, and at the point where the anterior retractor muscle joins the dorsal byssus retractor muscle (or the posterior byssus retractor muscle, in those species in which the dorsal retractor muscle is not distinguished), the nerve divides into two:

1. _the byssal nerve_

This is a small nerve, which runs superficially over the anterior byssus retractor muscle, in a ventral direction. It divides into a number of smaller nerves, which penetrate the byssus gland.

The byssal nerve of _A.magellanica_ (fig 21) is more complex. The ventral byssus retractor nerve passes ventrally and obliquely across the anterior byssus retractor muscle and gives rise to two byssal nerves:

(i) byssal nerve 1

This nerve runs across the outer lateral surface of the anterior byssus retractor muscle in a ventral direction. It gives rise to two smaller nerves, which penetrate the anterior region of the byssus, but the main nerve continues ventrally and superficially in the outer wall of the byssus gland, and then turns posterioly. It gives off numerous smaller nerve fibres (fig 21).

(ii) byssal nerve 2

The byssal nerve 2 arises from the ventral byssus retractor nerve a short distance from the origin of byssal nerve 1. Again, it runs over the anterior byssus retractor muscle, and divides into two equal branches. The most dorsal of these branches continues posteriorly to innervate the postero-dorsal region of the byssus gland, while the ventral branch continues along its course and divides into smaller nerves, innervating the median and lateral regions of the byssus.

2. the ventral byssus retractor nerve

Once the byssal nerve has been given off, the ventral byssus retractor nerve continues in a slightly postero-dorsal direction and then divides into smaller branches. These cover the area at the junction of the anterior byssus retractor muscles and the dorsal byssus retractor muscles, almost dorsally above the byssus apparatus.

(d) dorsal byssus retractor nerve

This nerve corresponds to the N.retractorum byssi (Np$_2$) of List (1902) and the dorsal byssus retractor nerve of Field (1922) and White (1937). Differences in the orientation of the dorsal and posterior retractor muscles in different species, are mirrored by differences in the course of this nerve. For the sake of simplicity, descriptions of this nerve, in each species, are dealt with seperately.

P.perna (fig 18)

In P.perna , the dorsal byssus retractor nerve is much thicker than in Mytilus latus or M.edulis, and is perhaps the most important nerve innervating the byssus retractor muscles. The nerve arises at the inner posterior angle of the pedal ganglion and travels posteriorly alongside the mid-line between the two anterior byssus retractor muscles. It continues postero-dorsally before giving off its first branch:

(a) this nerve runs latero-dorsally, to continue along the outer lateral surface of the dorsal retractor muscle. The nerve divides into a thinner branch, which runs more or less along the anterior surface of the muscle, and a thicker branch, which runs on the flat outer surface of the muscle.

The dorsal byssus retractor nerve continues postero-dorsally, and runs up each side of the mid-line through the V, formed by the junction of the dorsal byssus retractor muscles from each shell valve. Here it gives off two nerves:

(b) a median branch, which runs over the dorsal retractor muscle, and dives deeply into the posterior byssus retractor muscle, almost at the origin of that muscle.

(c) the second nerve runs dorsally along the inner lateral side of the dorsal byssus retractor muscle, towards its point of insertion on the shell valves.

The dorsal byssus retractor nerve then crosses over the dorsal byssus retractor muscle, onto the dorsal surface of the posterior byssus retractor muscle, and continues along this muscle towards its point of insertion on the shell valves. However, as it crosses onto the posterior retractor muscle, the nerve gives off another small branch:

(d) this nerve arises on the inner side of the dorsal byssus retractor nerve and loops under that nerve. It then runs laterally round the outer edge of the posterior byssus retractor muscle and along its ventral surface, towards the point of insertion of that muscle on the shell valves.

<u>S.bilocularis</u> (fig 23)

The dorsal byssus retractor nerve has its origin on the dorsal posterior side of the pedal ganglion. On leaving the ganglion, it runs postero-dorsally through the V, formed by the posterior byssus retractor muscles. Just before the V, it gives off a very fine branch, which runs latero-dorsally, along the outer lateral side of the posterior byssus retractor muscles. The main part of the nerve continues through the V and along the upper surfaces of the bundles of the posterior byssus retractor muscles. During this postero-dorsal course, it gives rise to smaller branch nerves at each of the muscle bundles.

<u>A.magellanica</u> (fig 21)

Although the origin of the dorsal byssus retractor nerve is similar to <u>P.perna</u>, in <u>A.magellanica</u>, the nerve is extremely fine. It runs in a postero-dorsal direction through the connective tissue, and then between the V, formed by the posterior byssus retractor muscles. It continues along the dorsal side of these muscles (along the muscular shelf) and just anterior to the last pair of muscle bundles, it divides into two nerves, both of which dive into the last bundle.

<u>M.virgiliae</u> (fig 22)

The dorsal byssus retractor nerve has a similar arrangement and course in <u>M.virgiliae</u> as it does in <u>P.perna</u>.

On reaching the muscular V, it gives rise to a very fine branch, which runs latero-dorsally along the anterior edge of the dorsal byssus retractor muscle. The main portion of the nerve continues posteriorly along the muscular shelf of the posterior byssus retractor muscles, giving off side branches to each of the muscle bundles as it does so.

L.capensis (fig 24)

Although there is no separate dorsal byssus retractor muscle in this species, ~~the course of~~ the dorsal byssus retractor nerve ~~is the same~~ follows the same course as in *M.virgiliae*.

C.meridionalis (fig 20)

The dorsal byssus retractor nerve has the same origin as in *P.perna*. The nerve runs posteriorly for a short distance and then postero-dorsally up through the muscular V. As it starts to turn dorsally, it gives off a branch from its inner lateral side, which runs under the main portion of the nerve, and onto the anterior and outer lateral surfaces of the posterior byssus retractor muscles. The main part of the nerve continues in a posterior direction through the V, and then runs along the muscular shelf, giving off smaller branch nerves to each of the muscle bundles of the posterior byssus retractor muscles.

Because of the lack of sufficient material, dissections of the nervous innervation of the foot/byssus musculature of

Semimytilus algosus were not done.

F. Alimentary Canal

Mussels are ciliary feeders on detritus and finely-divided, suspended matter in the water. Although Yonge (1946) is of the opinion that they are herbivorous, Mansour (1946, a, b) has shown that small copepods are often found in the stomachs of *Mytilus* specimens. A stream of water is drawn into the mantle cavity by ciliary activity (Atkins, 1936 - 1943) and the food particles, collected on the gills, are passed to the palps and then into the mouth (Ransom, 1926), which leads via a short oesophagus into the stomach. The stomach is perhaps the most important organ of the alimentary canal and is closely associated with the digestive gland (Owen, 1956), so that digestion can be both extra-cellular and intra-cellular (Mansour, 1946, a; Mansour-Bek, 1946). The complex arrangement of the ciliary tracts within the stomach (Graham, 1949), together with the rotation and dissolution of the crystalline style (Morton, 1960), allows further sorting to take place in the stomach. The worthless material and waste products from the digestive gland are then passed into the intestine, to be ~~excreted~~ discharged at the anus and ~~pass~~ passed out of the mantle cavity with the exhalent current of water.

Only the general gross anatomy of the alimentary canal has been studied in this paper; the histology of the different

FIGURE 25

The alimentary canal of P.perna from the left side. The outer gills and the digestive gland on the left side have been removed.

dig. gl. - digestive gland; oes. - oesophagus; mo. - mouth; lab. palps - labial palps; p. add. m. - posterior adductor muscle; cae. - caecum; dir. int. - direct intestine; term. int. - terminal intestine; rec. int. - recurrent intestine.

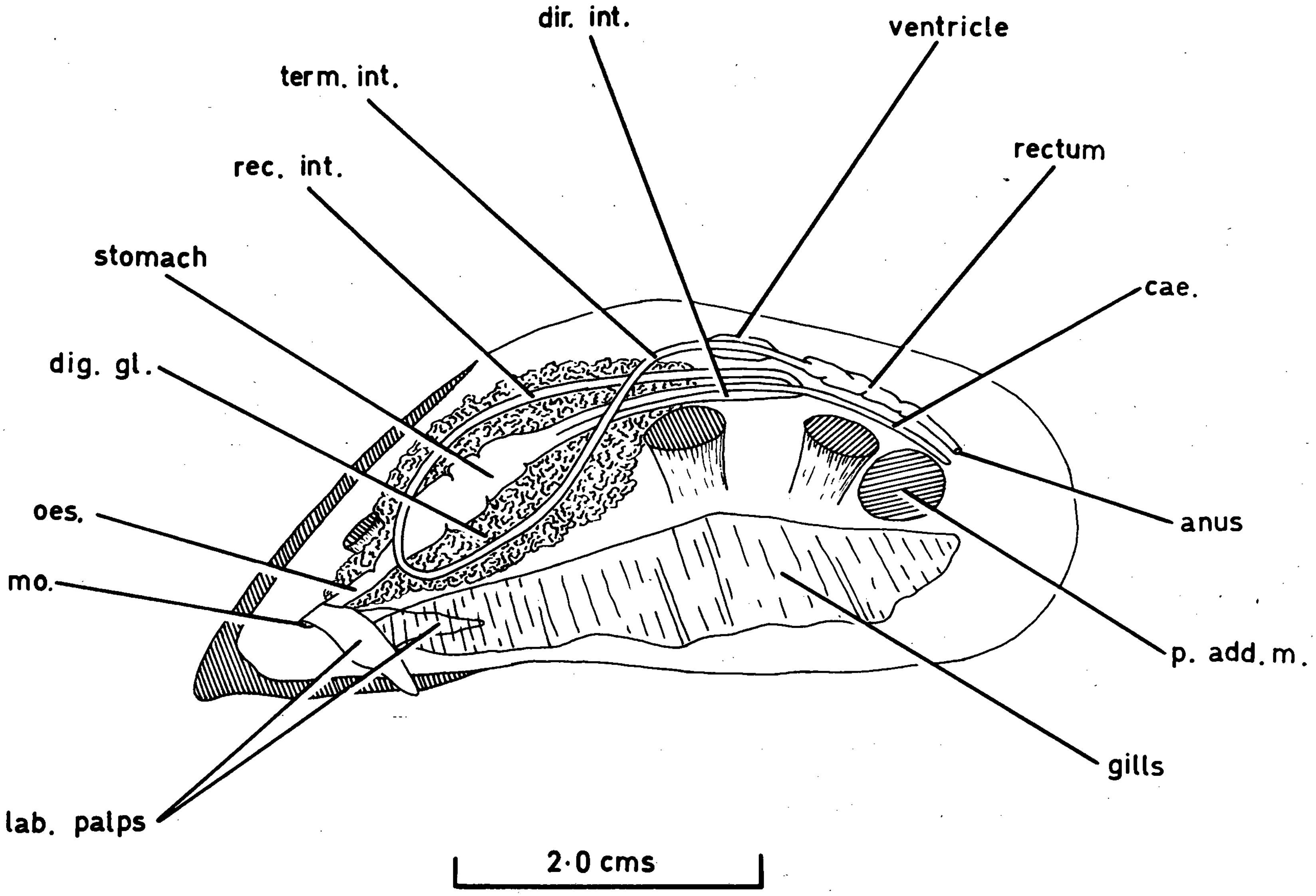
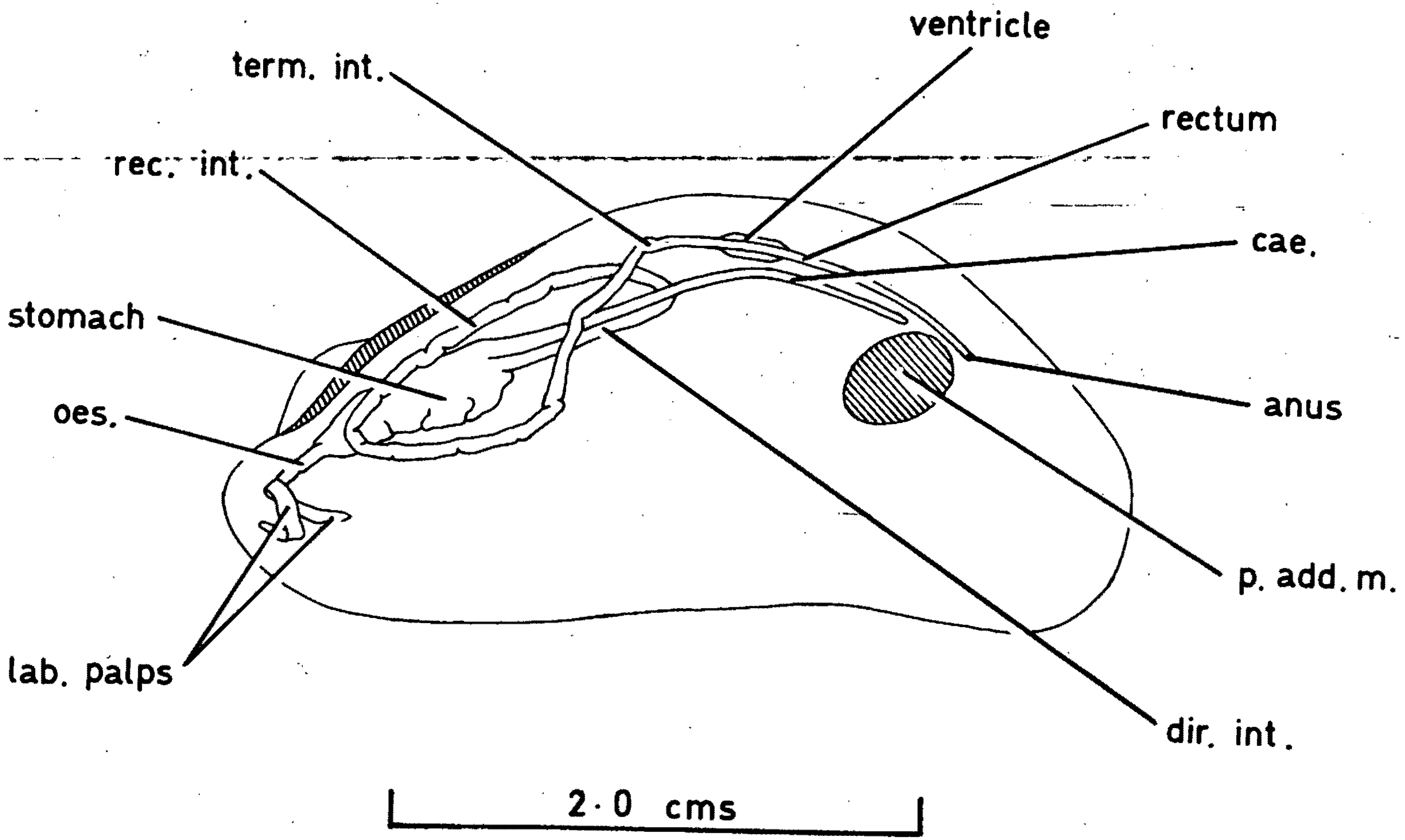

dir. int.
ventricle
term. int.
rectum
rec. int.
stomach
cae.
dig. gl.
anus
oes.
mo.
p. add. m.
gills
lab. palps
2·0 cms

FIGURE 26

The alimentray canal of a modioliform species from the left side.

oes. - oesophagus; lab. palps - labial palps; dir. int. - direct intestine; p. add. m. - posterior adductor muscle; cae. - caecum; term. int. - terminal intestine; rec. int. - recurrent intestine.


ventricle
term. int.
rectum
rec. int.
cae.
stomach
oes.
anus
p. add. m.
lab. palps
dir. int.
2·0 cms

regions of the canal has been given by List (1902), Field (1922) and White (1937).

The description of the alimentary canal up to, and including the stomach is the same for all species, except for the fact that there is a comparatively longer oesophagus in *A.magellanica* and *S.bilocularis* (figs 27, 28). There are however, differences in the intestine and crystalline style caecum, as the description will show.

The mouth is an elongate slit between the upper and lower lips, with which the outer labial palps and inner labial palps are continuous respectively. The palps are roughly triangular in shape, with a ridged inner surface and a smooth outer surface. The oesophagus arises a short distance behind the mouth opening, and continues posteriorly and dorsally, slightly to the right of the median line, between the paired anterior byssus retractor muscles. The stomach is irregularly shaped, more or less eliptical, with pouches in the ventral dorsal and lateral walls. The stomach is situated slightly to the right of the median line and almost below the posterior end of the ligament. Details of the internal anatomy of the stomach of related European species have been fully described by Graham (1949).

C.meridionalis, P.perna, S.algosus, L.capensis and *M.virgiliae*

(figs 25, 26)

The direct intestine arises at the posterior end of the stomach and passes backwards, slightly to the right of the mid-line of the byssus retractor muscles. At a point opposite the middle of the posterior retractors below, and the midpoint of the ventricle above, the intestine reflects on itself. It is then termed the recurrent intestine.

The recurrent intestine runs forwards and to the right of the mid-line, to a point under the posterior end of the ligament. Here it passes antero-ventrally and slightly to the left of the stomach, to form a loop in the digestive gland. The loop of the intestine is short in *C.meridionalis*, *M.virgiliae* and *S.algosus*, while in *P.perna* and *L.capensis*, the loop is comparatively longer and is tucked under the stomach. The loop marks the beginning of the terminal intestine.

The terminal intestine runs parallel with the anterior byssus retractor muscle for a short distance, and then turns dorsally and runs in a postero-dorsal direction, to cross over the direct intestine on the left. It then assumes a medial position. It runs posteriorly in this median plane above the recurrent intestine, and passes through the ventricle of the heart. After this, it continues as the rectum, dorso-ventrally flattened in *P.perna*, but almost cylindrical in *C.meridionalis*, *L.capensis*, *S.algosus* and *M.virgiliae*, to terminate at the anus, situated on the posterior surface of the posterior adductor muscle.

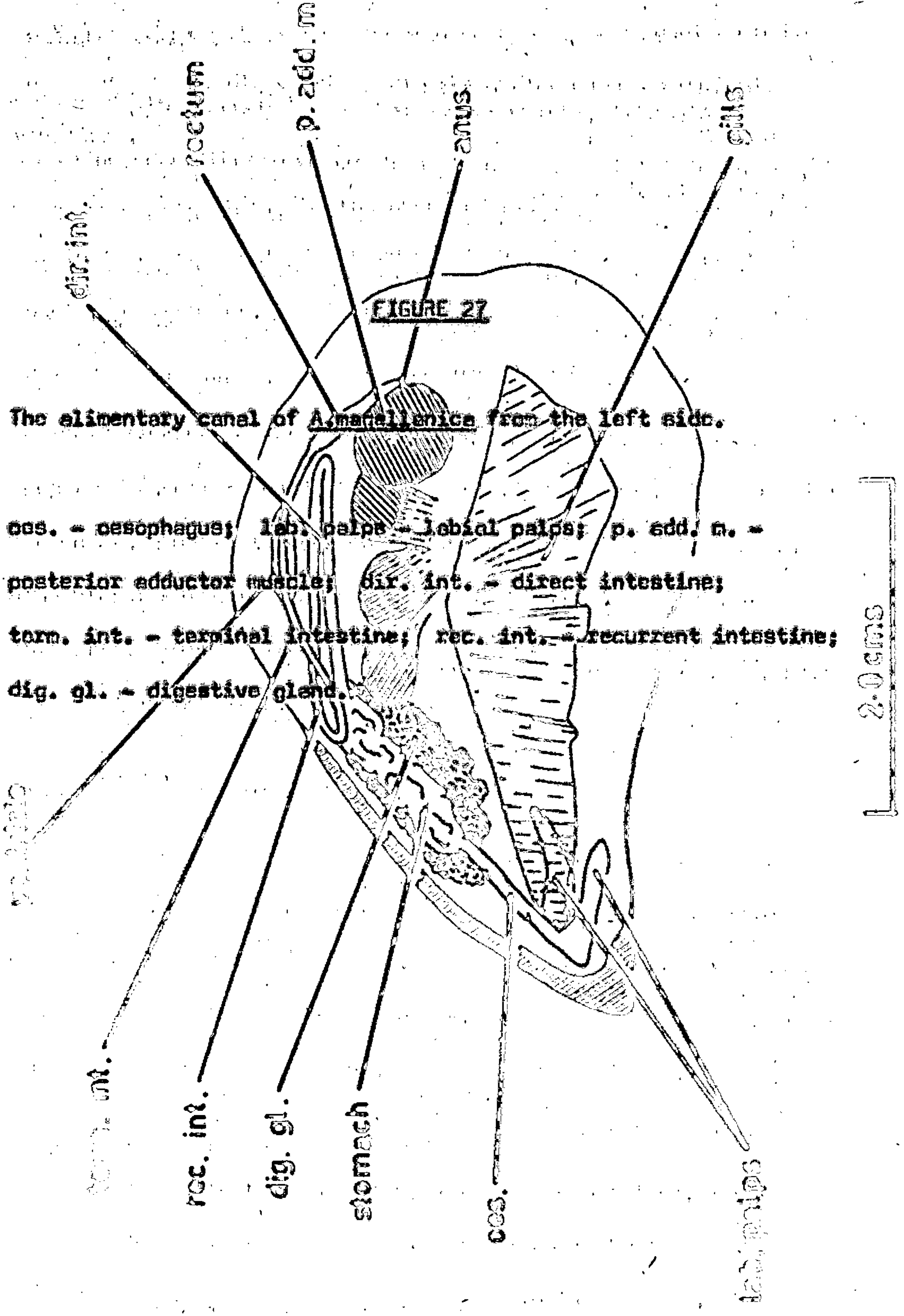
The caecum is an elongate structure, lying in the mid-line and directly above the origin of the direct intestine, with its origin at the posterior end of the stomach. It passes backwards under the floor of the pericardium, above the direct intestine and slightly to the left of the rectum, terminating alongside the anus on the posterior surface of the posterior adductor muscle. In C.meridionalis, L.capensis, S.algosus and M.virgilies, the caecum is about twice as long as the direct intestine, but in P.perna, it is only about a third longer than the direct intestine. The caecum is filled with a gelatinous substance, which extends throughout its entire length. This is the crystalline style.

A.magellanica and S.bilocularis (figs 27, 28)

The direct intestine arises at the posterior end of the stomach, and passes backwards in the plane of the mid-line of the byssus retractor muscles. At a point opposite the anterior end of the posterior adductor muscle, it reflects on itself, to run forwards and to the right of the direct intestine. The region is correspondingly called the recurrent intestine.

The recurrent intestine terminates in a loop, above the posterior end of the stomach. The loop is horizontal. This loop marks the beginning of the terminal intestine, which

FIGURE 27



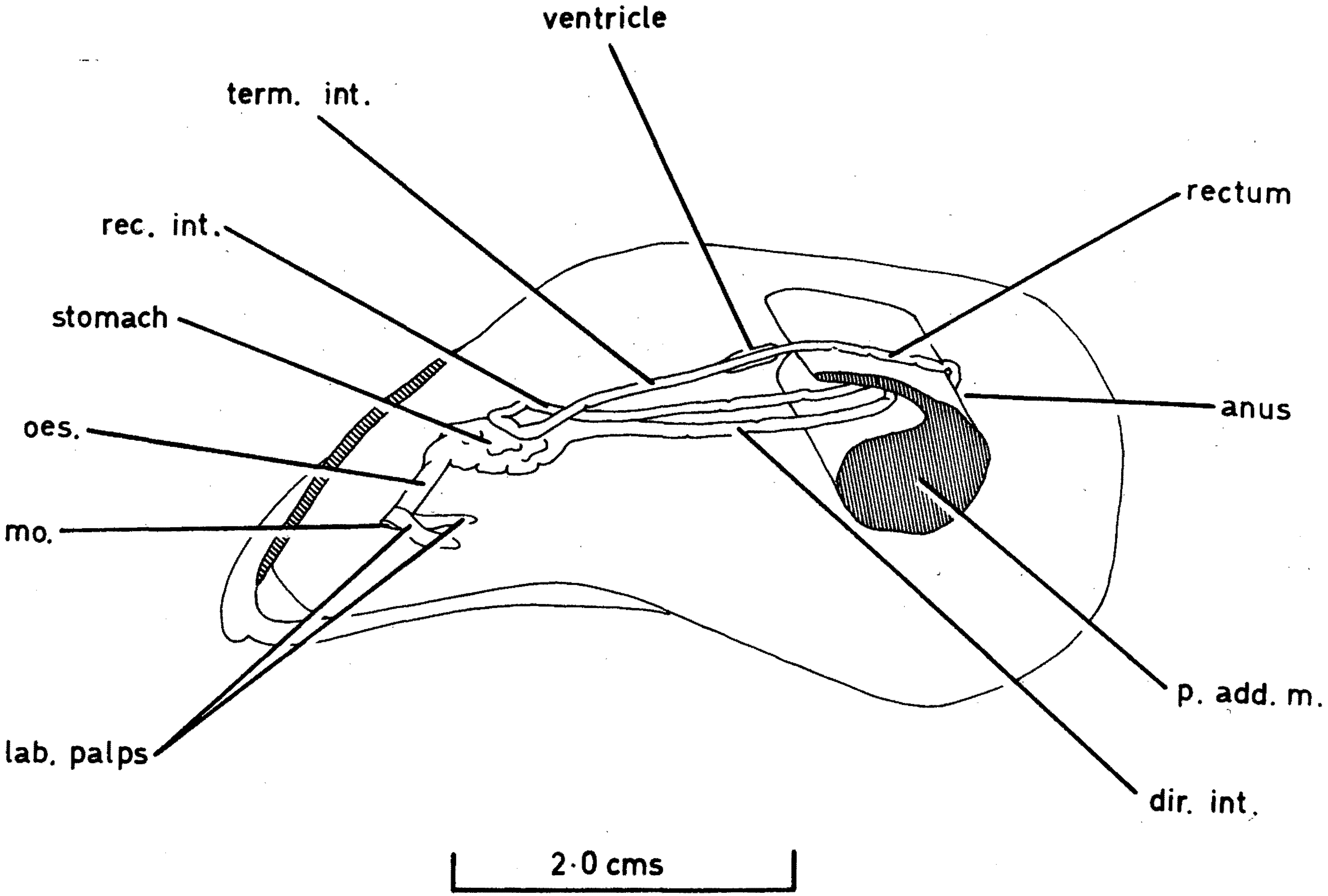
The alimentary canal of *A.magellanica* from the left side.

oes. = oesophagus; lab. palps - labial palps; p. add. m. - posterior adductor muscle; dir. int. - direct intestine; term. int. - terminal intestine; rec. int. - recurrent intestine; dig. gl. - digestive gland.

FIGURE 28

The alimentary canal of *S.bilocularis* from the left side, showing the looping of the direct intestine under the shelf of the posterior adductor muscle.

oes. - oesophagus; mo. - mouth; lab. palps - labial palps; dir. int. - direct intestine; p. add. m. - posterior adductor muscle; term. int. - terminal intestine; rec. int. - recurrent intestine.


ventricle
term. int.
rectum
rec. int.
stomach
anus
oes.
mo.
p. add. m.
lab. palps
dir. int.
2·0 cms

runs posteriorly in the mid-line of the byssus retractors and above the direct and recurrent intestines. At a point opposite and above the middle of the retractors, it passes through the ventricle.

After this, it continues posteriorly as the rectum, to terminate on the posterior surface of the posterior adductor muscle, ~~as~~ at the anus. The rectum of these two species is always surrounded by portions of the reproductive system.

Because of the anteriorly directing shelf of the posterior adductor muscle in *S.bilocularis* (fig 28), the posterior region of the direct/recurrent intestinal "loop" is flat and is separated from the rectum by the muscular shelf.

In both living and preserved specimens of *A.magellanica* and preserved specimens of *S.bilocularis* , the caecum was found to be absent.

Discussion on Anatomy

While gasteropods show a great variety in organisation and form, there are fewer structural patterns in lamellibranchs ~~have concentrated on fewer structural patterns~~. Morton (1960) has attributed their great success to the high degree of specialisation shown by them and to "the different ways in which a standard theme is given expression" (p. 48). The most remarkable feature, which this study has revealed, is the great similarity in the structure and arrangement of the internal organs. There is a single basic anatomical plan, which is only slightly modified in the different species. However, this is not altogether surprising, since all the species have a similar mode of life i.e. they are attached to a firm substratum by a byssus, and are all epifaunal. The environmental conditions are the only varying factors.

There is some variation in the size and number of the adductor muscles. Although no measurements were taken, it can be generally stated that the area of insertion of the adductor muscles is proportional to the size (total length) of the specimen. This applies equally to individuals within a species and to specimens of different species.

Both anterior and posterior adductor muscles are present in S.algosus, L.capensis and M.virgiliae; these species are typically heteromyarian, since the posterior adductor is much larger than the anterior adductor. In P.perna and C.meridionalis, the anterior adductor is absent, even in juvenile specimens i.e. these species are typically monomyarian. A.magellanica is unusual in that juvenile specimens are heteromyarian, while those above the size 15 - 20 mms (total length) are monomyarian.

Yonge (1962) has pointed out the significance of the byssus in evolution from isomyarianism, to heteromyarianism and finally to monomyarianism. In byssally attached genera, it is always the anterior half of the animal which becomes supressed, since due to the positions of the inhalent and exhalent currents (Yonge, 1954 : p. 452) "reduction of the anterior half of the body has survival value, reduction of the posterior half has none." Reduction of the anterior half therefore, leads to an anterior shift in position of the byssus and subsequent reduction of the anterior adductor. Followed to its ultimate conclusion, the anterior adductor is completely lost. The above anatomy confirms this, for as has been pointed out, the heteromyarian condition in A.magellanica is transitional, and that with increasing size, a monomyarian condition is achieved.

Lanistina (not examined in this study) seems to be an exception to this scheme. Barnard (1964 : fig 9d) has shown that although this species is modioliform in shape and is also byssally attached, it is the posterior half of the shell which is reduced, so that the posterior adductor becomes supressed and is smaller than the anterior adductor. However no work has been done on this species, with reference to the position of the inhalent and exhalent currents.

The peculiar anteriorly-projecting shelf of the posterior adductor muscle in *S.bilocularis* has already been noted by Pelseneer (1911), but no functional reason for this has been given. A similar condition is found in at least two other families, the Isognomonotidae (*Isognomum* and *Malleus*) and the Pteriidae (*Meleagrina*).

Differences in the size of the foot may account for differences in the size and insertion of the foot retractor muscles. In only two species, *M.virgiliae* and *S.bilocularis*, is there evidence of splitting of the foot retractor muscles. In *M.virgiliae*, the foot retractor possesses an anterior directing branch, which runs laterally and ventrally along the anterior byssus retractor muscle, while only some specimens of *S.bilocularis* possess a ventral foot retractor muscle (fig 13).

The byssus retractor muscles have been the subject of much neuromuscular physiological research. Of particular interest, has been the fact that these muscles (like the adductors) are capable of maintaining high tensions for long periods of time. The results and implications of these studies are beyond the scope of this paper, but the relevant literature has been reviewed by Hoyle (1957, 1964).

The muscle bridge, formed by the byssus retractor muscles, is essentually the same in all species. Williamson

(1907) has described the secretion and formation of the byssus threads and stem in the ventral groove of the foot, and observations in the laboratory have confirmed that during the secretion process, tensioning-up of the threads takes place. Once the first byssus thread has been fixed in position, the animal crawls away from this position until the thread becomes taught. The second thread is then secreted. This process is continued until the animal is firmly secured to the substratum. There appears to be no fixed pattern in the secretion of the threads, and it was noticed that during the tensioning-up process, some of the existing threads became slack. However, functional threads always appeared to be taught. Although it is the ends of the byssus threads which are fixed to the substratum, as a result of ~~by means of~~ this tensioning-up process, the byssus stem becomes the 'fixed' point. The byssus retractor muscles operate about the byssus stem. This would mean that not only is the byssus the fixed point about which the growth axes are orientated (Yonge, 1954), but it may also be considered as the fixed point about which the byssus retractor muscles operate.

There is no doubt that for basic movements of the shell valves, the anterior byssus retractor muscles are diagonally antagonistic to the posterior byssus retractor muscles i.e. the left anterior byssus retractor muscle would be antagonistic to the right posterior byssus retractor muscle. Such movements of the shell valves are presumably required when silting of the mussel beds takes place, since the animals can only survive as long as they can communicate with the exterior by their siphonal openings (Dodgson, 1928). Observations in the field have confirmed that for C.meridionalis at least, there is a general movement of shell valves in the mussel bank, on the incoming and outgoing tides. Also Maas (1942) has reported that juvenile specimens of M.edulis can orientate themselves so that the umbo is pointed downwards and is surrounded by as much of the substratum as possible. Perhaps the antagonistically arranged byssus retractor muscles bring about such movements. However, observations in the laboratory have shown that shell movement brought about by the byssus retractor muscles is slight.

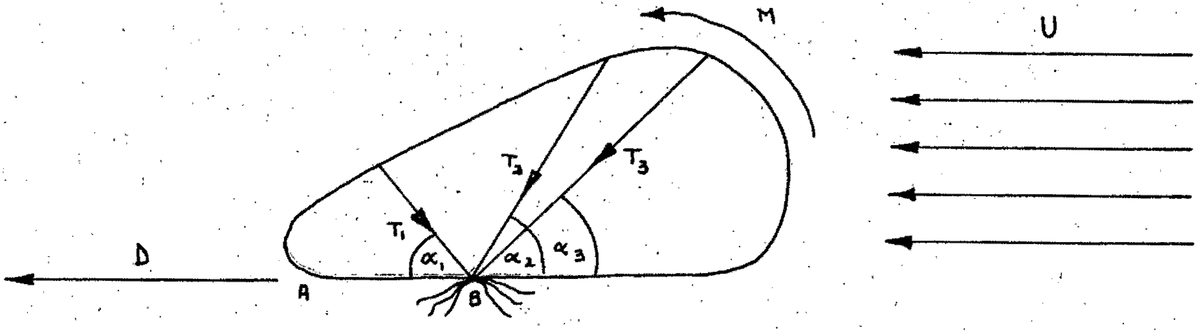
The byssus retractors consist of 2 or 3 pairs of muscles. All species possess an anterior pair (in S.algosus, there are two pairs), which insert on the shell at the apex of the umbo in modioliform species, or just behind the umbo and adjacent to the ligament in mytiliform species. Posterior byssus retractors are also present in all species, but in some, P.perna, M.virgiliae and some specimens of C.meridionalis and A.magellanica, the posterior retractors are organised into two separate and definite groups. In these cases, a pair of dorsal byssus retractor muscles is differentiated. It must be noted that each of the muscle groups may be split into numerous bundles of muscle fibres e.g. the dorsal byssus retractor of P.perna is usually composed of 3 - 5 such muscle bundles, each of which has its own area of insertion, so that their separate scars are easily seen. Small nacreous ridges separate the scars of the individual bundles, within the area of the dorsal retractor scar.

In those species without a definite pair of dorsal byssus retractor muscles, *L.capensis*, *S.algosus*, *S.bilocularis* and usually *C.meridionalis* and *A.magellanica*, the posterior byssus retractor muscle is split into numerous bundles, which insert on the shell in a line of separate scars (*A.magellanica* and *C.meridionalis*) or at one single extended scar (*L.capensis*, *S.bilocularis* and *S.algosus*), which is opposite the posterior end of the ligament. Examination of the nervous system of the byssus retractor muscles has revealed that these dorsal and posterior byssus retractor muscles are innervated by a single pair of nerves, which originate at the pedal ganglion, the dorsal byssus retractor nerves. In all cases, the dorsal byssus retractor nerve was similarly arranged, in that once passing through the muscular V, nerves were given off from it to each of the muscle bundles. No difference in arrangement of the side branches was observed either in *P.perna* (separate dorsal muscle) or in *A.magellanica* and *L.capensis* (no separate dorsal muscle).

It would appear therefore that the association of muscular bundles into dorsal and posterior retractors has no anatomical validity, and that the grouping of the more anterior bundles of the posterior retractor into a well separated dorsal retractor is only of functional significance to the animal. This is supported by the fact that the posterior byssus retractor muscles appeared to be separated into numerous smaller bundles in specimens of *A.magellanica* from exposed localities, while the single continuous scar was found in specimens of *A.magellanica* from less exposed localities.

The dorsal byssus retractor muscles (or those anterior groups of the posterior byssus retractors) are perhaps the most important muscles in the functioning of the byssus as a holdfast, for they act almost directly above the byssus stem, and can therefore exert maximum force on the byssus threads. In both *P.perna* and *A.magellanica*, these muscles are fairly large, suggesting that these species ~~are subject to~~ can resist strong wave action. This is found to be the case in their ecological distribution. On the west coast, *A.magellanica* occurs in more exposed localities than *C.meridionalis*, while on the south coast, *P.perna* occurs in the more exposed localities. Also Yonge (1967 : personal communication) has pointed out that *M.edulis* on the coast of California suddenly gives place to *M.californianus*, where exposure exceeds a certain point. The needs for attachment must be very different in different cases.

The grouping of the muscles of the posterior and anterior byssus retractors may then be explained in terms of their environment. This is presented in a simplified mathematical treatment below, where for the purposes of comparison, the byssus stem is taken as a theoretical fixed point, about which the retractor muscles opperate:



Because of the stream-lining of the shape, flow from ~~the~~ one direction (against the posterior or buff end) needs to be considered. For a flow of water with velocity U, a drag D is experienced by the body. Assuming that the muscles only exert a force by contraction, the muscles with tensions T_2 and T_3 do not influence the drag resistance, since they act in the same direction. The drag D is therefore counteracted by the muscle with tension T_1.

Therefore at equilibrium:

$$D = T_1 \cos \alpha_1 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

The drag in a body approximately increases with the square of the velocity of the water:

$$D \propto U^2$$

From equation (1):

$$\text{As } \alpha_1 \longrightarrow 0^\circ, \quad \cos \alpha_1 \longrightarrow 1$$

$$\text{and } T_1 \cos \alpha_1 \longrightarrow T_1$$

i.e. a greater resistance to the drag can be obtained by decreasing the angle α_1.

This means that a greater speed of water (and subsequent drag) may be resisted by having the anterior byssus retractor muscle positioned as far anteriorly as possible i.e. $\alpha_1 \longrightarrow 0^\circ$.

Besides the drag, the body will also experience a turning moment M about the point A (the anterior end). This moment M will be opposed by the forces in the muscles with tensions T_1, T_2 and T_3.

Therefore at equilibrium:

$$M = T_1 \sin \alpha_1 + T_2 \sin \alpha_2 + T_3 \sin \alpha_3 \quad \ldots\ldots(2)$$

From equation (2):

$$\text{As } \alpha \longrightarrow 90^\circ, \quad \sin \alpha \longrightarrow 1$$

$$\text{and } T \sin \alpha \longrightarrow T \quad \text{(in all three cases)}$$

i.e. a greater resistance to the moment can be obtained by increasing the angles α_1, α_2, α_3

NOTE: For the muscle with tension T_1, the angle α_1 must be the most suitable for resistance to both the drag and the turning moment.

FIGURE 30

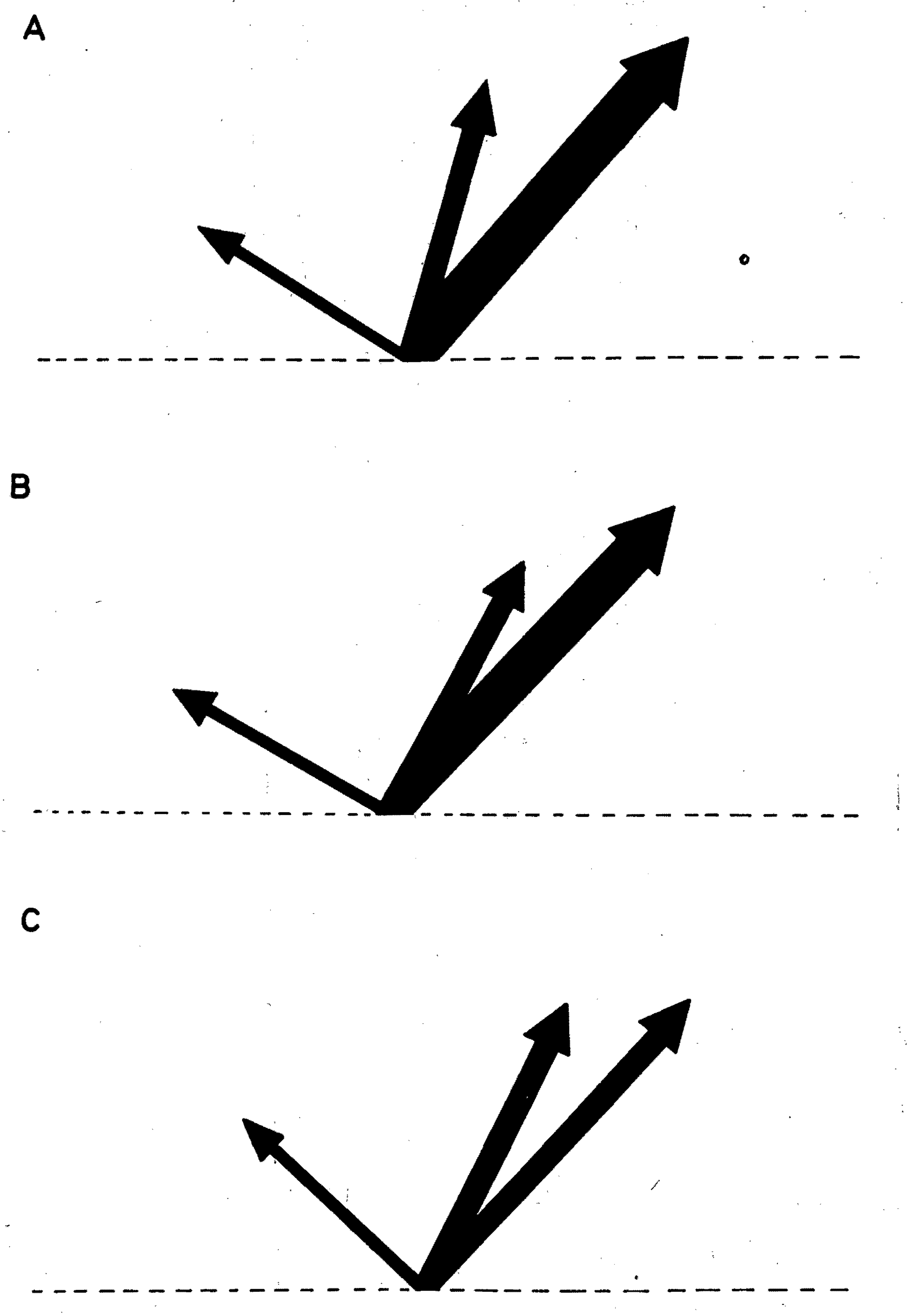
Force diagrams of the direction and strengths of the byssus retractor muscles of one valve, based on measurements from 10 specimens in each case.

A. *Perna perna*

B. *Aulacomya magellanica*

C. *Choromytilus meridionalis*

The direction of each muscle from the horizontal plane (ventral surface of the specimen) has been taken from measurement (Table 3) The strengths of each muscle, corresponding to the thickness of the arrow, is equivalent to the displacement volume of that muscle.


A
B
C

A series of measurements were taken on each of 10 specimens of *P.perna*, *A.magellanica* and *C.meridionalis* of approximately the same size. The position of the byssus stem (B) was fixed at a constant point, so that the distance AB was equal to one-third the total length. The positions of the muscles were constructed graphically from these measurements, and the average value of the angles calculated. These are given in Table 3. The displacement volume of each muscle bundle in every specimen was found; this volume corresponding to the relative strength of the muscle. The direction of tension and the relative strengths of the byssus retractor muscles in *P.perna*, *A.magellanica* and *C.meridionalis* are shown in fig 30.

Table 3: Average values of the angles of the byssus retractor muscles, relative to the ventral surface of the shell, calculated from 10 specimens (55 - 60 mms) of each of *P.perna*, *A.magellanica* and *C.meridionalis*.

	α_1	α_2	α_3
Perna perna	32.0°	74.0°	48.5°
Aulacomya magellanica	29.5°	62.0°	47.0°
Choromytilus meridionalis	44.0°	63.0°	47.0°

These measurements indicate that there is an anterior shift in the insertion of the anterior byssus retractor muscle in *P.perna* and *A.magellanica* as compared with *C.meridionalis*.

and that the relative strengths of this muscle are the same in all three species. Although there are differences in the relative strengths of the posterior byssus retractor muscles, these are constant in position in each of the species (Table 3). This would indicate:

$$\left(\frac{D}{M}\right)_{slow} < \left(\frac{D}{M}\right)_{fast}$$

i.e. that the drag is the more important factor, when the velocity of the water increases.

Therefore in those species living in exposed localities, the anterior byssus retractor muscle needs to be inserted on the shell as near the anterior end of the animal as possible.

It should be noted however, that in *P.perna*, the angle of the dorsal byssus retractor muscle is greater than the angle in *A.magellanica* and *C.meridionalis*, although the relative strengths of this muscle are the same in all three species, and that the relative strengths of the posterior byssus retractor muscle are greater in *P.perna* and *A.magellanica* than in *C.meridionalis*. This would seem to indicate that for this particular shape, the moment M increases in some complex manner with the increase in water velocity U.

The reason why there are never less than 2 muscle bundles in the posterior half of the shell, while there may be up to 7, is not evident. Presumably, splitting of the muscles into separate bundles occurs when more rigidity for the body is required.

However, it must be noted that the byssus stem does not necessarily occur at a distance one-third the total length from the anterior end. This distance was arbitrarily chosen for the purposes of comparison. The shell moves relatively to the byssus stem, so that the angles of the byssus retractor muscles are continually changing. The discussion therefore, does not attempt to describe the exact functioning of each muscle or set of muscles of the byssus. It is intended to show that the orientation of the byssus musculature, at least in the above three species, may be related to ecological habitat, and that while there may be differences in the position of the scars on the shell valves, these may only be of functional importance.

The above discussion has dealt with the orientation of the byssus retractor muscles in relation to the resistance to water movement and wave action. It has been suggested that resistance to predators may even be more important. However, Yonge (1962) has shown that the byssus is an essential agent in stability during metamorphosis of the post-larva. He points out that in those species in which the byssus is retained as a neotenous structure, it becomes massively developed and is "capable of maintaining the animal against powerful water movements" (p. 123) and may be associated with the change from an infaunal to an epifaunal mode of life. This would suggest that resistance to predators may be of secondary importance.

The Cape rock-lobster, *Jasus lalandii*, is one of the most important predators of *A.magellanica* and *C.meridionalis* (Heydorn, 1966). He states (p. 37) that "mussels which are loosely attached to the substratum by their byssus threads, and which can therefore be 'handled' by the rock-lobster, are selected for feeding." The rock-lobster manoeuvres the mussel into a suitable position and attacks the broad posterior end of the valves. Heydorn (1967 : personal communication) informs me that the mussels are attached to the substratum during the whole feeding process, and that "loosely attached specimens" are specimens occurring individually ~~individually occurring specimens~~ rather than those in clusters. There is however, no evidence to substantiate the fact that specimens occurring individually ~~individually occurring specimens~~ are more loosely attached to the substratum than those in clusters. This means therefore that mussels which can be easily manoeuvred are selected for feeding. i.e. ~~that in these cases,~~ gregariousness is of survival value, while the effectiveness of the byssus is ~~only~~ of secondary importance.

The alimentary systems of *C.meridionalis*, *P.perna*, *L.capensis*, *S.algosus* and *M.virgiliae* are essentially similar, except that the length of the loop of the intestine in *P.perna* and *M.virgiliae* is longer. Such a difference may be a secondary effect of muscle position.

The dorsal byssus retractor muscle in P.perna and M.virgilise has a more anterior insertion than in the other species. Consequently, the space between this muscle and the ligament is smaller. Since the intestine is looped within this space, the smaller the space, the greater the extent of looping.

The alimentary canals of A.magellanica and S.bilocularis are entirely different from the above-mentioned species. This difference may involve both specific differences (the absence of a caecum) and the secondary effect of muscle position (the horizontal loop of the intestine).

V. ORAL CONTRACTOR MUSCLE OF *C. meridionalis*

A. Anatomy

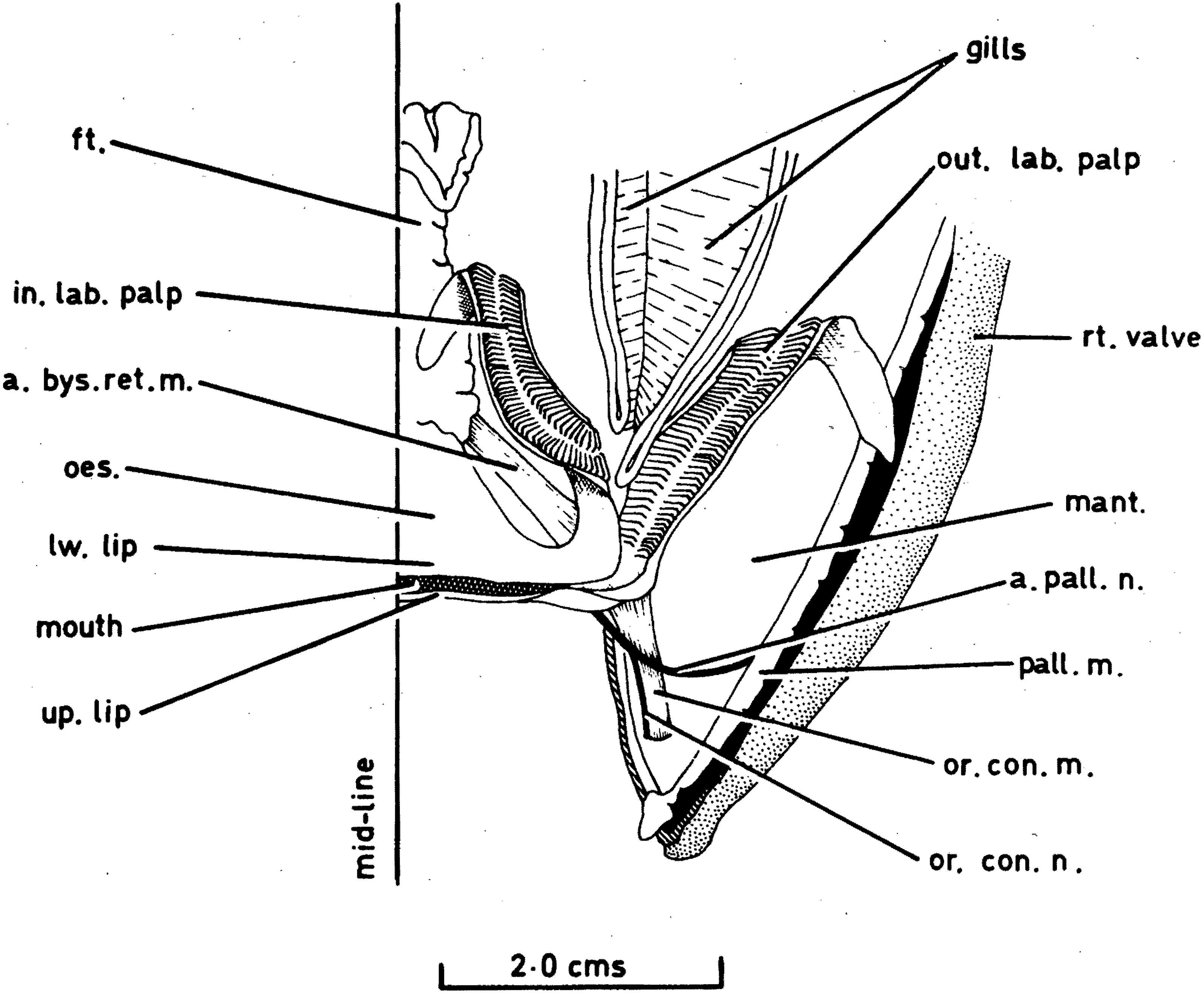
As has been pointed out above (see Muscle Impressions), the presence of this muscle in *C. meridionalis* was described as early as 1926 by Swart, and since the scar for this muscle was absent in all the other species examined, an investigation into the function of this muscle was deemed necessary. According to Swart (1926 : p. 285) this muscle "obviously serves the purpose of opening and closing the mouth by relaxing and contracting respectively", but such a statement warranted a more critical examination.

The oral contractor muscle is a small paired muscle arising from the anterior border of the proximal end of the upper labial palp on each side, where the latter is confluent with the mouth (fig 31). It inserts on the shell at the position of the oral contractor scar (fig 4), which is more anteriorly placed than the anterior byssus retractor scar. It is possible to see this muscle most easily ~~best~~ in living material, for once it is torn from its attachment to the shell, it withdraws into the tissues of the labial palp, whence it arises, and all traces are subsequently lost. The muscle is supplied by a nerve which arises in the cerebral ganglion, along with the anterior pallial nerve, with which it is confluent for some distance, before separating to run the length of the muscle to its insertion on the shell, while

FIGURE 31

The anterior region of the right shell valve of C.meridionalis, as seen from the ventral side, showing the origin and insertion of the oral contractor muscle.

ft. - foot; in. lab. palp - inner labial palp; a. bys. ret. m. - anterior byssus retractor muscle; oes. - oesophagus; lw. lip - lower lip; up. lip - upper lip; out. lab. palp - outer labial palp; rt. valve - right shell valve; mant. - mantle; a. pall. n. - anterior pallial nerve; pall. m. - pallial muscles; or. con. m. - oral contractor muscle; or. con. n. - oral contractor nerve.


gills
ft.
out. lab. palp
in. lab. palp
rt. valve
a. bys.ret.m.
oes.
mant.
lw. lip
a. pall. n.
mouth
pall. m.
up. lip
or. con. m.
mid-line
or. con. n.
2·0 cms

the pallial nerve runs ventrally under the muscle (fig 31). This nerve is called the oral contractor nerve.

B. Muscle Function

1. Method

(i) Mechanical and electrical stimulation

The oral contractor muscle in C.meridionalis was ~~both~~ mechanically stimulated with a needle and electrically stimulated by means of electrodes, connected to an induction coil circuit, and the effect of contraction noted.

(ii) Feeding experiments

These series of experiments were performed mainly with specimens of C.meridionalis, although they were repeated with P.perna and A.magellanica for control purposes, to show the significance of the oral contractor muscle, present only in C.meridionalis.

Specimens were kept in clean sea water, which was changed daily and kept constantly aerated. Tides were simulated by the removal of the water from the tank and exposure of the mussels for two hours in every twelve hours. During this time, the specimens were kept moist by infrequent sprinklings of sea water. It was noted that the feeding behaviour was at maximum intensity when the specimens were again covered by sea water after exposure, and consequently the feeding experiments were performed at this time.

In the case of C.meridionalis, the specimens for these experiments were opened by cutting the posterior adductor muscle and splaying the valves open. Although this method was of some significance, it tended to pull the oral contractor muscles taught, keeping them continually in a state of tension, ~~unless cut~~. Specimens opened in such a manner were then covered with sea water, which was kept constantly aerated. This allowed for a recovery period, usually from 15 to 20 minutes.

(a) Feeding on carmine particles

In these experiments, a suspension of carmine particles in sea water was used as a substitute for food, although Artemia eggs, and milk stained with Congo-red, were also tried. Due to the method of opening the valves, the oral contractor muscles were pulled taught, as pointed out above. Experiments were first performed on specimens in which the oral contractor muscle was left intact i.e. in its taught state (contracted), and then on specimens in which the muscle had been cut. In all experiments the carmine particles were transported to the palps, where they were sorted and then either rejected (regarded in the analysis as "not feeding") or transported to the mouth and eaten. The presence of carmine particles in the pouches of the stomach was confirmed by dissection, and such specimens were then said to have fed.

Small quantities of the carmine/sea water suspension were used at a time, since it was found that large quantities tended to clog, so that the mucous thread was simply rejected.

(b) Feeding with sand

Observations on the localities of *C.meridionalis* were responsible for this series of experiments.

Experiment 1

In this experiment, the specimens were not opened in the usual way. The anterior point of the specimen was cut off in both control and experimental animals. Only a small region of the shell was removed i.e. that region anterior to the insertion of the oral contractor muscle. In the control animals the oral contractor muscle was kept intact, but in the experimental animals, this muscle was broken from its attachment to the shell. The specimens were then placed in a tank containing clean sea water, which was changed daily and kept constantly aerated, for 2 to 3 days. Tides were simulated. This period was to allow for any sand particles present in the alimentary canal to be ~~excreted~~ discharged. All the specimens were then transferred to a tank containing aerated sea water, in which fine sand particles had been placed, and kept continually in suspension with the aid of an electrical stirrer. After 2 - 3 hours, the specimens were removed and their stomachs cut open, to ascertain the presence of sand particles. Due to the fact that there might be a positional effect in the tank, this experiment was performed twice, involving a total of 14 control animals and 14 in which the muscle had been cut.

In the case of _P.perna_ and _A.magellanica_, an aerated tank of sea water was used in which the sand was kept in suspension with the aid of an electrical stirrer. Specimens were placed in this tank intact, and left for 2 - 3 hours, so that feeding could take place. The specimens were then dissected and the presence or absence of sand in the stomach recorded.

Experiment 2

This experiment was undertaken as confirmatory evidence for the function of the oral contractor muscle.

50 similar-sized specimens of _C.meridionalis_ (40 - 60 mms total length) were collected in the field, at each of three different levels of the tide:

(a) at low tide - when the mussel bank was exposed

(b) 1 hour before exposure on the outgoing tide - when the mussel bank was just covered by sea water

(c) 1 hour after exposure on the incoming tide - when the mussel bank was again just covered by sea water.

The specimens were killed instantly in 90% ethyl alcohol to prevent defaecation. Each animal was removed from its shell in the laboratory, and thoroughly washed under running water.

It was then placed in a strong solution of boiling sodium hydroxide and dissolved. The remaining sand, from the alimentary canal, was then collected by filtration, and heated to constant weight.

Living specimens of *C.meridionalis* (40 - 60 mms total length) were also collected and transported to the laboratory. Here they were divided into two batches of 50 specimens each:

(i) the umbones in front of the oral contractor muscle were removed and the oral contractor muscle broken at its attachment on the shell.

(ii) the umbones in front of the oral contractor muscle were removed, but the oral contractor muscle was left intact.

These specimens were kept in the laboratory, under tidal conditions for 3 days, until byssal attachment was achieved and all traces of sand in the alimentary canal had disappeared. This was done in plastic trays.

At an appropriate height of the tide, the trays plus animals were taken back to their locality of collection, and were fixed in position by half burying the trays in the sand. The tide was allowed to rise over the trays and after a period of 1 hour, the animals were killed. The specimens were removed from their shells in the laboratory and processed as before. The sand was heated to constant weight.

2. Results

(i) Mechanical and electrical stimulation

When the taught oral contractor muscle was pricked with a needle, it contracted, and in the majority of experiments, this was accompa~~g~~nied by an undulating movement in the outer labial palp, with a curling back of the mouth corners. No conclusive evidence could be gleaned from these experiments, except for the fact that the oral contractor muscle may close the mouth by contracting, as originally postualted by Swart (1926).

Despite the fact that glass-encased electrodes were used, together with a small voltage output from the induction coils i.e. the coils were placed some 12 cms apart for a response, the results were as inconclusive as those mentioned above, probably due in this case to the high specific conductivity of the sea water medium acting as a shunt.

(ii) Feeding experiments

The results obtained from the feeding of carmine particles to C.meridionalis are shown in Table 4. The method of opening the valves resulted in the oral contractor muscle being in a state of tension; experiments were therefore performed with the muscle intact and taught, and with the muscle cut and relaxed.

Table 4: Effect of stretching (equivalent to contraction) and severing (equivalent to relaxation) of the oral contractor muscle of *C.meridionalis* on its ability to take up carmine particles into the gut.

	cut muscle (relaxed)	uncut muscle (contracted)	total
Feeding	11	2	13
Not feeding	5	8	13
Total	16	10	26

Statistical analysis of Table 4:

$$X^2 = \frac{(ad - bc)^2(a + b + c + d)}{(a + c)(b+d)(c + d)(a + b)}$$

$$= \frac{(11.5 \times 8.5 - 1.5 \times 4.5)^2(26)}{16 \times 10 \times 13 \times 13}$$

$$= 7.95 \text{ for one degree of freedom}$$

The probability of the difference in results being due to chance is less than 0.01, and the muscle in a state of contraction therefore, prevents particles from entering the mouth. The function attributed to the muscle by Swart (1926) is thus confirmed.

Substituting fine sand for carmine particles and comparing the sand intake of animals allowed free control over their oral contractor muscles, with animals in which the muscle had been cut, yielded the results shown in Table 5.

In these experiments, the method of opening i.e. removal of the apex of the shell, was such, that if the muscle is left intact, it is capable of functioning and shutting the mouth. If the muscle is cut, it can no longer function properly and the mouth remains open.

<u>Table 5</u>: Comparison between the sand intake of normal specimens of <u>C.meridionalis</u> and specimens in which the oral contractor muscle had been severed.

	cut muscle	intact muscle	total
sand present	6	0	6
sand absent	8	14	22
total	14	14	28

<u>Statistical analysis of Table 5</u>:

$$X^2 = \frac{(6.5 \times 13.5 - 7.5 \times 0.5)^2 (28)}{14 \times 14 \times 6 \times 22}$$

$$= 7.64 \text{ for one degree of freedom}$$

Therefore the probability of the difference being due to chance is less than 0.01, and it seems as if the oral contractor muscle serves to close the mouth in the presence of small particles of sand, which are normally not rejected by the palps.

These results were compared with the sand intake by intact specimens of A.magellanica and P.perna (Table 6), and it was found that there was no significant difference between the numbers of C.meridionalis with severed muscles and normal specimens of P.perna and A.magellanica, which had taken in sand.

Table 6: Sand intake of normal specimens of P.perna and A.magellanica.

	sand present	sand absent	Total
P.perna	3	2	5
A.magellanica	2	3	5
Total	5	5	10

Table 7: Comparison of sand intake between specimens of C.meridionalis with severed oral contractor muscles and normal specimens of P.perna and A.magellanica.

	sand present	sand absent	Total
C.meridinnalis	6	8	14
P.perna & A.magellanica	5	5	10
Total	11	13	24

Statistical analysis of Table 7:

$$X^2 = \frac{(6 \times 5 - 5 \times 8)^2(24)}{11 \times 13 \times 14 \times 10}$$

$$= 0.12$$ for one degrees of freedom.

The probability coefficient for these results is 0.99 and indicates no significant difference between *C.meridionalis* with severed muscles and intact specimens of *P.perna* and *A.magellanica*.

The quantities of sand from specimens of *C.meridionalis* naturally occurring and experimental, and isolated by boiling the specimens with sodium hydroxide and collecting the residue at constant weight, is given in Table 8.

Table 8: The dry weight of sand obtained from the alimentary canals of naturally occurring and experimental specimens of *C.meridionalis*. 50 specimens (40 - 60 mms total length) taken in each case.

	dry weight of sand in gms/50 specimens
Naturally occurring specimens:	
Incoming tide - just covered	0.190
Outgoing tide - just covered	0.203
Low tide - exposed	0.114

Table 8: continued

	dry weight of sand in gms/50 specimens
Experimental specimens:	
Oral contractor muscle intact	0.455
Oral contractor muscle cut	0.748

One function attributable to the oral contractor muscle of *C.meridionalis* therefore, is to close the mouth in order to prevent the entry of inedible particles, such as sand into the gut. However, small quantities of sand are always present in the gut (Table 8). The significance of such a function, in terms of the activities and ecology of the animals, will be considered in the following discussion.

Discussion on the Oral Contractor Muscle of *C.meridionalis*

The absence of the oral contractor muscle in *P.perna* and *A.magellanica*, and its presence in *C.meridionalis*, warranted further investigation, for the presence of this muscle must be included among the diagnostic specific characters of the latter species. As was pointed out by Swart (1926), it serves the purpose of opening and closing the mouth, by relaxing and contracting respectively. However, besides describing the anatomy of this muscle, Swart ignored the conditions under which such a muscle would operate.

There can be no doubt that this muscle performs the function ascribed to it by Swart (1926), and this is shown in the experiment using carmine particles as a substitute for food, so long as small quantities of the suspension are used at a time. When the muscle is contracted, the lips of the mouth are pressed firmly together, so that no food may pass into the oesophagus, but instead is transported by ciliary action towards the distal ends of the labial palps and rejected as pseudofaeces into the mantle cavity. However, relaxation of the muscle allows the lips to part, and ciliary activity moves the food, sorted on the palps, into the mouth and into the oesophagus.

It was also noted that in the three species dealt with, the major feeding activity took place a short time after the animals had been exposed and then replaced in water, as they are at periods of low tide. Thus the localities of the mussels were studied and together with the experimental evidence, the correct functioning of the oral contractor muscle is postulated.

The three species of mussels dealt with in this section, ~~can~~ may be discriminated ecologically as follows (~~Stevenson~~ Stephenson, 1944):

P.perna

This is a warm water species, having a maximum density at the lower Balanoid zone, where they form thick clusters on the rocks. Strong wave action seems to be one of the factors regulating the zonation of this species. *P.perna* is always situated on wave-washed positions on the seaward faces of rocks and platforms (see Discussion on Anatomy).

A.magellanica

This is the cold water counterpart of *P.perna*, being mainly distributed on the west and south coasts (see Distribution). It is found on the seaward faces of rocks and reefs, in areas of strong wave action.

C.meridionalis

A cold water endemic species, which is found mainly on inshore rocks. This species has ~~taken~~ great advantage in exploiting those areas of rock, which are almost entirely covered by sand, almost to the exclusion of all other mytilids. ~~Stevenson~~ Stephenson (1943) goes as far as to point out that the occurrence of *C.meridionalis* seems to be favoured by the proximity of sand.

This species must therefore have some device whereby it can tolerate the high concentrations of suspended sand in the sea water, which it filters.

It must be noted however, that this species cannot live when completely buried under sand for long periods. Certain rocks, which are covered by sand in the summer months at Llandudno, and are exposed during the winter months, ~~have~~ support populations of small *C.meridionalis* ~~on them~~ only in the winter.

Yonge (1962 : p. 113) states that "the Bivalvia are perhaps the best animals suited for life in soft substrata. It is surprising to find such animals, and often with supreme success, exploiting the possibilities of life on hard, sometimes highly surf-beaten substrata." It is therefore not surprising to find *C.meridionalis* in sandy habitats.

As long as the specimens are covered by water, the ciliary mechanism works for 97 - 99% of the time (Loosanoff, 1942), during which time feeding takes place, provided that the conditions are suitable; the average adult filtering from 1.5 to 2.4 litres of water per hour (Linke, 1954). Schlieper (1963) has shown experimentally that feeding is not a continuous process during the period of submersion, and that *Mytilus* can regulate its feeding mechanism, in relation to the food content of the water.

At low tide, the animal closes its shell, and carbon dioxide accumulates within the mantle cavity. It is said that such a chemical change depresses the ciliary activity, until the cilia come to rest and the oxygen in the tissues is conserved. Since the average oxygen consumption for M.edulis has been assessed at 22 cc/kg/hr at 20°C (Nicol, 1960), it is possible that an oxygen debt is manifested during the periods of exposure. Some respiratory exchange may take place, as the shell may be slightly open allowing some air to enter. When the tide rises, and the mussel bank is covered, the cilia resume their activity.

Now considering the locality of C.meridionalis; the incoming tide will lift up sand from the bottom and carry it in suspension over the mussel bank. Kellogg (1915) is of the opinion that lamellibranchs can only feed in comparatively clear water, but Nelson (1923) and Churchill and Lewis (1924) have shown that lamellibranchs can and will feed in water with a high sand content. Specimens of C.meridionalis must therefore be able to carry on respiration and yet prevent fine particles of sand from entering the alimentary canal, when the tide is rising. How is this possible?

The answer to this problem is presumably in the functioning of the oral contractor muscle. It was seen in the laboratory, that specimens of all three species feeding in a tank of sea water, tended to close up to a small extent and form their pallial tentacles into a kind of sieve, when fine sand was added and the water continually stirred. Stirring alone without the addition of sand, did not ~~do this.~~ produce such an effect. Hence, by means of this pallial filtering mechanism, the larger particles of sand are prevented from entering the mantle cavity with the inhalent current of water. Results (Table 8) seem to indicate that this method of regulation is fairly important, since when the pallial mechanism is intact, only 0.203 gms of sand was found in the gut contents of 50 specimens; and on destroying the effectiveness of this mechanism, by removal of the umbonal region, 0.455 gms of sand was found in the gut contents of 50 specimens. Ashcroft (1899) has commented on the importance of this mechanism.

Secretion of mucous sheets by the gill epithelia will tend to capture the food particles (MacGinitie, 1941) and also the sand particles, although the gills do not produce the mucous nets when inedible matter alone is present. In this case, the efficiency with which particles are retained is entirely dependant on the particle size. The mucous sheet, plus particles, is transported to the labial palps and the particles sorted.

Controversy has arisen as to whether the selection of food by the palps is qualitative or quantitative. Lotsy (1893), Allen (1914) and Jorgensen (1949) have suggested that the food value of the particles is discerned by the palps, but List (1902), Kellogg (1915), Yonge (1923, 1926), Nelson (1923) and Churchill and Lewis (1923) have failed to find anything other than a purely mechanical selection of food, based on particle size. The examination of stomach contents, both by Savage (1925) and the present author seems to confirm this.

Carmine particles, obviously inedible, were shown in experiments to be readily taken into the gut, and sand particles were shown to be present in all the specimens examined (Table 8). This would seem to suggest that the palps discriminate on the size (? or weight) of the particle alone, and that those within a certain range are taken into the mouth. Critical particle size retained by the filtering mechanism has been determined as 1 - 3 µ (Jorgensen, 1949, 1952, 1955). Particles of larger size are passed off the palps as pseudofaeces. There may, however, be sensory receptors on the palps (Cobb, 1918) which distinguish edible from inedible particles, but if the particles are of suitable size, they are carried to the mouth regardless of this factor.

Now in the case of C.meridionalis, where the sand suspension, as approximately sampled, is 10 gms/litre (Table 9), some sand particles must enter the mantle cavity and hence be transported to the labial palps, where they are sorted for size. If there were some mechanism for closing the mouth, an excess of such particles could be shunted off the palps as pseudofaeces. Although small amounts of sand were found to be present in natural populations (Table 8), the case of the feeding experiments, employing a swirling sand suspension, has shown that another regulating mechanism applies.

<u>Table 9</u>: The dry weight of sand obtained from water samples of the same volume, taken above a bank of <u>C.meridionalis</u> on an incoming tide.

Sample	Wt of sand gms	Mean Wt gms	Mean Vol ccs
1	0.1772		
2	0.1679		
3	0.2477		
4	0.1646		
5	0.2700	0.2013	20.1
6	0.1846		
7	0.2096		
8	0.1603		
9	0.1497		

Quantity of sand suspended in the sea water is 9.9 (5) gms/litre

<u>10 gms/litre</u>

Note: This is an arbitary figure and will vary with the amount of wave action and the direction of the wind on any given day. It does however, give an indication as to the high value of the concentration of the sand in suspension.

The method of opening the point of the shell obviously leads to unnatural conditions, where more sand might enter the gut than under natural conditions (Table 8). None the less, it has been shown statistically that, in those specimens with an intact oral contractor muscle, the mouth could be closed off and so prevent the entry of sand. Table 8 shows that nearly four times as much sand enters the gut, when the oral contractor muscle is not functioning.

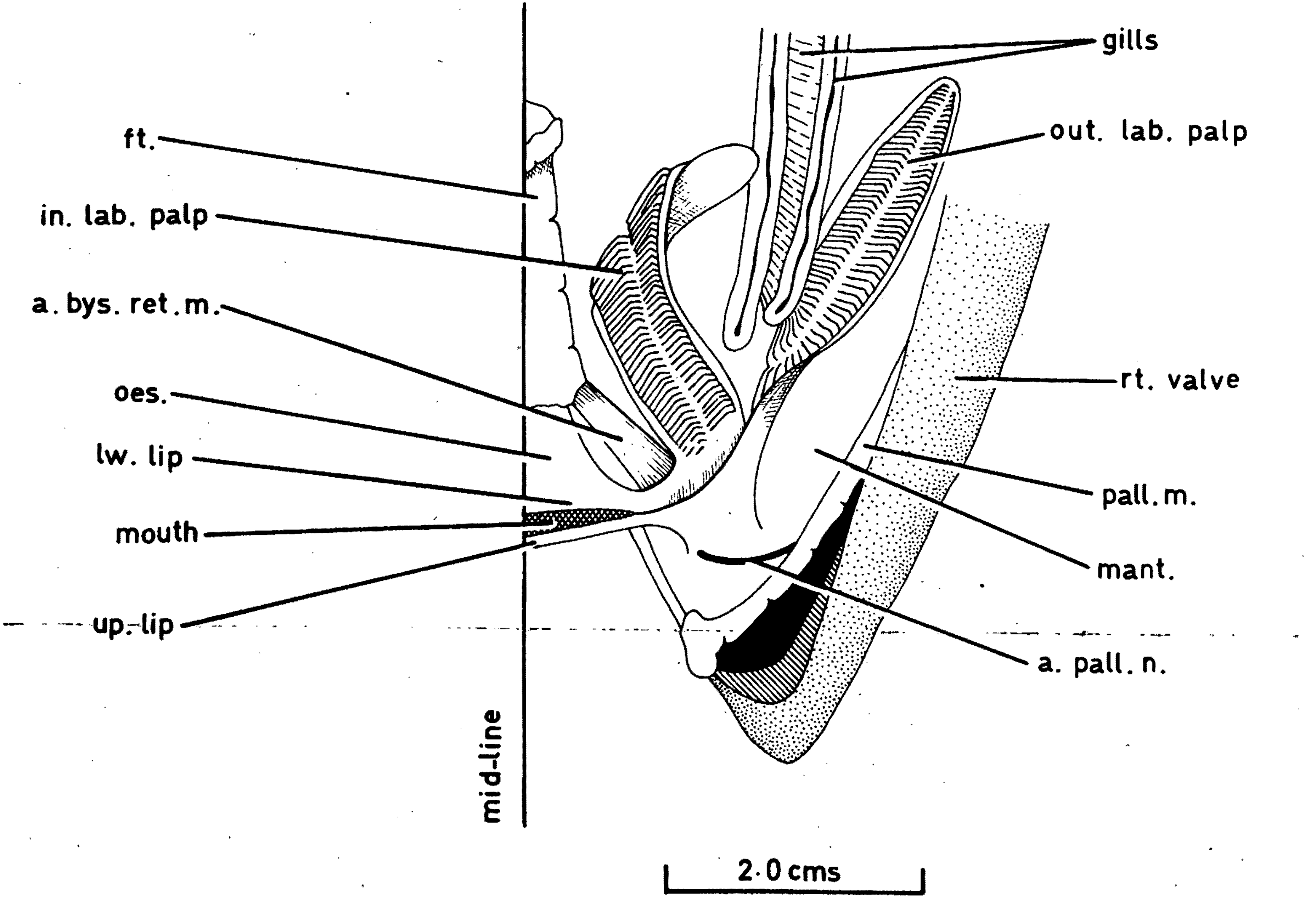
The function of the oral contractor muscle therefore seems to be that of a breaking mechanism on the food intake, and in the presence of high concentrations of sand, may close the mouth and prevent the entry of inedible material. It seems that this is a far more likely occurrence than the discrimination of the particles by the ciliated labial palps, and would involve a much simpler nervous co-ordination. However, it is suggested that this method of regulation is one of several operating simultaneously within the animal i.e. closure of the shell valves, the pallial tentacle sieve, secretion of mucous nets by the gills and the sorting on the palps.

It has been suggested that the oral contractor muscle might act in conjunction with closure of the shell valves, for the expulsion of pseudofaeces from the mantle cavity. In the light of the experiments, this seems unlikely. Anatomical examination has also revealed that none of the muscle fibres enter the palps.

FIGURE 32

The anterior region of the right shell valve of P.perna from the ventral side, showing the absence of the oral contractor muscle.

ft. - foot; in. lab. palp - inner labial palp; a. bys. ret. m. - anterior byssus retractor muscle; oes. - oesophagus; lw. lip - lower lip; up. lip - upper lip; out. lab. palp - outer labial palp; rt. valve - right valve; pall. m. - pallial muscles; mant. - mantle; a. pall. n. - anterior pallial nerve.


gills
ft.
out. lab. palp
in. lab. palp
a. bys. ret. m.
rt. valve
oes.
lw. lip
pall. m.
mouth
mant.
up. lip
a. pall. n.
mid-line
2·0 cms

What happens in the case of P.perna and A.magellanica? Ecological distribution seems to indicate that these species are unsuited in the main to such a sandy ecological niche. However, in certain localities, specimens of both species are found on the wave washed surfaces of rocks. These are usually in the lower Balanoid zone. Such small groups, in the case of P.perna, or larger banks, in the case of A.magellanica, will also be influenced by the entry of sand particles into their mantle cavities. However, when the tide rises to the extent where these are concerned, the water level has risen considerably above the sandy substratum, and this water will be comparatively free from suspended sand. In the case of experiments with both P.perna and A.magellanica, employing a swirling sand medium, sand was found in the stomachs of three out of five specimens of P.perna and two out of five in A.magellanica. Thus besides closure of the pallial tentacles, these species have little control on the entry of correctly sorted particles into the alimentary canal. Dissections of these two species indicated that the outer labial palps were attached to the mantle at the position on the corner of the mouth (fig 32). Stimulation of these regions in P.perna and A.magellanica yielded no response in the mouth.

The oral contractor muscle must therefore be one of the factors enabling C.meridionalis to take full ecological advantage of sandy niches, almost to the exclusion of P.perna and *A.magellanica*.

It is interesting to note that the South American species, *Mytella* and *Arcuatula*, which possess a scar in a similar position (see Muscle Impressions) to the oral contractor scar of *C.meridionalis*, but do not have a muscle (Soot-Ryen, 1955), have been taken from muddy and sandy localities (Soot-Ryen, 1955).

VI. VARIATION IN SIZE OF *A.magellanica* WITH EXPOSURE TO WAVE ACTION

A. Method

The locality selected as suitable for this series of measurements was the outer wall of the Breakwater of Table Bay Harbour, where it was known that *A.magellanica* occurred from the lower Balanoid zone, down to a depth of 50 ft below the level of low water ~~low water~~ of neaps. ~~of neaps mark.~~ Five different depths were chosen as the stations: surface (lower Balanoid zone), 10 ft, 20 ft, 30 ft and 40 ft below the surface of the water at low tide. The depths were ascertained by direct reading of Dräger wrist depth gauges.

Random samples were collected in labelled plastic bags at each depth by divers. The total length of each specimen was measured in the laboratory with sliding calipers, before preservation of the material. Only specimens above 10 mms (total length) were measured. The results of these measurements are given in Tables 12 - 16 and are plotted on graphs (fig 33). The collections were made on two different occasions (November and December, 1966) in order to increase the randomness of selection.

Recordings of the temperature at the Breakwater have been obtained from Heydorn (1966) and from the Diving Logs of the Division of Sea Fisheries (Heydorn and Newman, unpublished). These recordings are presented in Tables 10 and 11.

Table 10: Water temperatures (^{o}C) and salinities (^{o}/oo) recorded from the Breakwater, Table Bay Harbour. (after Heydorn, 1966)

Date	Depth metres	Temp ^{o}C	Salinity ^{o}/oo
26 : 5 : 62	32	13.1	-
	42	12.9	-
19 : 7 : 62	16	13.8	34.39
	35	13.9	34.63
	43	14.0	34.84
11 : 10 : 62	35	13.9	34.88
	43	11.8	34.89
10 : 12 : 62	20	9.8	34.69
	40	9.7	34.79

Table 11: Water temperatures (°C) recorded at the surface and at 60 ft below the surface (bottom), from the Breakwater, Table Bay Harbour (after Heydorn and Newman, unpublished).

Date	Temp °C		Date	Temp °C	
	bottom	surface		bottom	surface
2:6:64	-	14.3	20:7:64	14.5	14.5
17:8:64	-	13.4	21:9:64	-	11.5
26:10:64	-	15.5	26:11:64	10.2	10.2
14:12:64	-	15.8	4:3:65	16.5	17.8
27:4:65	-	14.7	19:5:65	11.0	11.5
17:6:65	13.8	13.9	14:7:65	13.2	13.4
7:8:65	13.4	17.8	8:9:65	13.0	13.3
4:10:65	11.4	12.3	4/11:65	9.0	9.2
1:12:65	-	14.8	10:1:66	8.9	12.3
23:2:66	10.2	13.2	30:3:66	14.4	15.5
12:4:66	11.6	15.3	5:7:66	-	13.6
22:8:66	-	11.4	6:9:66	-	13.8
21:11:66	-	14.8			

Table 12: *A.magellanica.* Lengths of specimens (in mms) obtained at the Breakwater, Table Bay Harbour in November and December, 1966, from the surface station (lower Balanoid zone).

Class Interval in mms	No. of specimens	% sample
10.0 - 14.9	347	37.8
15.0 - 19.9	214	23.3
20.0 - 24.9	135	14.7
25.0 - 29.9	89	9.7
30.0 - 34.9	66	7.2
35.0 - 39.9	39	4.2
40.0 - 44.9	22	2.4
45.0 - 49.9	5	0.5
50.0 - 54.9	1	0.1

<u>Table 13</u>: <u>A.magellanica</u>. Lengths of specimens (in mms) obtained at the Breakwater, Table Bay Harbour in November and December, 1966, from the 10 ft depth station.

Class Interval in mms	No. of specimens	% sample
10.0 - 14.9	101	22.3
15.0 - 19.9	62	13.8
20.0 - 24.9	56	12.5
25.0 - 29.9	50	11.2
30.0 - 34.9	50	11.2
35.0 - 39.9	25	5.6
40.0 - 44.9	25	5.6
45.0 - 49.9	13	2.9
50.0 - 54.9	17	3.8
55.0 - 59.9	9	2.0
60.0 - 64.9	6	1.3
65.0 - 69.9	14	3.1
70.0 - 74.9	8	1.8
75.0 - 79.9	8	1.8
80.0 - 84.9	2	0.4
85.0 - 89.9	2	0.4

Table 14: *A.magellanica.* Lengths of specimens (in mms) obtained at the Breakwater, Table Bay Harbour in November and December, 1966, from the 20 ft depth station.

Class Interval in mms	No. of specimens	% sample
10.0 - 14.9	67	15.9
15.0 - 19.9	45	10.7
20.0 - 24.9	39	9.3
25.0 - 29.9	41	9.8
30.0 - 34.9	47	11.2
35.0 - 39.9	34	8.1
40.0 - 44.9	35	8.3
45.0 - 49.9	39	9.3
50.0 - 54.9	33	7.8
55.0 - 59.9	18	4.3
60.0 - 64.9	14	3.3
65.0 - 69.9	9	2.1

<u>Table 15</u>: <u>A.magellenica</u>. Lengths of specimens (in mms) obtained at the Breakwater, Table Bay Harbour in November and December, 1966, from the 30 ft depth station.

Class Interval in mms	No. of specimens	% sample
10.0 - 14.9	32	13.3
15.0 - 19.9	32	13.3
20.0 - 24.9	32	13.3
25.0 - 29.9	21	8.7
30.0 - 34.9	15	6.2
35.0 - 39.9	16	6.6
40.0 - 44.9	7	2.9
45.0 - 49.9	4	1.7
50.0 - 54.9	8	3.3
55.0 - 59.9	16	6.6
60.0 - 64.9	13	5.4
65.0 - 69.9	9	3.7
70.0 - 74.9	13	5.4
75.0 - 79.9	6	2.5
80.0 - 84.9	7	2.9
85.0 - 89.9	6	2.5
90.0 - 94.9	3	1.2
95.0 - 99.9	1	0.4

Table 16: *A.magellanica*. Lengths of specimens (in mms) obtained at the Breakwater, Table Bay Harbour in November and December, 1966, from the 40 ft depth station.

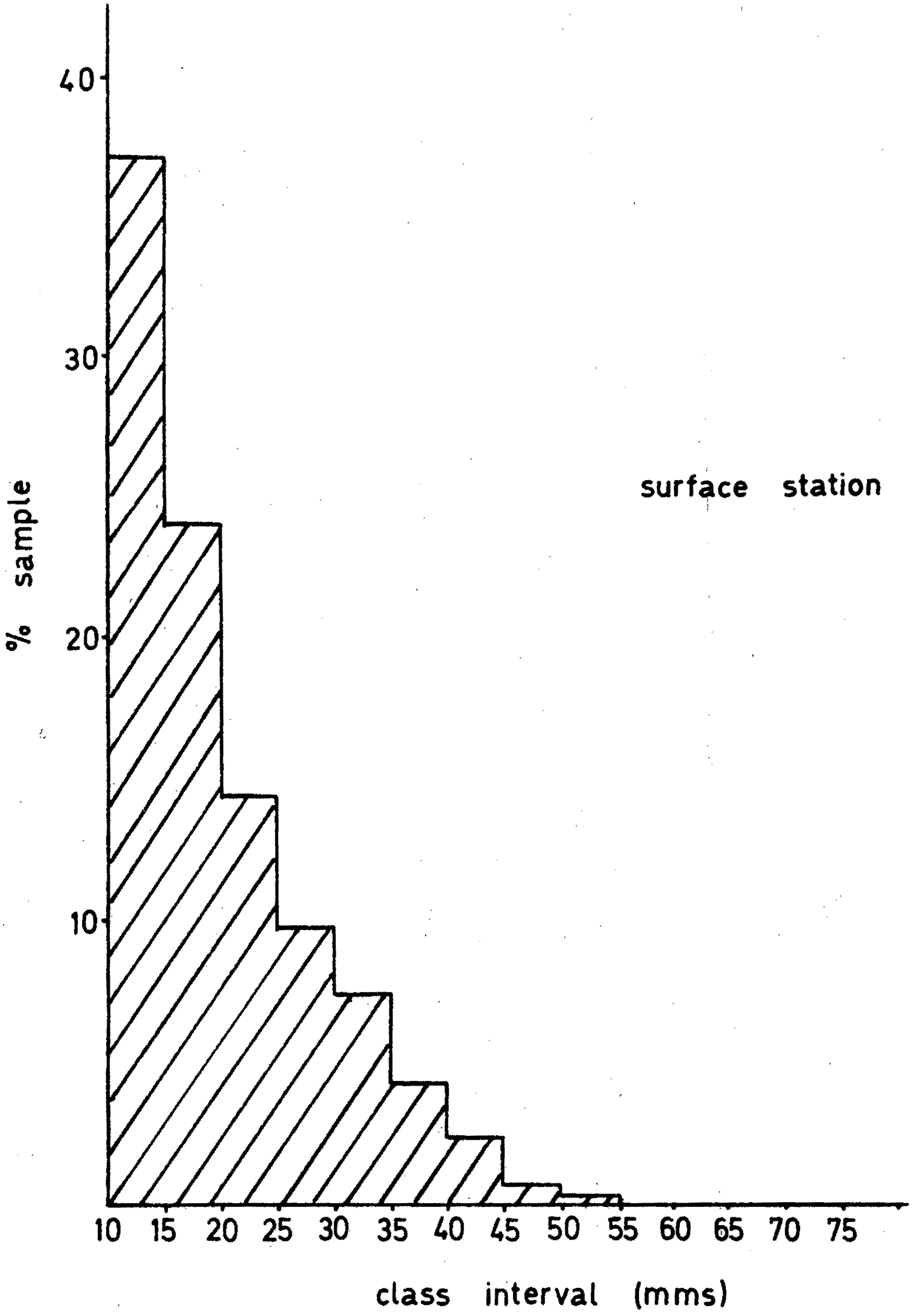
Class Interval in mms	No. of specimens	% sample
10.0 - 14.9	20	11.1
15.0 - 19.9	29	16.1
20.0 - 24.9	16	8.9
25.0 - 29.9	10	5.6
30.0 - 34.9	2	1.1
35.0 - 39.9	0	0
40.0 - 44.9	1	0.5
45.0 - 49.9	3	1.7
50.0 - 54.9	10	5.6
55.0 - 59.9	2	1.1
60.0 - 64.9	11	6.1
65.0 - 69.9	13	7.2
70.0 - 74.9	23	12.8
75.0 - 79.9	16	8.9
80.0 - 84.9	9	5.0
85.0 - 89.9	7	3.9
90.0 - 94.9	5	2.8
95.0 - 99.9	0	0

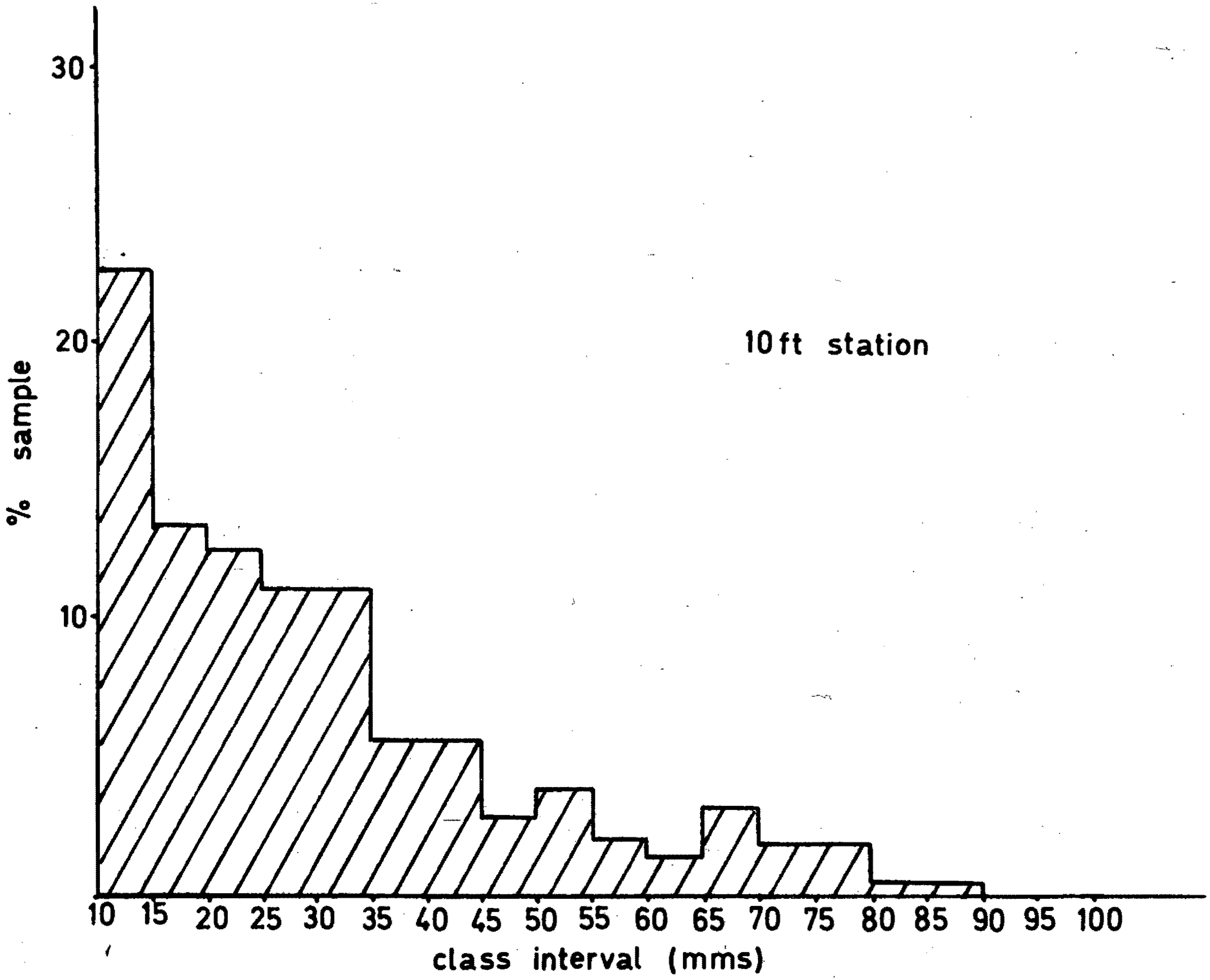
<u>Table 16</u>: continued

Class Interval in mms	No. of specimens	% sample
100.0 - 104.9	1	0.5
105.0 - 109.9	0	0
110.0 - 114.9	2	1.1

FIGURE 33

Size distribution of populations of A.magellanica collected from the Breakwater, Table Bay Harbour in November and December 1966.


40
30
20
10
% sample
surface station
10
15
20
25
30
35
40
45
50
55
60
65
70
75
class interval (mms)



30
20
10
% sample
10 ft station
10
15
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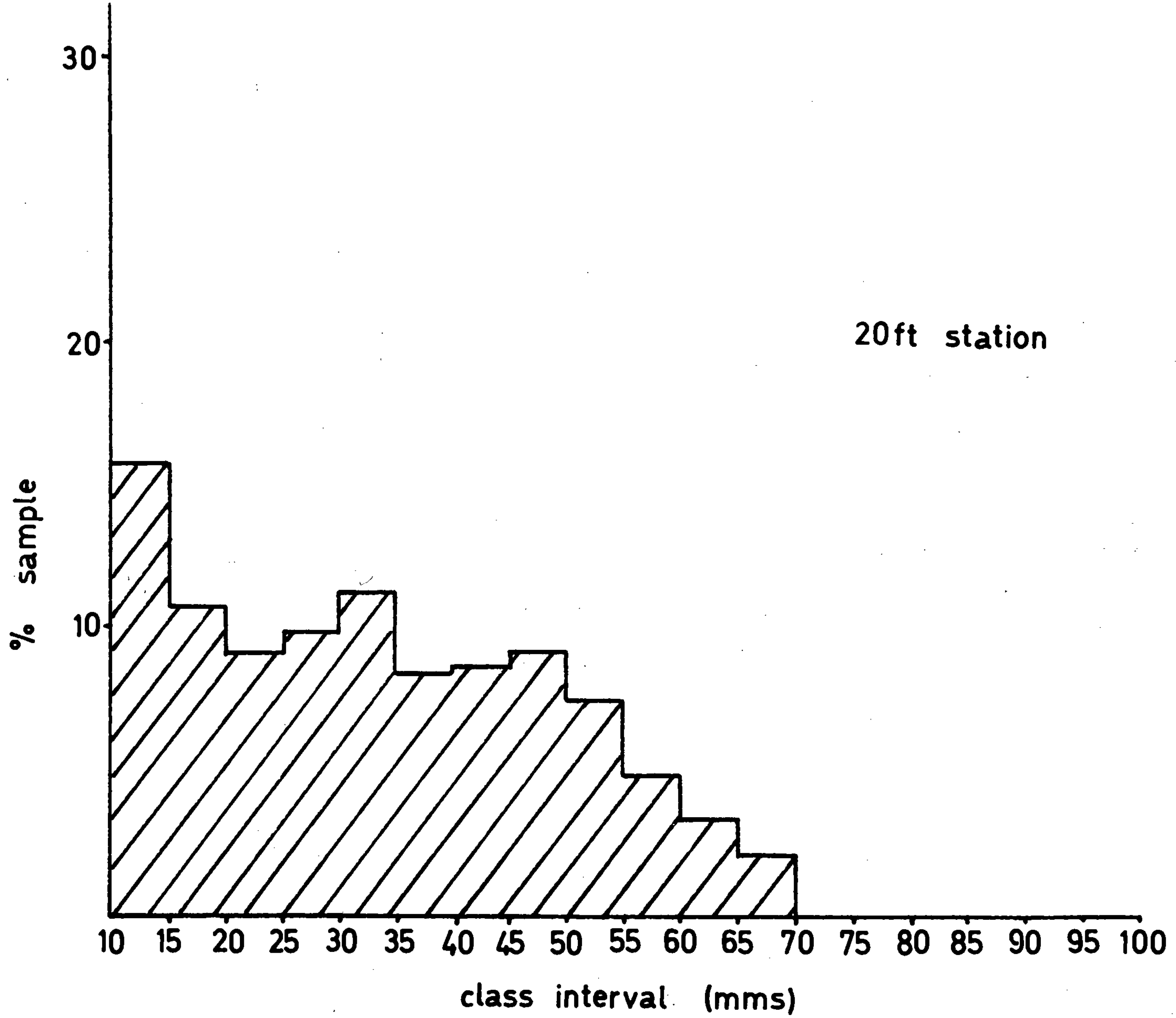
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
class interval (mms)


20ft station
% sample
30
20
10
10
15
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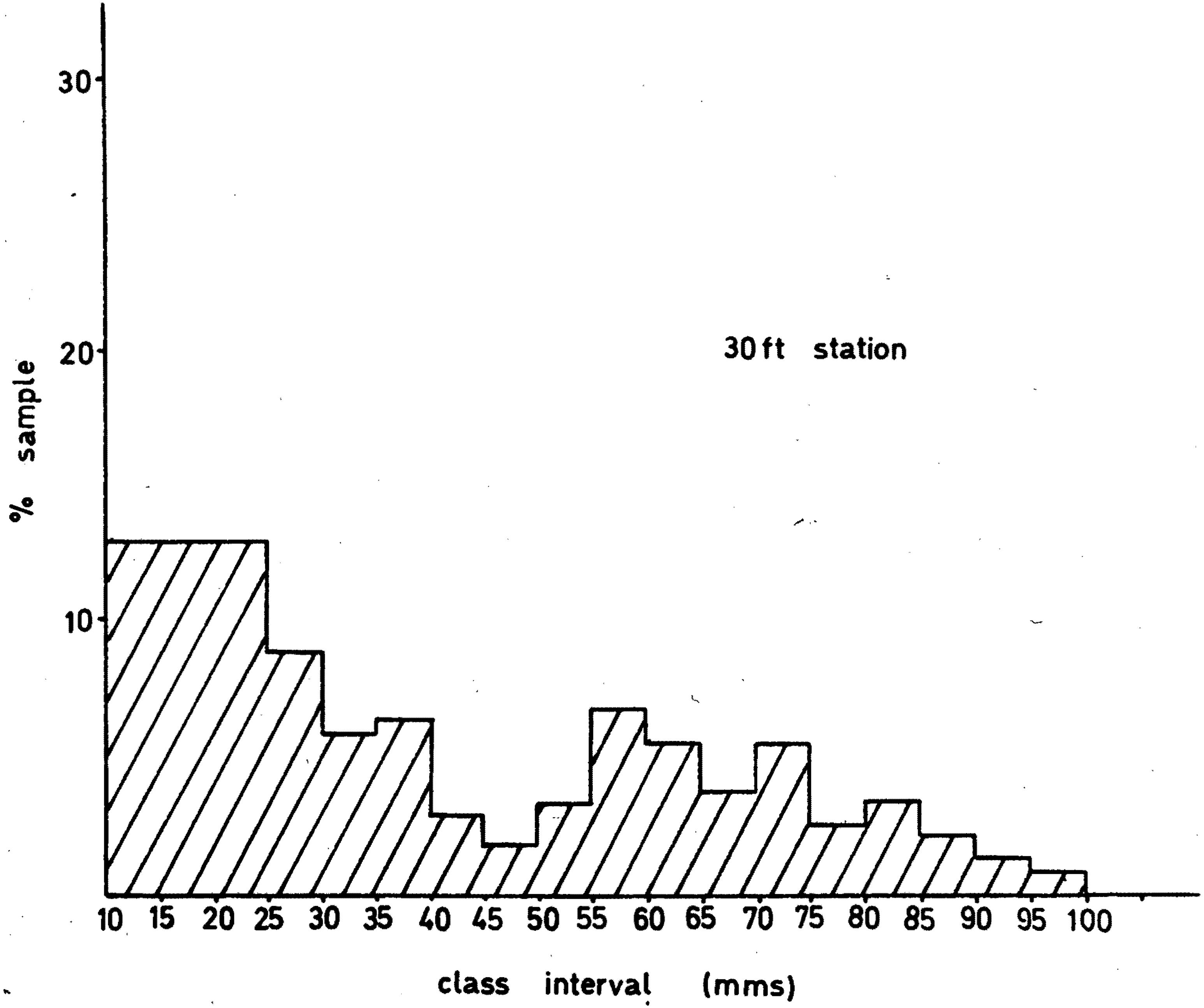
35
40
45
50
55
60
65
70
75
80
85
90
95
100
class interval (mms)



30 ft station
% sample
30
20
10
10
15
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45
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55
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65
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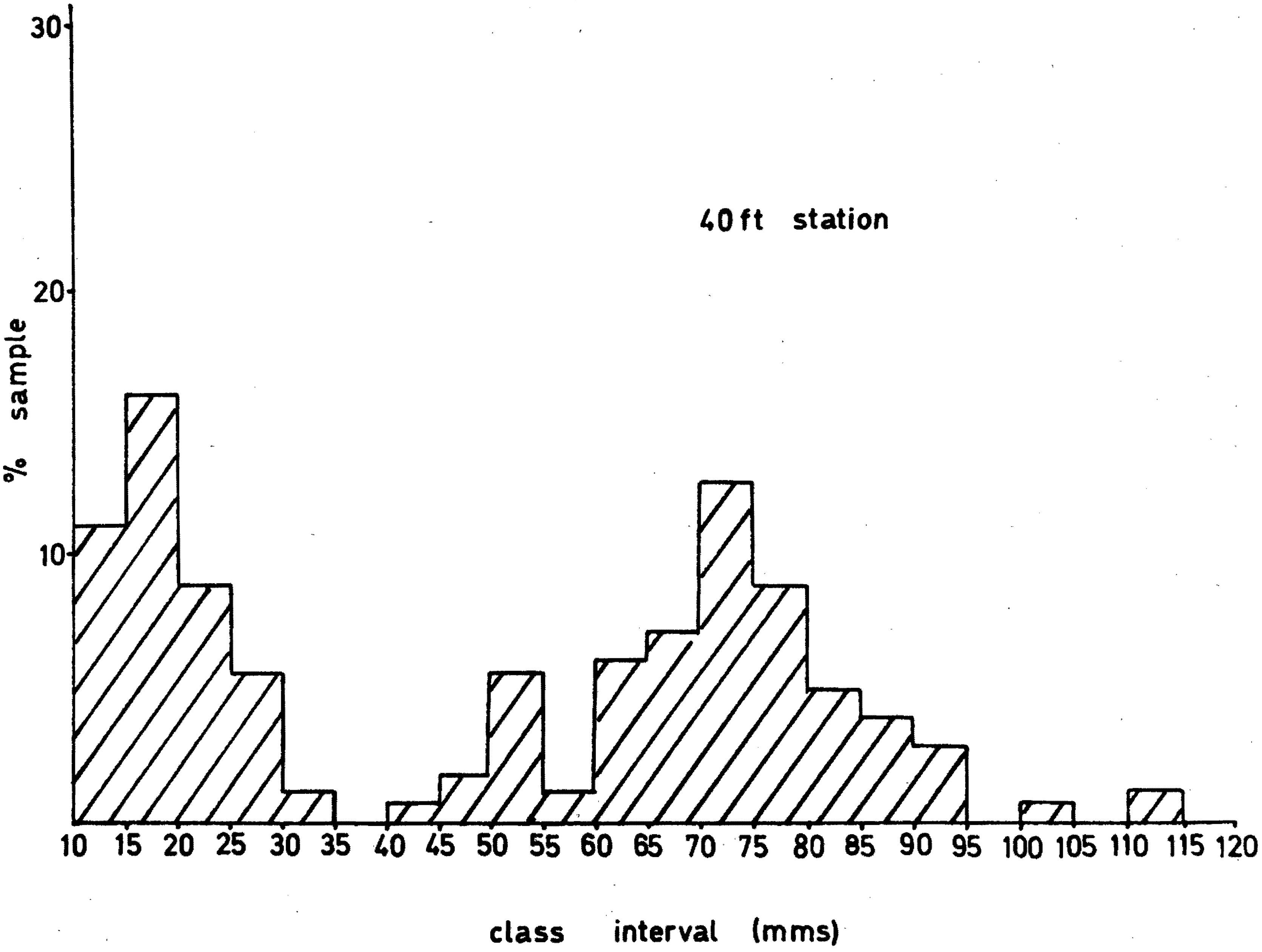
75
80
85
90
95
100
class interval (mms)


40 ft station
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65
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75
80
85
90
95
100
105
110
115
120
class interval (mms)

Discussion on Variation in Size with Exposure to Wave Action

Although this series of measurements was carried out to determine variations in size of A.magellanica due to wave action, it must be noted that the effects of any single factor of the environment cannot readily be isolated. The factors always act jointly, and it is their resultant action which produces the variations. As yet, no adequate study has been made on the joint effect of several factors, although Galtsoff (1964) has employed a points system for his studies on Crassostrea virginica.

Variations due to the environment manifest themselves in bivalves with both changes in the shape of the animal and changes in the rate of growth. Orton and Awati (1926) found that in Ostrea angulata, specimens from deeper water had broader shells than those from shallow water. However, they offered no explanation for this. Hamai (1934) has attributed differences in the shape of Merètrix merètrix to temperature, while stating in later papers that the nature of the substratum and other chemical conditions of the sea water also contribute to changes in shape (Hamai, 1935 a, b). Pelseneer (1893) has shown that in mussels, the shell form is influenced by the movement of water.

Since it is reported (Walford, 1946) that the higher the growth rate, the greater the ultimate length, environmental factors influencing the growth rate in mussels have been studied (Genovese, 1958 - 1959; Ricci, 1957; Plessis, 1958; - all as given in Allen, 1963). Fox and Coe (1943) have shown that there is a general positive correlation between increment in growth and average monthly temperature, with a decrease during the month with highest temperature. Dodgson (1928) has noted that mussels can function between 0°C and 20°C, but it appears that temperatures between 10°C and 20°C are optimal for growth (Coulthard, 1929).

Although both White (1937) and Baird (1966) report that Mytilus can tolerate great variations in salinity, Brandt (1898) found that the size is inversely proportional to the salinity.

Field (1922) is of the opinion that food supply is the chief factor influencing growth, and Baird (1966) further states that the temperature has an indirect influence, in that it affects the point at which mussels will feed. Also related to feeding is the fact that mussels can only feed when they are submerged, so that specimens which are submerged for longer periods should have an increased growth rate. White (1937) finds that in M.edulis, smaller specimens are found in deeper water, but Field (1922), Coulthard (1929), Zenkevitch (1963) and Baird (1966) find that the largest specimens are found below the surface of the water at LWST.

Lamy (1936 - 1937) reports that wave action effects the size of the animal, since the movement of sea water renews the supply of food. Hence, larger specimens should be found in more exposed regions. However, Fox and Coe (1943) have shown that exposure to wave action reduces the size, and that mussels exposed to heavy seas, grow more slowly than those from sheltered positions. The choice of their two localities in this case was unfortunate, for they were widely separated and therefore subjected to other environmental differences besides wave action.

The choice of the Breakwater at Table Bay Harbour was made because it was known that the species concerned (A.magellanica) has a large vertical range in distribution. It occurs from the lower Balanoid zone, down to a depth of 50 ft below the surface of the water at LWST. There can therefore be no variation in feeding time at stations other than the lower Balanoid zone, for these stations are completely submerged at all times. It was also thought that at the Breakwater, movement of the water against the wall would result in mixing of the water layers, so that temperature, salinity and food supply would be more or less constant at all stations, while wave action would be the only varying factor.

As will be seen (Table 10 and 11), there is a difference in the temperature between the surface water and the bottom water. The magnitude of this difference on any particular day will be dependant on the strength and direction of the prevailing winds.

However, the maximum recorded difference in temperature between the surface and bottom water is 4.4°C, and the difference in the mean recorded temperatures for the surface and bottom water is only 1.5°C. It is therefore held that mixing of the water layers does take place at the Breakwater, and that besides wave action, conditions are similar at each of the stations. The brief recordings of salinity seem to confirm this (Table 10).

It was noticed during diving, for the collection of the material, that there was an appreciable difference in the wave action /swell, at each of the stations, and that with increasing depth, the effect of the swell became less noticeable.

The measurements taken of the specimens for each of the stations have been plotted as histograms (fig 33). At the surface station (fig 33), there is a large percentage of juveniles and a steady decrease in numbers with increasing size. More than 50% of the specimens are shorter than 20 mms in length, and the maximum recorded length at this station was 51.8 mms. At the 10 ft station, there is again a decrease in numbers in each size group, with increasing size. Here 35.5% of the sample are shorter than 20 mms, and 50% of the sample shorter than 25 mms. The largest specimen recorded at this level was 88.7 mms. At the 20 ft level (fig 33), the maximum recorded length was only 69.9 mms, but 50% of the population was longer than 30 mms. The largest specimen from the 30 ft station was 98.8 mms long, while almost 50% of the population was longer than

35 mms. It will be seen from figure 33, the graph of the 40 ft station, that 50% of the population are larger than 60 mms in length, and that the largest specimen obtained measured 113.0 mms. There is a sharp decrease in numbers up to the 30 - 35 mms size group, followed by an increase in numbers. 12.8% of the population at this level fall into the 70 - 75 mms size group. This peak is followed by a steady decrease in numbers with increasing size.

Therefore, it can be concluded that, with increasing depth, the size of the specimens also increases. That is, with a decrease in the effect of wave action, there is an increase in the size which specimens of A.magellanica attain. That this statement holds true for A.magellanica, Mytilus californianus (Fox and Coe, 1943) and Mytilus edulis (Baird, 1966), would seem to indicate that in all the Mytilidae, an increase in exposure to wave action results in a decrease in size.

Examination of figure 33 shows that for larger specimens a series of peaks are obtained on the graphs. These may be explained as the results of the growth of larvae from successive periods of settling, but as yet the spawning cycle of A.magellanica is unknown. Also it can be seen that there is a steady decrease in the numbers of very small specimens (10 - 15 mms total length), with increasing depth. This would suggest that fairly well wave washed rocks are more suitable for the young specimens.

This of course raises the question of overcrowding and its effect on the ultimate size of the specimen. Moore (1935) has already pointed out that in Balanus balanoides, overcrowding results in a decreased growth rate. Fox and Coe (1943) have reported that in M.californianus, thicker and broader shells are found in specimens living in crowded wave-washed localities. Lamy (1936) considers that mussels may become so tightly pressed against one another, that circumstances are unfavourable for their development. However during the collection of the material in this experiment, it was noticed that at all stations, the specimens were packed one against the other, and the record of a specimen of total length 88.7 mms from the 10 ft station, seems to indicate that overcrowding may not be so important. This is further supported by the fact that overcrowding is dependant upon the available settling space between existing individuals, so that larger individuals would limit the settling space more than smaller specimens.

How wave action effects the size of the animal is unknown. Exposure to wave action may have a direct effect on the size, or it may be that in exposed positions, particularly heavy seas at certain times of the year, result in the mass mortality of individuals which are exposed, so that they can never achieve their maximum size.

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