Geographical studies on the interaction between the pear limpet, Patella cochlear, and the encrusting coralline alga, Spongites yendoi

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I declare that

"Geographical studies on the interaction between the pear limpet, Patella cochlear, and the encrusting coralline alga, Spongites yendoi" is my own work and that all sources I have used or quoted have been indicated and acknowledged by means of complete references.

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GENERAL INTRODUCTION

1. Geographical patterns and their control

Recently, there has been much debate about the present geographical distribution of marine organisms. Although it was van den Hoek (1975, 1982a, b, 1984), Pielou (1977, 1978, 1979), Vermeij (1978), and Michanek (1979, 1983) who revived interest in the subject of marine biogeography, the concept had already become familiar in the middle of the 19th century. It was the British marine zoologist and paleontologist Forbes who said: "The student of history follows, with intense interest, the march of a conqueror, or the migration of a nation .... yet, absurd as it may seem to those who have not thought of such things before, there is deeper interest in the march of a periwinkle, and the progress of a limpet" (cited in Lüning 1990).

Two pioneers of the biogeography of marine algae (marine phycogeography) were the Swedish phycologist F.R. Kjellman (1883) and the North American phycologist W.A. Setchell (1920). Kjellman was interested in the comparison of Northern Hemisphere floras, while Setchell emphasized the rôle of temperature in algal distributions. Setchell (1917) gave a history of phycogeography before 1900, and since then, entire symposia have been dedicated to the subject of seaweed biogeography (e.g. The Vth international Seaweed Biogeography Workshop held in Cape Town, July 1993).

It is not surprising that terrestrial biogeography has been well documented, and Pielou (1979) especially gives an extensive account thereof. It is so much easier and less costly to explore the world's forests and mountains, than it is to explore sea shores or the canyons of the deep oceans or even the shallow subtidal zone. Biogeography of the marine realm has only relatively recently become a somewhat popular topic of research among marine scientists.

There appear to be three chief contrasts between the marine and terrestrial environments which affect their biogeography profoundly (Werger 1978, Pielou 1979). Firstly, the world's ocean is continuous and composed of a fluid medium in constant movement; different parts of it can therefore never be as isolated as can the separate parts (continents and islands) of the world's land surface. Secondly, the vegetation responsible for primary production in the open sea is simple microscopic phytoplankton, consisting of minute floating organisms (diatoms, dinoflagellates, etc) dispersed through the water; it does not, as does the vegetation of the land, form a large structural environment. Third, the ocean is far more three dimensional; a far greater fraction of the marine realm is light-limited and its local properties as they affect the organisms present, vary more markedly with depth as well as with geographic location (Pielou 1979, Nybakken 1988, Lüning 1990, Norse 1993).

The contrasts between marine and terrestrial biotas are equally striking. Taxonomically, marine organisms present far more variety than terrestrial organisms; in the fauna of the sea, all but one animal phylum is represented and on land, fifteen phyla lack representation (Norse 1993). While the land is species diverse (most of the phenomenal species diversity comes from the phylum Arthropoda), the sea is phylum diverse (Norse 1993).

This and all the above-mentioned contrasts should be borne in mind as we consider the biogeography of the sea.

During the past twenty years, the benthic marine algal flora of the Northern Hemisphere has been subject to extensive floristic analysis (van den Hoek 1975, 1982a, b, 1984, Adey et al. 1976, Masaki et al. 1982, South 1987, Breeman 1988, Prud'Homme van Reine and van den Hoek 1988, 1990, Stam et al. 1988, Bot et al. 1989, Whittick et al. 1989, Kooistra et al. 1992, Chen and Chen 1993, Pearson and Davison 1993, van Oppen et al. 1993) with the result that the general distribution patterns of species are reasonably well known. It is only in the past ten years that extensive work has begun in the Southern Hemisphere (Harlin et al. 1985, South 1979, Peters and Breeman 1993) with much work concentrated around southern Africa (Branch 1984, Bolton 1983, 1986, 1987, 1994, Bolton and Anderson 1987, 1990, Bolton and Levitt 1985, Bolton and Stegenga 1987, Anderson and Bolton 1989, Bolton and Lutjeharms 1993, Critchley et al. 1994, Farrell et al. 1994, Bustamante 1995).

The study of the biogeographical distribution of marine organisms around the coasts of southern Africa was pioneered by Stephenson (1948). In his studies of intertidal communities, Stephenson concluded that three distinctive provinces could be delineated: a cold temperate west coast, a warm temperate south coast, and a subtropical east coast. A re-assessment of the seaweed flora of the west coast however, suggests that it is better described as warm temperate, although its flora is still distinctive from the south coast flora, and with a sharp discontinuity in distribution patterns related to temperature regimes, in the vicinity of Cape Agulhas (Bolton 1986, Bolton and Anderson 1987, Bolton and Stegenga 1987, Lüning

1990). This notion had already been suggested by Ekman (1953) and Briggs (1974).

The geographical distribution patterns of marine organisms are controlled by a number of factors, including sea water temperature, salinity, nutrient stress, light, water movement, past events or history (e.g. continental drift), biological interactions, etc (Lubchenco 1980, Hay 1981, Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Branch 1984, Hockey and Branch 1984, van den Hoek 1984a, b, Bolton 1986, Bolton and Anderson 1987, 1990, Bolton and Stegenga 1987, South 1987, Breeman 1988, Lüning 1990, Prud'Homme van Reine and van den Hoek 1988, 1990, Anderson and Bolton 1989, Kooistra et al. 1989, McClanahan 1992, Karban and Strauss 1993, Norse 1993, Peters and Breeman 1993). These factors may be defined as barriers since they obstruct species' dispersal (Rapoport 1982). Since the distribution patterns of many species are so distinct, it is easy to imagine the existence of barriers.

Sea water temperature has been continually emphasised in the literature as an overriding factor controlling the distribution of seaweeds. The evidence for the control of seaweed distribution by sea water temperature can be divided into two categories (Bolton and Anderson 1990):

1. correlations of floral discontinuities with discontinuities in ambient temperature patterns (van den Hoek 1984, Branch 1984, Bolton 1986, Bolton and Stegenga 1987, South 1979, 1987, Bolton and Anderson 1990);
2. detailed laboratory studies in culture linking physiological temperature tolerance limits to geographic distribution limits (Bolton and Anderson 1987,

Breeman 1988, Anderson and Bolton 1989, Peters and Breeman 1993, Breeman and Pakker 1994,Gierdien 1994).

Salinity too may be important as a controlling factor in determining species distributions in some geographical regions (Harlin et al. 1985, Kooistra et al. 1989, Lüning 1990, McClanahan 1992). Not only does a salinity barrier prevent most aquatic plants from passing from marine to freshwater habitats and vice versa (Hay and Gaines 1984), but it has a significant effect on survival and growth of marine organisms (Zimmeman and Rechenik 1991, Chen and Chen 1993), growth of invertebrates (Laughlin 1983), and even fertilization success (Bush and Weis 1983). It would not be difficult to predict that control of distribution patterns by reduced salinity would be important in areas with large river influxes, and tropical areas experiencing unpredictable typhoons; high salinity would be important to seaweeds adapted to high intertidal pools.

Apart from temperature and salinity, there are a host of other physical factors which have been shown to control distributional patterns. These include desiccation tolerance (Vermeij 1978, Kooistra et al. 1989), nutrient stress (Lobban et al. 1985, Coutinho and Zingmark 1993), light (Lüning 1990, Péres-Lloréns et al. 1993), water movement (Bolton 1986, Bolton and Levitt 1987), hydromechanical adaptations (Vermeij 1978), the degree of separation of the shallow-water areas and in particular of the continental shelves of the landmasses (Werger 1978, Pielou 1979), and the existence of solid substrate along any coast (Hay and Gaines 1984, Lüning 1990). Examples of simultaneous control of species distributions by the interactions of more than one factor are common (MacArthur 1972, Vermeij 1978, Rapoport 1982, Hay and Gaines 1984, Chen and Chen 1993) but are less well worked out.

Besides the factors already mentioned, there are a variety of instances where temperature and salinity have failed to account for distribution patterns (MacArthur 1972, Pielou 1979, Masaki et al. 1982, van den Hoek 1984, Mendoza and Cabioch 1986, Breeman 1988, Bot et al. 1989, Peters and Breeman 1993). In detailed laboratory studies in culture linking physiological temperature tolerance limits to geographic distribution limits, quite a few species' thermal responses could not account for their geographical distributions (Breeman 1988; A.K. Peters, personal communication). Laughlin (1983) studying the effects of varying factorial combinations of temperature and salinity on larval growth of the horseshoe crab Limulus polyphemus (Linnaeus), found that lowest survival occurred at combinations of low temperature and low salinity. Nevertheless, the larvae are sufficiently provisioned with yolk to survive the prevailing ranges of these variables in the habitat where adults normally deposit eggs. Laughlin suggests that other unexamined physical factors, or more likely biological factors such as predation or competition among the feeding larval stages and adults, are important for larval survival of L. polyphemus.

Similarly, apart from temperature or salinity control of species distributions, there appear to be few possible other reasons for some species' geographic distribution patterns. These may include different survival strategies of a species or its reproductive phases (Breeman 1988, Peters and Breeman 1992, van Oppen et al. 1993); differential capability for deep water dispersal (Pielou 1979, Childress 1995); differential response to physical disturbance (Wilce

1963, unpublished manuscript, Dayton 1971, 1975, Menge 1976, Hay 1981, Hooper and Whittick 1984, Keats et al. 1985, Lüning 1990); and biological control of species distributions (MacArthur 1972, Vermeij 1978, Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Rapoport 1982, Hockey and Branch 1984, Kikkawa and Andersen 1986, Nybakken 1988, Klump and Polunin 1989, Lüning 1990, Branch et al. 1992, Johnson 1992, Anderson et al. 1993, Karbon and Strauss 1993).

Different survival strategies of species (or of their reproductive phases) in response to environmental stress have even been suggested to control some species' geographical distributions. Experimental temperature tolerance studies in algae (Breeman 1988) have shown that both Northern and Southern Hemisphere gametophytes of Desmarestia viridis O.F. Müller can survive for extended periods at temperatures of 26 to 27°C (Peters and Breeman 1992). The microscopic gametophyte is more resistant to environmental stress than the macroscopic sporophyte. Resistant microscopic stages in algae such as D. viridis may provide a mechanism for continuous coastal migration (van Oppen et al. 1993).

Deep water dispersal should also not be excluded as a mechanism for continuous coastal migration (Pielou 1979). If a species' tolerance of low light intensities, low temperatures, elevated hydrostatic pressure, and decreased O_2 is high, such a species could survive by deep water dispersal. Animals should find it easier to disperse via deep water since they apparently have less of a problem coping with low temperatures, low light intensities and elevated hydrostatic pressure (Childress 1995).

Physical disturbances have continually been emphasized as having important effects on the abundance and geographical distribution patterns of many sessile species (Wilce 1963, unpublished manuscript, Dayton 1971, 1975, Menge 1976, Hay 1981, Hooper and Whittick 1984, Keats et al. 1985, Lüning 1990, Keats 1991). In particular, exposure to wave action (Dayton 1971, 1975, Menge 1976, Hooper and Whittick 1984) and ice scour (Wilce 1963, Hooper and Whittick 1984, Keats et al. 1985, Keats 1991) have a major influence on the distribution patterns of seaweeds. Dayton (1971) studying the geographical distribution patterns of algae of the Olympic Peninsula region of Washington State along a gradient of physical exposures, indicated that Postelsia palmaeformis Ruprecht dominated in exposed areas, while Fucus distichus Linnaeus and Gigartina papillata (C. Agardh) J. Agardh dominated in sheltered to moderately exposed areas. Furthermore, what becomes obvious, is that in exposed areas, interspecific competition for space mediates the replacement of species while in relatively sheltered areas, predation influences patterns of space utilization (Dayton 1975, Menge 1976). Wilce (1963) studying the benthic algal vegetation of north-west Greenland, particularly of the Thulé District and Disko Bay, concluded that the dissimilarities in the floras were due to two factors, one of which was ice scour.

As well as physical factors, the dynamics of the euphotic zone are governed by biological factors such as competition between species, and the activity of herbivores and predators (MacArthur 1972, Vermeij 1978, Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Rapoport 1982, Hockey and Branch 1984, Kikkawa and Andersen 1986, Nybakken 1988, Keats 1991, Klump and Polunin 1989, Lüning 1990, Branch et al. 1992, Johnson 1992, Anderson et al. 1993, Karbon and Strauss 1993). Even body form has been suggested to determine species distributions (Vermeij 1978, Branch 1981). The encrusting coralline alga, Leptophytum foveatum Chamberlain et Keats is a thin coralline undoubtedly having a fast lateral growth rate which possibly accounts for the coralline's dominance of the lower shore on the South African west coast (G.W. Maneveldt, personal observation). Furthermore, Keats and Maneveldt (1994) have shown that this coralline is able to retaliate to competitive overgrowth by thicker encrusting algae. These factors may very well allow this species to broaden its geographic range.

2. Ecological interactions on a geographical gradient

Physical factors, in particular sea water temperature, has continually been emphasized as an overwhelming factor controlling the distribution of seaweeds (Branch 1984, van den Hoek 1984, Bolton 1986, Bolton and Anderson 1987, 1990, Bolton and Stegenga 1987, South 1987, Breeman 1988, Prud'Homme van Reine and van den Hoek 1988, 1990, Anderson and Bolton 1989, Kooistra et al. 1989, McClanahan 1992, Peters and Breeman 1993). There are however cases where it has been found that several seaweed species have higher temperature optima in laboratories than in their natural habitats (Breeman 1988, Peters and Breeman 1993). It therefore becomes obvious that other factors (biological) may determine their true field boundaries.

Although it has been suggested that biological factors can influence large-scale geographical distributions (Lubchenco 1980, Hay 1981, Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Hockey and Branch 1984, Lüning 1990, Karban and Strauss 1993), there are only a few known cases with well documented evidence supporting this hypothesis. Hay (1981) showed that because of differential competitive abilities, sand-plain algal genera are better adapted for temperate areas than are reef-slope genera (since there are relatively fewer grazing species of fish in temperate regions) as long as they are not selectively removed by reef-associated grazers. Similarly, Hay and Gaines (1984) demonstrated that the primary barrier to the successful transport and establishment of shallow water Caribbean seaweeds appears to be herbivore activity along with the lack of reef-generated refuge areas on the Pacific coast, and not the salinity of the Panama Canal. Wethey (1983) also showed that the northern limit of the barnacle Chthamalus fragilis Darwin was set not by factors directly related to cold acting on C. fragilis. Rather, it appears to be set by cold which allows the dominant competitor, the barnacle Semibalanus balanoides (Linnaeus) Newman et Ross, to exclude C. fragilis from its refuge. South of its northern limit, C. fragilis survives because S. balanoides is excluded from the high shore where it dies from desiccation or heat stress. Brenchley and Carlton (1983) studying the interaction between native mud snails and introduced periwinkles in the New England intertidal zone, showed experimentally that the historical change in the distribution of the mud snail Ilyanassa obsoleta Say was due to competitive exclusion by introduced Littorina littorea Linnaeus.

3. Herbivores and the control of abundance, competitive dominance, and morphology of algae

If there is one truism that has developed from experimental studies on rocky shores, it is that herbivores have the capacity to control the structure and dynamics of communities

(Stimson 1970, 1973, Branch 1971, 1975a, b, c, Dayton 1971, 1975, Ayling 1981, Lubchenco and Gaines 1981, Lubchenco 1978, Paine 1984, Johnson and Mann 1988, Chapman and Johnson 1990, Dethier et al. 1991, Sousa and Connel 1992, Foster 1992, Anderson et al. 1993). Besides denuding rock surfaces, limpets, littorines, sea urchins and other herbivores may potentially prevent the establishment of seaweeds. Herbivory is also thought to be a primary factor in maintaining the between-habitat diversity of seaweeds (Lubchenco 1978, Ayling 1981, Hay 1981, 1984, Johnson and Mann 1988, Worthington and Fairweather 1989). Herbivory has also been hypothesized to be important in maintaining distributional boundaries on a geographic scale (Lubchenco 1980, Hay 1981, Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Lüning 1990, Hawkins et al. 1992).

On a local scale, algal diversity is notably the one factor most affected by herbivory. Lubchenco (1978) has stated that the effect of herbivores on local species diversity patterns is confusing, in part because few experimental studies (e.g. Keats et al. 1991) have been done. In some instances, herbivores appear to increase algal diversity (Dayton 1975, Lubchenco 1978, Hay 1981, Breitburg 1984), decrease algal diversity (Dayton 1971, Lubchenco 1978, Steneck 1983, Dethier et al. 1991, Foster 1992), or both (Paine and Vadas 1969, Lubchenco 1978). The answer to understanding such variable results may reside in understanding characteristics of both the herbivore(s) (e.g. foraging rates, densities, etc.) and the plant(s) (productivity, rates of competitive displacement, etc.) (Lubchenco and Gaines 1981). Subsequently, Lubchenco and Gaines (1981) developed an "intermediate intensity of herbivory" hypothesis which may be likened to the intermediate disturbance hypothesis probably first formulated by Joseph H. Connell (1978).

Herbivores have even been suggested to affect the geographic patterns of algae ((Hay 1981, Sousa et al. 1981, Gaines and Lubchenco 1982, Hay and Gaines 1984, Foster 1992, Vadas and Elner 1992) and influence assemblage structure. According to Foster (1992) there are great differences in the biota at the latitudinal extremes of the north-east Pacific (the coasts of California, Oregon, and Washington [ca. 32° - 50°N]). Sousa et al. (1981) suggested that reduced grazing at more northern latitudes may be one reason why, in the low intertidal zone, there are more kelp assemblages in the north and more turf assemblages in the south. Furthermore, Dethier and Duggins (1988) have shown that even if community composition is similar, the effect of grazers can be quite different in different geographical regions.

It is generally well known that tropical habitats have smaller and more calcified plants, while many temperate habitats are dominated by the Laminariales, Fucales, Durvilleales and Desmarestiales (Gaines and Lubchenco 1982, Lüning 1990). Numerous authors have suggested that an increase in the intensity of herbivory in the tropics, have favoured small size and calcification of algae (Dawson 1966, Earl 1972a, b, Menge and Lubchenco 1981, Brosnan 1992); herbivorous fish are apparently more common in the tropics, while invertebrate grazers dominate temperate regions (Dawson 1966, Earl 1972a, Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Sousa et al. 1981, Brosnan, 1992). Crustose coralline algae in particular, although they live in a variety of habitats, tend to thrive in tropical areas (Dawson 1966, Gaines and Lubchenco 1982), dominating these environments of intense herbivory (Adey 1973, Steneck 1982, 1983, Breitburg 1984, Sousa and Connel 1992, Dethier 1994, Steneck and Dethier 1994). D.W. Keats (personal communication) states that corallines dominate equally well everywhere; they are just not covered by kelps on coral reefs. Kelps are however a very prominent feature in temperate and colder water habitats (Gaines and Lubchenco 1982, Lüning 1990).

There is however, probably only one well documented case supporting the hypothesis that herbivory may influence large-scale geographic distributions. Several dominant, shallow-water seaweeds from the Caribbean are physiologically capable of transiting the freshwater of the Panama Canal, surviving both the marked salinity changes, and the required time spent in freshwater. Even though boats provide a direct method of transport for the seaweeds through the canal, Hay and Gaines (1984) found that herbivory (and the lack of reef-generated refuge) is the primary barrier to the successful transport and establishment of these seaweeds.

Competition among seaweeds is yet another biological interaction that is often controlled by herbivory and the rôle of herbivory in influencing plant competitive interactions is a well known phenomenon (Dayton 1975, Lubchenco 1978, 1980, Lubchenco and Gaines 1981, Quinn 1982, Paine 1984, 1990, Steneck 1985, 1986, Steneck et al. 1991, Dethier 1994, Steneck and Dethier 1994). One might argue that the coexistence of many plant species is dependent upon the chronic disturbance by herbivores. Among encrusting algae, which compete for space mainly by overgrowth (Paine 1984, Steneck 1985, 1986, Steneck et al. 1991, Maneveldt 1992, Keats and Maneveldt 1994, Keats et al. 1994a), herbivores may prevent monopolization by one or a few competitive dominants (Quinn 1982, Steneck 1985, 1986, Steneck et al. 1991); herbivores often cause competitive reversals in encrusting algal communities (Paine 1984, Steneck et al. 1991).

Even along a broader geographic scale, herbivores may allow competing plants to coexist by selectively grazing the competitively dominant alga. Such a case was supported by Lubchenco (1980) who suggested a factor other than cold water for the latitudinal distribution of Fucus serratus Linnaeus. Fucus serratus occurs from Nova Scotia to Greenland to the European Atlantic shores. This range coincides with intense limpet grazing which according to Lubchenco presumably prevents the red algae Chondrus crispus Stackhouse and Gigartina stellata (Stackhouse) Batters from monopolizing space in the low intertidal zone; it is in this zone that F. serratus coexists with these competitively dominant algae. Outside this range, in the absence of intense herbivore-induced disturbance, C. crispus and G. stellata continue to dominate the low intertidal zone and competitively exclude F. serratus. Even though this suggestion has not been tested experimentally, it certainly highlights the possible importance of herbivory in the control of competitive dominance along a geographic gradient.

In addition to controlling the species diversity (and abundance in particular) and the competitive abilities of algal stands, herbivores have the capacity to control the morphology of some algae (Steneck & Adey 1976, Steneck 1985, Steneck and Paine 1986, Dethier et al. 1991). Coralline crust morphology in particular has been shown to be affected by herbivory (Steneck and Adey 1976, Steneck and Paine 1986, Littler et al. 1995). Studying the rôle of the environment in the control of morphology in Lithophyllum congestum (Foslie) Foslie, a Caribbean algal ridge builder, Steneck and Adey (1976) showed experimentally that besides water motion and light, grazing by parrot fish also influenced the development and branch form of L. congestum. They further showed that all individuals of L. congestum below a depth of 0.25m showed net losses of their thalli due to grazing. Pseudolithophyllum whidbeyense (Foslie) Steneck et Paine on the other hand develops irregular protuberances as a result of healing grazer-induced wounds (Steneck and Paine 1986). In the absence of grazers, this crustose coralline alga's surface is smooth. Furthermore, when irregular crusts were transplanted into herbivore-free environments, a smoothing of the crusts surface morphology was observed. It has even been reported that many fleshy algae may increase their survival under intense herbivory by incorporation of a crustose phase or basal system in their life history (Lubchenco 1980).

On a larger scale, Littler et al. (1995) recently showed that the intimate association between the chiton Choneplax lata (Guilding) and its primary prey, the encrusting coralline alga, Porolithon pachydermum (Foslie) Foslie, results in a mutualistic association. The coralline serves as a predictable source of food and refuge substratum, while the grazing activity of the chiton results in increased biomass and accretion of the alga, and simultaneously removes superior competitors that can overgrow and smother or shade the coralline. More strikingly, the grazing activity of the chiton completely alters the morphology of the coralline.

4. The ecology of Patella cochlear Born. and Spongites yendoi (Foslie) Chamberlain in South Africa

The pear limpet Patella cochlear reaches its highest abundance along the South and southern West coasts of South Africa where it dominates the lower eulittoral zone by achieving densities of over 3600 individuals per m^{-2} (Branch and Griffiths 1988). At densities above 300 per m^{-2}, it excludes most other species, leaving only a band of encrusting coralline algae

(Branch 1975b, 1976, Branch et al. 1992) and a garden of Gelidium micropterum Kuetzing or Herposiphonia heringii (Harvey) Falkenberg. Whereas species richness and biomass tend to increase in a downward direction, in the lower eulittoral zone they are abruptly reduced (Branch and Branch 1988, Branch and Griffiths 1988), increasing again in the sublittoral fringe.

The high densities of P. cochlear appear to be maintained as a result of its territorial behaviour (Branch and Griffiths 1988). Territoriality is defined here as the prolonged occupancy of an area and its defense against intrusions by other species (Stimson 1973). This behaviour is considered an adaptive response to intense intra- and interspecific competition for algal food (Stimson 1970, 1973, Branch 1975a, b, 1976, 1981, 1982, Creese and Underwood 1982, Hockey and Branch 1984, Klump and Polunin 1989, Branch et al. 1992, Wright and Shanks 1993), and it has been repeatedly established that these limpets may regulate the abundance of littoral zone algae (Branch and Griffiths 1988, Keats et al. 1994a).

Selection for territorial behaviour would be based on the advantage it confers on the territory holder. Two possible advantages to individuals as a result of defending territories are, the protection of a thick algal film (Stimson 1970, Branch 1975a, b, Branch and Griffiths 1988, Branch et al. 1992, Klump and Polinin 1989, Wright and Stank 1993), and the maintenance of a sufficiently large smooth grazing surface (Stimson 1973, Steneck 1982, Steneck and Paine 1986). It may be a combination of these features which allows P. cochlear to maintain such high densities.

Territories of adjacent P. cochlear are known to touch but apparently do not appear to overlap, as indicated by narrow ungrazed strips between territories (G.W. Maneveldt, personal observation). These narrow ungrazed strips often become filled in by the encrusting algae Ralsia verrucosa (Areschoug) J. Agardh or Spongites impar (Foslie) Chamberlain which are in turn prevented from overgrowing the limpet territories by the grazing activities of these limpets (G.W. Maneveldt, personal observation). Unless disturbed, the P. cochlear territories are very stable and longevity is high, up to 30 years (Branch and Newell 1978), favouring a low metabolic rate relative to other patellid limpets (Branch and Newell 1978, Branch 1979), slow growth (Stimson 1973, Branch 1974b), and a low reproductive output (Branch 1974a, 1976).

P. cochlear relies on a highly specific association with a fringing "garden" of fine red algae (Branch 1971, 1975a, b, 1976, 1981, Branch and Griffiths 1988). Usually this comprises G. micropterum or less often H. heringii. Branch and Griffiths (1988) further state that these algae are extremely productive and potentially can supply all the energetic needs of the limpet.

There does however exist at the base of the mid- and lower eulittoral zones, a species of encrusting coralline alga Spongites yendoi which notably grows in association with P. cochlear throughout the Western Cape (Branch and Branch 1988, Keats et al. 1993, 1994b). Seagrief (1967), Branch (1971, 1975a, b, 1976), and Branch and Newell (1978) have recorded P. cochlear grazing on S. yendoi (as Lithothamnion). Earlier, Branch (1971, 1975a, 1975b, 1976) had gone as far as stating that P. cochlear feeds almost entirely on S. yendoi (as

Lithothamnion); later (1980), reporting on the energy requirements of *P. cochlear*, he states that *P. cochlear* cannot survive on *S. yendoi* alone. Steneck and Branch (*unpublished manuscript*) have however indicated that juvenile *P. cochlear* rely on *S. yendoi* for all their energy requirements as they lack gardens of their own. This study will determine whether *S.yendoi*, which occurs much further north along the West coast, may indeed be as important a supplement to *P. cochlear* as *G. micropterum* or *H. heringii*, irrespective of the limpet's size group. Furthermore, it will be determined whether *P. cochlear* is the primary grazer of *S. yendoi* along this coast.

Spongites yendoi is one of the most abundant West and South coast intertidal encrusting coralline algae (Chamberlain 1993, Keats et al. 1993, 1994a). It is a relatively thin species that grows abundantly from the mid- to lower eulittoral zones on rocky shores throughout South Africa (Chamberlain 1993, Keats et al. 1993, 1994a, b). At its upper limits, *S. yendoi* forms thin sheets mainly in crevices and pools (Chamberlain 1993, Keats et al. 1993), while in the lower eulittoral zone, it forms relatively thicker sheets on open rocks and is often found growing on the shells of the molluscs *P. cochlear*, *P. argenvillei* Krauss, *P. granatina* Linnaeus, *Oxystele sinensis* (Gmelin), *Turbo sarmaticus* Linnaeus, and *T. cidaris* Gmelin (G.W. Maneveldt, *personal observation*). Somewhat thicker and protuberant expanses of *S. yendoi* are often also found growing on the sheltered vertical aspects of low shore rocky outcrops (G.W. Maneveldt, *personal observation*). *P. cochlear* shells are often coated with thalli of the marine lichens *Pyrenocollema* spp.[1] and *S. yendoi* frequently even grows over the lichens (D.W. Keats, *personal communication*; G.W. Maneveldt, *personal observation*).

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[1] This is probably a new species of marine lichen (Y. M. Chamberlain, *personal communication*).

Individual thalli of S. yendoi are usually not discernible because of extensive fusion of margins (Keats et al. 1993). The thallus of S. yendoi is frequently heavily grazed by P. cochlear (Keats et al. 1994a, b).

Apart from Steneck and Adey's (1976) Caribbean algal ridge builder, and Steneck and Paine's (1986) boreal northeastern Pacific examples, there are no documented cases of herbivores controlling the morphology and abundance of encrusting coralline algae on a local scale, and only one recent study of this nature on a larger scale (see Littler et al. 1995); there are no studies of this nature along a geographic gradient. The present study hopes to determine whether herbivores have the capacity to control both the morphology and abundance of algal species along a geographic gradient.

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GEOGRAPHIC STUDIES ON THE INTERACTION BETWEEN THE LIMPET, PATELLA COCHLEAR, AND THE ENCRUSTING CORALLINE ALGA, SPONGITES YENDOI

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Abstract. The territorial pear limpet, Patella cochlear, occurs along the South and southern West coasts of South Africa, while one of its primary prey, the encrusting coralline alga, Spongites yendoi, occurs much further north along the West coast. This has presented the ideal situation to develop and test hypotheses concerning the importance of grazing in the ecology of encrusting coralline algae along a geographic gradient.

Variation in the abundance of P. cochlear has various implications for the morphology and ecology of S. yendoi. The coralline comprises the major portion (roughly 85 %) of the limpets diet while fleshy algae (Gelidium micropterum) comprise roughly 7 % of its diet. Grazing by the limpet reduces the thallus thickness of the coralline producing a relatively smooth coralline; in the absence of herbivory, or under low grazing frequencies, the coralline is thick and highly protuberant. As far as overgrowth (interference) competition is concerned, grazing reduces the corallines competitive ability; as far as exploitative competition is concerned, grazing enhances the corallines competitive ability (increased growth rate means increased rate of substratum occupancy). Grazing also reduces the fecundity of the coralline. Manipulation experiments support the observed geographic trends.

Although grazing is commonly perceived as a negative factor in marine ecosystems, the intimate herbivore-coralline association between P. cochlear and S. yendoi shows characteristics of a facultative mutualistic association. Grazing increases the corallines' lateral growth rate; thinner forms of the coralline grow significantly faster (0.58 ± 0.24 $mm.month^{-1}$) than thicker forms (0.10 ± 0.02 $mm.month^{-1}$). An increased lateral growth also resulted in the thinner form of the coralline being very abundant on South and southern West coasts occupying as much as 79 % of all surfaces in the lower eulittoral zone; there is thus a positive correlation between limpet and coralline abundance. Preliminary nutrient analyses reveal that

the coralline is equally high in organic content per volume as compared with the limpet's garden of G. micropterum and possibly also Herposiphonia heringii.

Key words: competitive ability; facultative mutualistic association; fecundity; geographic gradient; growth rate; herbivore-coralline association; herbivory; morphology; Patella cochlear; Spongites yendoi; thallus thickness.

Key phrases: Effects of grazing on: thallus thickness, lateral growth rate, general physiognomy, fecundity, competitive ability, and abundance; Facultative mutualistic association; Grazing as a positive factor; Nutrient status of coralline vs that of alga from limpet's garden; Results of limpet manipulation vs geographic trends.

INTRODUCTION

With a few notable exceptions (Brenchley and Carlton 1983, Wethey 1983, Hay and Gaines 1984, Dethier and Duggins 1988, Foster et al. 1988, Foster 1990, Andrew and Underwood 1992, Schaff et al. 1992, Kennelley and Underwood 1993, Steneck and Dethier 1994), ecologists rarely have the opportunity to study interactions at levels beyond the "within ecosystem" scale. As a result, the importances of changes in biotic interactions along geographic gradients remain a little explored area of ecology and most often generalizations from small scale studies have been applied to entire regions to explain certain observed patterns (Kennelley and Underwood 1993). An example where such generalizations have proven false was provided by Foster (1990). Foster sought to determine whether the generally accepted causes of intertidal zonation and factors affecting subtidal kelp assemblages along the Northeast Pacific coast were true for the central and northern Californian coast. He found instead that the algal assemblage structure was highly variable as were its causes, and stated that "the generality of commonly accepted causes .... may be an illusion based on assumptions of environmental homogeneity". Foster (1990) then suggested that geographic studies were the most realistic way to evaluate our understanding of ecosystem assemblage structure. The purpose of this research therefore, is to examine the consequences of changes in the abundance of two strongly interacting species, a limpet and its coralline food, along a geographic gradient.

Encrusting coralline algae are important occupiers of space in shallow, hard-bottom, marine environments, yet there have been relatively few studies of interactions involving encrusting coralline algae (Adey and McIntyre 1973, Paine 1984, Steneck 1982, 1983, 1985, 1986, Dethier et al. 1991, Steneck et al. 1991, Keats et al. 1993, 1994a, b, Keats and Maneveldt 1994), and only two (Steneck and Paine 1986, Steneck and Dethier 1994) have examined such interactions along a geographical gradient. There have however been discussions on interactions involving encrusting coralline algae from several biogeographically distinct localities (Steneck and Watling 1982, Steneck 1983, 1985, 1986). Encrusting algae usually show distinct hierarchies of competitive superiority in which thicker crusts and those with raised margins are superior competitors over thinner crusts and those with adherent margins of equal or greater thallus thickness (Paine 1984, Steneck 1986, Maneveldt 1992, Steneck et al. 1991, Keats and Maneveldt 1994). The nature of the competitive hierarchy can however change in relation to the abundance of excavating herbivores and the intensity of their grazing (Quinn 1982, Paine 1984, Steneck 1985, Dethier et al. 1991, Steneck et al. 1991). One observation common to many of the studies involving encrusting coralline algae, is that corallines are often the only algal form to thrive under, and often even require, intense herbivory (Adey 1973, Steneck 1982, 1983, Breitburg 1984, Sousa and Connel 1992, Dethier 1994, Steneck and Dethier 1994).

Limpets (Mollusca, Gastropoda) are important grazers and many of them include encrusting coralline algae in their diets (Branch 1971, 1981, Steneck 1982, 1983, 1986, Steneck and Watling 1982, Paine 1984, Steneck and Paine 1986, Steneck et al. 1991). They are even known to form associations with encrusting coralline algae (Steneck 1982, Steneck and Paine 1986, Steneck et al. 1991). It has been suggested by Steneck (1982) that the limpet Tectura testudinalis Müller and the encrusting coralline alga Clathromorphum circumscriptum (Strömfelt) Foslie for example, have coevolved toward an interdependency since there are a number of apparently specific adaptations between these two organisms. The population density of T. testudinalis is highest on the coralline alga and the association apparently has mutual advantages for both organisms.

Three similar associations have been reported from the Eastern North Pacific. The limpets Lottia pelta (Rathke) (= Collisella pelta) and Tectura scutum (Rathke) (= Notoacmea scutum) preferentially graze the encrusting coralline alga, Lithophyllum impressum Foslie (Steneck et al. 1991). In low-shore tide pools of the same shore, the limpet Acmaea mitra (Rathke) Eschscholtz preferentially grazes another encrusting coralline alga Pseudolithophyllum whidbeyense (Foslie) Steneck et Paine (Steneck and Paine 1986, Steneck et al. 1991) and significantly alters the competitive hierarchy along these shores. By preferentially grazing P. whidbeyense, A. mitra reduces the thallus thickness of the crust. Pseudolithophyllum whidbeyense, having a rapid lateral growth, including over its own deep wounds, subsequently dominates the low shore; the crust overgrows itself, thereby developing a thicker thallus and improving its competitive success over L. impressum (Steneck et al. 1991). Besides their competitive abilities, grazing by limpets have also affected the morphologies of these corallines (Steneck and Paine 1986, Steneck et al. 1991).

The South and West coasts of South Africa are characterised by a shore that has been divided into four zones: the supralittoral fringe (Littorina-zone), the upper eulittoral zone (upper balanoid zone), the mid-eulittoral zone (lower balanoid zone) , and the lower eulittoral zone (the cochlear-zone along the South coast, the cochlear-argenvillei-zone along the West coast) (Branch and Branch 1988). The pear limpet, Patella cochlear Born., and the encrusting coralline alga, Spongites yendoi (Foslie) Chamberlain, are the most characteristic species of the lower eulittoral zone (Fig. 1).

The distribution patterns of these two organisms are somewhat similar (Fig. 2). Spongites yendoi occurs from at least Swakopmund in Namibia, all the way round to the east coast of Mozambique, just south of Vilanculos. Patella cochlear occurs from Luderitz in Namibia to just south of Richards Bay (Branch et al. 1994). Both organisms reach their highest abundances along the South and southern West coasts of South Africa (Branch 1976, Branch and Griffiths 1988, Chamberlain 1993). North of Groenriviermond along the West coast, P. cochlear is progressively replaced by another limpet, P. argenvillei Krauss, which occurs in equally dense populations (Branch and Griffiths 1988). However, S. yendoi is abundant well north of Groenriviermond, at least as far as Luderitz, Namibia (G.W. Maneveldt, personal observation). At its southern extent S. yendoi is relatively thin while further north of Groenriviermond, an extremely thick, very protuberant form of this coralline is found. Also, at many South and West coast sites, on the vertical aspects of many sheltered rocky outcrops lacking any apparent herbivores, the coralline is very protuberant. Variation in the abundance of P. cochlear therefore has various implications to the morphology and ecology of the encrusting coralline alga, S. yendoi, and presents the ideal situation to develop and test hypotheses concerning the importance of grazing in the ecology of encrusting coralline algae on a local and along a geographic gradient.

In this thesis a number of questions concerning the interaction between P. cochlear and S. yendoi were addressed: Is the thicker, more protuberant encrusting coralline alga found along the South African north West coast indeed S. yendoi? If so, is P. cochlear the primary grazer of S. yendoi, and does the alga comprise a substantial portion of the limpet's diet? Does grazing by P. cochlear reduce the thallus thickness of S. yendoi and thus affect its competitive ability? If grazing by P. cochlear does reduce the thallus thickness of S. yendoi, does this affect the crusts growth rate? Are populations of S. yendoi more abundant in the presence or absence of P. cochlear? Does differential grazing affect morphological traits in S. yendoi? Does grazing by P. cochlear affect the fecundity of S. yendoi? What is the energy status of S. yendoi compared to the limpets' algal garden? Is there a difference in the energy status of the thin and thick forms of S. yendoi? All of these questions are addressed on a geographical gradient in relation to the distribution of P. cochlear.

METHODS

This study was conducted within the eulittoral zone along a geographic gradient from the West to the South West coasts of South Africa. The study sites included Port Nolloth (Northern Cape), Groenrivier (Northern Cape), and Holbaaipunt, South West coast (Western Cape) (Fig. 3). Collections and measurements were made of thin (plants growing in the mid- to lower eulittoral zone in the presence of P. cochlear) and thick forms (at Holbaaipunt and Groenrivier, these plants grow on the vertical aspects of sheltered rocky outcrops lacking any apparent herbivores; at Port Nolloth, these plants grow in the mid- to lower eulittoral) of S. yendoi.

To determine whether the thicker, more protuberant crustose coralline alga found along the north West coast of South Africa is indeed S. yendoi, a morphological study of the 2 forms was carried out. Field collections were made from all study sites. Plants were examined as far as possible when fresh, or were air dried, or fixed in 10 % commercial formalin in seawater (4 % formaldehyde) and stored in 70 % ethanol: 10 % glycerol: 20 % distilled water solution. For light microscopy, formalin-preserved plants were decalcified for sectioning in 10 % nitric acid, the thallus was hardened in 70 % ethanol and sectioned at 10-30 μm thickness on a Leitz CO_2 freezing microtome. Sections were mounted on a microscope slide containing aniline blue in 60 % Karo syrup. Observations and thallus measurements were compared with those of Chamberlain (1993, 1994) for identification. For scanning electron microscopy, air dried material was mounted whole or fractured and mounted on stubs, using double-sided adhesive tabs (Agar Scientific, 66a Cambridge Rd., Stanstead, Essex CM24

8DA, UK). The stubs were stored in a desiccator for at least 24hrs prior to examination, coated with gold for 4-6 minutes in a 5000-V Edwards S150B sputter coater (Edwards High Vacuum, Manor Royal, Crawley, West Sussex RH10 2LW, UK), and examined with a Hitachi X650 scanning electron microscope (Hitachi, Ltd., Tokyo, Japan), equipped with a Mamiya 6X7 camera. In cell measurements, length denotes the distance between primary pit connections, and diameter the width of the cell lumen at right angles to this. Conceptacle measurements follow the method of Adey and Adey (1973). Thallus terminology follows Chamberlain (1990, 1993, 1994). Drawings were made from individual representative slide preparations and are not composite representations.

The grazing scars observed at the surface of the two forms of S. yendoi were examined under a scanning electron microscope and compared with the distinctive radular marks made by molluscan grazers. Grazing marks were also simulated by gently scraping the radulae of the molluscs commonly found on S. yendoi over a chalk cube and comparing these to the actual grazing scars. Limpet grazing frequency (bite rate per unit area) experiments similar to Steneck et al. (1991), were carried out. Grazing was measured in the field by recording the rate at which pencil (graphite) dots were removed from the surface of S. yendoi by P. cochlear. Dots were 2mm in diameter and their positions were determined by a 100 cm^2, 50 cm^2, 25 cm^2, and 16 cm^2 perspex template perforated respectively with 81, 36, 16, and 9 evenly spaced holes (results were expressed as percentages). Different sized quadrats were used since S. yendoi at Port Nolloth and Groenrivier have somewhat patchy occurrences, and individual patches are often smaller than 50 cm^2. The number of dots removed by limpets was recorded daily for 2 days (n = 15 for each form of S. yendoi from each site). Dots removed by limpets were marked again each day in the same place. Ungrazed dots persist for several days on the coralline surface. Grazing intensity (bite depth) was measured under a scanning electron microscope. For gut content analysis, the entire gut of 20 individuals from each of three limpet species and one chiton were dissected and using a dissection microscope equipped with an eyepiece quadrat divided into 100 squares, the percentage of coralline algae and other food items found in the gut was determined; coralline "chalk" was not included as contributing toward the percentage of coralline algae in the gut. All limpets and chitons sampled were collected from within the "S. yendoi zone".

For margin and thallus thickness measurements of S. yendoi, air-dried material was used. Crude sections were made perpendicular to the growing margins of the thalli simply by breaking the crusts between two forceps or using a diagonal cutters or a small hammer and cold chisel. Using an eyepiece micrometer the thickness of the margins and thalli were measured under a dissection microscope. For competitive interactions, approximately 1200 contact zones between two species were randomly sampled along transect lines run at all sites. The overgrowth (symbol > on graph) of one species by another was scored as a win for the overgrowing species against the overgrown species (Fig. 4). Retaliations were also recorded where species normally overgrown resisted overgrowth or reversed the normal pattern by regenerating margins and thereby raising their thalli over the encroaching alga (e.g. symbol A >< B on graph: A overgrows B, but B retaliates to competitive overgrowth by A)(Fig. 4) (see Keats and Maneveldt 1994). To determine crust thickness at the point of overgrowth, 10 pieces of the margin of each species involved in a competitive interaction were collected. The competitors' margins were fractured perpendicular to the line of contact, and the thallus thickness at the point of overgrowth was measured for both species using an eyepiece micrometer in a dissecting microscope.

Marginal extension rates of both forms of S. yendoi from all sites were monitored over a 12 month period at 10-weekly intervals. To measure the lateral growth of S. yendoi, holes were drilled, away from the margin, through the thallus into the substratum. A numbered, tagged screw inserted into plastic wall anchors was embedded in the substratum. A second untagged screw was embedded in the substratum approximately 5 - 10 centimetres from the margin. The tagged and untagged set of screws represented a transect line (Fig. 5). The advance of the leading edge of the crust from the tagged screw, indicating growth, was measured to the nearest 0.05 of a millimetre using plastic callipers (N = 25 for each form at all sites).

To measure the abundance of S. yendoi at all sites, a 30 cm x 30 cm perspex quadrat perforated by 100 holes was used. The percentage cover of S. yendoi and other algae was measured randomly along a transect line running more or less perpendicular to the shore at the various sites. Since P. cochlear territories are so stable, percent cover of all herbivores were also measured to determine the relative importance of P. cochlear and other herbivores.

To determine the effects of grazing on the general physiognomy of S. yendoi, various morphological data were obtained. Under a dissection microscope the number of protuberances per cm^2, the protuberance height, the protuberance diameter, and the percentage of the thallus covered by the protuberances were measured. Protuberance percentage cover of the planar area of the thallus was measured under a dissection microscope equipped with an eyepiece quadrat divided into 100 small squares. Averages per specimen were obtained, and then the mean for 10 specimens was calculated. This procedure was carried out for all morphological variants from all three sites.

To determine the effects of grazing on the reproductive output of S. yendoi, a dissection microscope equipped with an ocular quadrat lens was used. The number of conceptacles across a 0,25 cm^2 (0,5 cm X 0,5 cm) area of the crust was measured. An average for each specimen was measured, and an average for 10 specimens was obtained. This procedure was carried out for both forms of S. yendoi.

Apart from the various field analyses, a limpet manipulation experiment was set up to test against the observed geographic trends. A portion of the randomly selected territories of P. cochlear were cordoned off by sinking screws into the substratum (Fig. 6). The distance between screws was sufficiently close to prevent the resident limpet from having access to the cordoned off portion of its territory. This design essentially represented an area of "0" grazing. It was assumed then that the remaining uncordoned portion would receive approximately twice as much grazing since the area was essentially halved. This represented an area of "2X" grazing. The natural state acted as the control. Fifteen replicates of each of the three experimental designs were set up. A series of data collections were made after 5 months. These included:

1. Spongites yendoi's thallus thickness;
2. Spongites yendoi's marginal extension (every month for the 5 months);

3. the general physiognomy, i.e. protuberance data; and

4. the corallines' fecundity, i.e. conceptacle data.

A preliminary nutrient status of S. yendoi was determined and compared against that of G. micropterum by measuring the organic content per volume. Ten samples for each of the two forms of S. yendoi and for G. micropterum were used for organic content analysis. Samples were dry ashed for 16 hours at 450 ^{0}C in a Naber L47T muffle furnace (Naber Industrieofenbau, 2804 Liliethal/Bremen, West Germany) following the procedure of Moore and Chapman (1985).

RESULTS

Taxonomy

The thicker, more protuberant encrusting coralline algae found along the South African North West coast is indeed S. yendoi. The coralline possesses three of the four characters diagnostic of Spongites Kützing namely:

1. simple spermatangia restricted to the floor of the male conceptacles (Penrose 1991, 1992, Verheij 1993)(Figs 7 and 8);
2. a tetrasporangial conceptacle roof which is formed only by filaments surrounding the sporangial initials (Penrose and Woelkerling 1991)(Fig. 9); and
3. the pore canals of the tetrasporangial conceptacles lined by cells that arise from peripheral roof filaments, protrude into the pore canal, and are orientated more-or-less parallel to the roof surface (Penrose and Woelkerling 1992) (Fig.10).

The fourth distinct character i.e. 'that carposporangia are borne peripherally from the fusion cell' (Penrose 1992, Verheij 1993), could not be evaluated since no female material was found. Furthermore, the thick, more protuberant coralline found at Port Nolloth conforms well to a recent description of the vegetative and reproductive anatomy of Spongites yendoi (Foslie) Chamberlain (Table 1, Figs 11-31) (Chamberlain 1993, 1994).

Grazing on S. yendoi

Patella cochlear is the primary grazer of S. yendoi at the Holbaaipunt and Groenrivier sites. The feeding apparatus and grazing traces of the various molluscs are very distinct (Figs 32-52) and examination of graze marks on the surface of these crusts (Figs 14, 16, and 20) as well as simulated grazing marks (Figs 33, 39, 45, and 49) show that the grazing scars at the surface of S. yendoi at Holbaaipunt and Groenrivier are indeed made by P. cochlear. The majority of the grazing scars on the Port Nolloth population of S. yendoi (Figs 27 and 28) are made by the smaller P. granularis Linnaeus; some chiton scars were also visible (Fig. 50). Grazing intensity (depth of bite) of P. granularis is lower than that of P. cochlear (Fig 53) as the radula of P. cochlear (Figs 35, 41, and 53) clearly penetrates deeper into the thallus of S. yendoi.

Patella cochlear's distinctive grazing trace, appearing similar to that made by an eight-pronged garden rake (Figs 32 and 33), is clearly evident at the surface of S. yendoi (Fig. 34). The grazing scars made by P. granularis, P. argenvillei and chitons, are different (Figs 38, 39, 40, 44, 45, 48, and 49). On soft chalk P. granularis produces two broad grazing strokes which are relatively close together (Fig 39) resulting from the overlap of its lateral teeth (Fig. 38), the actual grazing scar on S. yendoi's surface is an extremely narrow, superficial, four to six-stroked grazing trace (Figs 38 and 40). This grazing scar is shallow and has multiple strokes because only the tips of the teeth are effective at excavating the coralline's surface. On chalk, P. argenvillei produces a grazing scar similar to that of P. granularis (Figs 44 and 45) and since their radula are somewhat similar in the shape of the teeth ends and the relative amounts of hardening, one would expect a similar grazing scar on coralline surfaces.

Although P. argenvillei has a broader radula with larger teeth than either P. cochlear or P. granularis (Figs 46 and 47), its radula appears to be, like that of P. granularis, relative ineffective at excavating the thallus of S. yendoi despite its close resemblance to the radula of P. cochlear; this idea is supported by the presence of relatively thick and very protuberant individuals of S. yendoi around individuals of P. argenvillei at Groenrivier and sites further north (D. W. Keats and G.W. Maneveldt, personal observation). Chitons leave two narrow, relatively broad spaced grazing strokes which penetrate deeper into the thallus of S. yendoi (Figs 48, 49, and 50). Radulae with shovel-like teeth (P. cochlear and chitons) are deeper excavators of coralline algae than those with rake-like, pointed teeth (P. argenvillei and P. granularis). It thus seems feasible to suggest that those molluscs which are relatively ineffective at excavating coralline surfaces, have relatively high radula-to-shell/body length ratios (Fig. 53).

Spongites yendoi comprises a substantial portion (85.40±0.58 %) of P. cochlear's diet (Fig. 54). Compared with the coralline, fleshy algae from its garden comprise 6.75±0.43 % of the limpet's diet. The remaining 7.85±0.30 % of the gut contents of P. cochlear probably comprise a mixture of diatoms, larvae and other microscopic algae and unidentifiable material.

At Holbaaipunt, 86.9 % of the surface of S. yendoi in the lower eulittoral zone is grazed every 24 hours as compared with 55.05 % at Groenrivier ($P < .0001$, TWOSAMPLE TUKEY'S test, hereafter referred to as 'T' test). When comparing the actual rate of the graphite dots removed per unit area (grazing frequency), that of Holbaaipunt (ca 0.57) is significantly higher than the grazing frequency at Groenrivier (ca 0.30, $P < .0001$, TWOSAMPLE 'T' test) (Figs 55 and 56). The grazing intensity at Holbaaipunt and Groenrivier are relatively similar and grazing scars may achieve depths of up to 21 μm (Fig. 57). The grazing frequencies at Port Nolloth are so low that even after 48 hrs, the graphite dots were still visible on the surface of S. yendoi.

Thallus thickness, growth rate, physiognomy and fecundity in natural populations

Both the margin and thallus in the Holbaaipunt population of S. yendoi are extremely thin (Figs 58A and B). The thalli of S. yendoi at Groenrivier are thicker than those at Holbaaipunt (Fig. 58B). There are no significant differences in the margin thicknesses of both forms of S. yendoi (i.e. thin form in the lower eulittoral and thick form on vertical aspects of rocky outcrops) at either the Holbaaipunt or Groenrivier sites ($P = .42$, TWOSAMPLE 'T' test) (Fig. 58A); these two populations do, however, have thinner margins and thalli than the Port Nolloth population ($P < .001$, ANOVA) (Figs 13, 23, 58A and 58B). The margin and thallus of S. yendoi at Port Nolloth are extremely thick and have been observed to attain thicknesses of up to 15 mm (Fig. 31). It is likely that the high grazing frequencies and intensities experienced by S. yendoi in the lower eulittoral zone at Holbaaipunt have resulted in the thallus of the coralline being so thin. Reduced grazing frequencies (Fig. 56) yet similar intensities have resulted in the thallus of S. yendoi at Groenrivier being somewhat thicker than the Holbaaipunt population. At Port Nolloth, even though P. granularis grazes S. yendoi, the frequencies and intensities (Figs 56 and 57) are not great enough to significantly reduce the thallus thickness as in the Groenrivier and Holbaaipunt populations.

The thin form of S. yendoi found in the lower eulittoral zone at Holbaaipunt grows significantly faster (0.58 ± 0.24 mm.month^{-1}) than the thicker form of S. yendoi (0.18 ± 0.05 mm.month^{-1}, $P < .0001$, 'T' test)) found growing on the vertical aspects of rocky outcrops lacking any apparent herbivores. A similar trend exists at Groenrivier. The thin form of S. yendoi at Holbaaipunt also grows significantly faster than the thick form of the coralline at Port Nolloth (0.10 ± 0.02 mm month^{-1}, $P < .0001$, 'T' test) (Fig. 59). The thin form at Groenrivier grows at 0.38 ± 0.08 mm month^{-1} which appears to be slower, but is not significantly different from the thin form at Holbaaipunt ($P = .42$, 'T' test). Thick forms of S. yendoi at all sites grow at roughly the same rate ($P = .064$, ANOVA). There is thus a negative correlation between thallus thickness and lateral growth rates ($r^2 = .806$, $P = .017$, ANOVA) (Fig. 60).

Grazing by P. cochlear also affects the general physiognomy of S. yendoi. Besides being thicker, S. yendoi in the absence of P. cochlear as well as those experiencing reduced grazing frequencies, are more protuberant ($P = .02$ for thin forms of S. yendoi 'T' test, $P = .087$ for thick forms of S. yendoi, ANOVA, see Figs for differences between sites) (Figs 27, 30, 31, 61, and 62). Not only do the protuberances cover a larger percentage of the thallus of thicker S. yendoi ($P = .0084$ for thin forms of S yendoi 'T' test, $P = .001$ for thick forms of S. yendoi, ANOVA, see Figs for differences between sites) (Fig 61D), but the protuberance height ($P = .009$ for thick forms of S. yendoi, ANOVA, see Figs for differences between sites) and diameter ($P < .001$ for thick forms of S. yendoi, ANOVA, seee Figs for diferences between sites) also increases with a decrease in grazing frequency (Fig. 61B and C). Despite the thick form of S. yendoi at Holbaaipunt having the greatest number of protuberances, and the largest percentage of the thallus surface covered by protuberances (Figs 61A and D), these protubernaces are much smaller than those of the Port Nolloth population (Figs 61B and C).

Conceptacles are generally not restricted to any one part of the thallus of S. yendoi. Conceptacles may occur on top of protuberances, on the sides and base of protuberances, or on areas lacking protuberances (Fig. 30) so that the greater the surface area, the greater the area for conceptacle production (Fig. 62). Populations of S. yendoi in the absence of P. cochlear have a greater number of conceptacles than those experiencing grazing from P. cochlear (Fig. 63A). Notably, the Port Nolloth population has the greatest number of conceptacles per unit area than either the Holbaaipunt or the Groenrivier populations ($P = .013$, ANOVA, see Figs for differences between sites). Not only is the number of conceptacles at the surface of S. yendoi located within the lower eulittoral zone lower at Holbaaipunt and Groenrivier, but the conceptacles themselves are generally flattened due to the more intense grazing activities of P. cochlear (Fig. 16).

Thallus thickness, growth rate, physiognomy and fecundity in response to manipulated grazing

The margin and thallus thickness of S. yendoi varies with the three experimental designs (Fig. 58C). Margins and thalli become increasingly thicker upon limpet exclusion ($P < .001$, ANOVA, see Fig. 58C for differences between sites). Spongites yendoi grows significantly faster under increased grazing conditions ("2X" grazing) than under "Normal" and "0" grazing conditions ($P < .001$, ANOVA) (Fig. 64C). The margin extensions of S. yendoi under "Normal" and "0" grazing conditions are virtually identical to those of the margin extensions of the thin population of S. yendoi at Holbaaipunt (P = .509, ANOVA) and the thick population at Port Nolloth (P = .969, ANOVA) respectively (Fig. 59). The general physiognomy of S. yendoi also differs with the three experimental designs (Fig. 61E). Under reduced grazing conditions ("0" grazing), the thallus surface of S. yendoi becomes more protuberant (P < .001 for percent cover, P = .002 for height, P = .015 for diameter, ANOVA, see Fig. for differences between treatments). Even the fecundity under the different experimental designs differs dramatically (Fig. 63B), with the number of conceptacles being extremely low under intense ("2X") grazing conditions (P < .001, ANOVA, see Fig. for differences between treatments).

Competitive ability

It appears that the competitive ability of S. yendoi is also affected by the presence or absence of P. cochlear. At Holbaaipunt, with a 32.40±1.82 % cover of P. cochlear in the lower eulittoral zone (Fig. 65), S. yendoi is ranked below Ralfsia verrucosa (Areschoug) J. Agardh in the competitive hierarchy; 93 % of all competitive interactions between the two crusts involve R. verrucosa overgrowing S. yendoi (Fig. 66). At Groenrivier, with a reduced cover (22.86±0.67 %), and reduced grazing frequency of P. cochlear (Figs 65 and 56), there is the potential for S. yendoi to be the superior competitor; roughly 56 % of all competitive interactions between S. yendoi and R. verrucosa, involves S. yendoi overgrowing R. verrucosa. No competitive interactions between the two crusts were found at Port Nolloth, so a possible complete reversal could not be determined (Fig. 66). Thallus thickness is positively correlated with the rank in overgrowth competition (see Fig. 67 for correlation and p values).

Abundance of S. yendoi

There is a positive correlation ($r^2 = .813$) between *P. cochlear* and *S. yendoi*'s abundance; at least in the lower eulittoral zone (Fig. 65). *Spongites yendoi* achieves its highest abundance in the lower eulittoral zone at Holbaaipunt (79±2.88 %) when considering that the coralline encrusts the shells of the limpet as well (Fig. 1), and has its lowest abundance in the lower eulittoral zone at Port Nolloth (Fig. 65). *Spongites yendoi*'s cover in the lower eulittoral zone at Groenrivier is somewhat patchy (Fig. 68) and much of the primary substratum is occupied by *Leptophytum foveatum* (Chamberlain et Keats) (Figs 65, 68, and 69). *Leptophytum foveatum* and a species of *Peyssonnelia* Decaisne are the most abundant encrusting algae in the lower eulittoral at Port Nolloth and particularly occupy much of the primary substratum in low shore tide pools (G.W. Maneveldt, *personal observation*). While *R. verrucosa* occupies much of the ungrazed space between limpet territories along the South coast (Fig. 1), *S. impar* is characteristically the dominant encrusting alga between limpet territories along the southern West coast (Fig. 69). Interestingly enough, as *L. foveatum* replaces *S. yendoi* as the basal encrusting coralline within the lower eulittoral zone along the West coast (Figs 68 and 69), *S. yendoi* characteristically finds a refuge within the ungrazed portions between limpet territories (Fig. 68).

Nutrient status

Although a large proportion of the volume of *S. yendoi* comprises calcium carbonate, there is no difference in the organic content per volume for either of the two forms of *S. yendoi* and *G. micropterum* ($P = .858$, ANOVA,) (Fig. 70). In *G. micropterum*, much of this volume is water. Interestingly, most of the dry weight in *G. micropterum* is organic matter (Fig. 70).

DISCUSSION

The habit and vegetative features of all forms of S. yendoi studied here correspond well with those reported by Chamberlain (1993, 1994) at both the generic and specific levels (Table 1, Figs 7-31). Chamberlain (1993) found that many variations of S. yendoi, particularly in external morphology, exist and she suggested that these morphological variants are directly attributable to habitat factors such as grazing pressure. The present study confirms these suggestions.

The differences in feeding apparatus of gastropods and chitons (see Steneck and Watling 1982) are well known and graze marks produced by these herbivores are easily distinguished from each other (Steneck 1982; 1983, Steneck and Watling 1982, Steneck et al. 1991). An examination of the different grazing scars clearly show that P. cochlear is the primary grazer of S. yendoi. It appears that primarily the shape of the ends of the teeth and the relative amounts of hardening agents (iron and silicate compounds), and secondarily the size of the "dominant teeth" and the radula are important. Shovel-like teeth (P. cochlear and chitons), as opposed to rake-like, pointed teeth (P. argenvillei and P. granularis) are more effective at excavating coralline surfaces. This feature combined with the relative amount of hardening agents on the distal ends of the "dominant teeth" (to minimize wear), provide for a greater excavating capability on coralline surfaces. Large "dominant teeth" possessing all the above features (i.e. shovel-like and high iron and silicate content as in the radulae of chitons) are thus the ultimate in an effective rasping tool.

Molluscs with the most effective excavating capabilities (chitons and P. cochlear) have the smallest radula-to-shell/body length ratios. This should perhaps not be surprising since the greater iron and silicate content, and the shovel-like shape of the "dominant teeth" of these two groups would seem to minimize wear of these teeth. Limpets with pointed rake-like teeth would certainly have their teeth worn out quicker by a calcareous diet and would thus need a relatively long radula. In my opinion, despite the larger size of P. argenvillei and its radula being broader and having larger "dominant teeth" than P. cochlear, the pointed nature of the distal ends of P. argenvillei's teeth prevents this limpet from being an effective coralline grazers. It would seem thus that within the Patellacea, the docoglossan radula appears to have levels of differentiation. Chitons (with polyplacophoran radulae) are superior excavators over the other herbivorous molluscs and their excavating abilities are probably due to the reduced number of points contacting the substratum; two to six, depending on the number of cusps present and the applied pressure of the radula (Figs 48, 51, 52, and 53) (Steneck and Watling 1982). The superior excavating capabilities and feeding apparatus of chitons means that they do not need a long radula. However, even though P. cochlear is ranked below the chitons as effective coralline excavators, their high grazing frequencies (and relative high grazing intensities) make them formidable coralline grazers.

Numerous studies have shown that grazing may affect the thallus thickness and the morphology of encrusting coralline algae (Steneck 1982, 1983, 1985, 1986, Steneck and Paine 1986, Steneck et al. 1991, Littler et al. 1995). Not only is the grazing intensity (bite depth) important, of equal importance is the frequency of grazing (Steneck 1982, 1983, Steneck and Watling 1982, Steneck et al, 1991). The varying grazing frequencies of P. cochlear are the main cause for the differences in thallus thickness and external morphology of S. yendoi. Both field observations and limpet manipulation experiments support the idea that P. cochlear is the main herbivore responsible for the differences in thallus thickness of S. yendoi. Even though chitons have a greater coralline excavation ability than limpets (Steneck and Watling 1982), and even though P. granularis has been shown to graze S. yendoi at Port Nolloth, these two herbivores do not graze the Port Nolloth population of S. yendoi often enough to reduce its thallus thickness as much as P. cochlear does. Reduced thallus thickness resulting from the grazing activities of P.cochlear, have various effects on the ecology of S. yendoi.

Thallus thickness is strongly correlated with success in overgrowth (interference) competition and in general, thicker crusts and those with raised margins have a competitive advantage over thinner ones and those with adherent margins of equal or greater thallus thickness (Steneck 1982, 1985, 1986, Steneck et al. 1991, Maneveldt 1992, Keats and Maneveldt 1994, Keats et al. 1994a). It follows then that any factor which potentially affects crust thickness of competing species may mediate their competitive success (Steneck et al. 1991, Maneveldt 1992). Grazers have been shown to control the ability of crusts competing by overgrowth competition (Paine 1984, Steneck 1985, 1986) and competitive reversals involving encrusting coralline algae do exist (Steneck et al. 1991). Grazing by P. cochlear reduces the thallus thickness of S. yendoi and subsequently affects the competitive (interference) ability of the coralline alga. There is the potential for a complete competitive reversal between Ralfsia verrucosa (the superior competitor to S. yendoi along the South and south West coasts) and S. yendoi at Groenrivier and north thereof. The tendency for this competitive reversal already exists at Groenrivier (Fig. 66) and it was expected that interactions between S. yendoi and R. verrucosa at Port Nolloth would reveal this competitive reversal. A complete competitive reversal does however not exist at Port Nolloth since the two encrusting species of algae do not interact at all, north of Groenrivier. The reason for this is because along the West coast, the encrusting coralline alga, Leptophytum foveatum becomes increasingly more abundant and replaces S. yendoi in the lower eulittoral zone north of Groenrivier, restricting S. yendoi to the mid-eulittoral, a zone which is devoid of R. verrucosa. Furthermore, it should be noted that all the other competitive interactions retain the same ranking at the different sites. Consistency of competitive ranking is therefore much more of a feature than competitive reversals.

It is well known that thinner crusts generally grow faster than thicker crusts (Steneck 1985, 1986, Maneveldt 1992, Keats et al. 1994b); it is thought that thicker crusts maintain more living non-photosynthetic cells than do thinner crusts (Steneck 1983) and that this investment in vertical expansion depletes photosynthate that would normally be used for lateral expansion (Steneck 1985). The greater grazing activities of P. cochlear along the South and south West coasts of South Africa result in the thallus of S. yendoi being extremely thin. This geographical observation is supported by the limpet manipulation experiments and clearly the thinner crusts grow faster than the thicker ones (Figs 59 and 64). There is no significant difference between the margin thickness at either the Holbaaipunt or Groenrivier sites, yet lateral margin extensions of S. yendoi at the two sites differ slightly (Fig. 59). This suggests that lateral expansion is a function of both the margin thickness, as well as the thallus thickness away from the margin. Differential grazing frequencies and intensities experienced by S. yendoi are therefore responsible for the differences in lateral growth rates. Grazing by P.

cochlear thus indirectly increases the exploitation competitive ability of S. yendoi by allowing the coralline to grow rapidly and occupy much of the primary substratum, reducing the availability of this limited resource.

It has been reported (Keats et al. 1993, 1994b) that S. yendoi undergoes deep-layer sloughing twice a year, losing up to 50% of its thallus with each sloughing event. Keats et al. (1994b) suggested that this type of cell sloughing (as compared with epithallial sloughing) is an effective way of remaining thin because it allowed for higher lateral growth. The present study has however shown that grazing by P. cochlear is primarily responsible for the thinning of the thallus of S. yendoi. Furthermore, G.W. Maneveldt and D.W. Keats (personal observation) have observed the thick form of S. yendoi at Port Nolloth undergoing sloughing which also negates deep-layer sloughing as being an effective way of remaining thin.

Thick corallines are more susceptible to invasion from boring organisms (Paine 1984, Steneck 1986, Steneck and Paine 1986). Keats et al. (1993) have shown experimentally that the thicker Leptophytum ferox (Foslie) Chamberlain et Keats, which was much more heavily burrowed that the thinner S. yendoi, was more weakly attached. It is thus highly likely that the thicker, more protuberant form of S. yendoi (which results from reduced grazing activity) found along the West coast, has a weaker attachment strength than the thinner form at Holbaaipunt and other South and Southwest coast sites because of its greater susceptibility to invasion from boring organisms. This presumably weaker attachment strength of the thicker, more protuberant S. yendoi, could be one of the reasons for the low abundance of the coralline at Port Nolloth.

Spongites yendoi reaches its highest abundance in the lower eulittoral when P. cochlear dominates the lower shore. Numerous authors have also shown that coralline abundance is usually positively correlated with that of their grazers (Adey and Macintyre 1973, Branch 1975, Steneck 1982, 1985, Branch and Griffiths 1988, Littler et al. 1995). If space is available for growth, or if it is continually renewed, a thin crust with a faster lateral growth rate than a thicker crust, could rapidly dominate the shore (Keats and Maneveldt 1994). Differential grazing frequencies and intensities which have been shown to be responsible for differences in thallus thickness and lateral margin extensions of S. yendoi, (and subsequently increasing the corallines exploitation competitive ability) may have thus indirectly affected the corallines abundance.

Steneck (1982) reported an association between the limpet Tectura testudinalis and the encrusting coralline alga Clathromorphum circumscriptum and in both tide pools and subtidal communities, the population density of T. testudinalis is highest on C. circumscriptum. Steneck (1982) reported that juvenile limpets recruit preferentially to the alga. Branch and Griffiths (1988) have also shown that juvenile P. cochlear appear to settle specifically in the lower eulittoral zone and suggest that one of the cues for such apparently specific settlement, is that the larvae are responding to the presence of S. yendoi (as Lithothamnion) which forms such a conspicuous component of the lower eulittoral zone. Many other authors (Morse and Morse 1984, Morse 1992, Johnson et al. 1991a, 1991b) have documented a number of species whose larvae have exhibited selective settlement on encrusting coralline algae and Johnson et al. (1991b), and Morse et al. (1994) have recorded a number of these cases paralleling the substratum-specificity of settlement, metamorphosis, and recruitment in the natural environment. It is often assumed that inducers associated with encrusting coralline algae are algal in origin (Steneck 1982, Morse and Morse 1984), but an alternate hypothesis is that these inducers originate from bacteria on the corallines surface (Johnson et al. 1991a). Morse et al. (1994) have however demonstrated that the apparently specific settlement and metamorphosis of invertebrates are algal in origin and are specifically in response to a chemosensory recognition of a morphogen found at the surfaces of certain species of encrusting coralline algae. Morse et al. (1994) further concluded that this morphogen was a component of the cell walls of the encrusting coralline algae themselves rather than a product of any non-calcified microbial epibionts. Whether the question of algal or bacterial origin of inducers has been resolved, is uncertain, but all authors do agree that the inducing agent is a chemical stimulus.

A more obvious effect of grazing by P. cochlear is on the general physiognomy of the coralline. It seems that the genetic disposition of S.yendoi is to produce a lumpy to very protuberant crust, with protuberances often being in excess of 15mm high and 5mm wide (Fig. 31). Grazing by P. cochlear is primarily responsible for the occurrences of large populations of relatively smooth plants of S. yendoi. This is a common phenomenon as it has been documented that other grazers influence the morphologies of their coralline food (Hay 1984, Steneck 1985, 1986, Steneck and Paine 1986, Steneck et al. 1991, Littler et al. 1995).

Grazing by P. cochlear clearly also affects the reproductive output of the coralline. Since grazing tends to reduce the number of protuberances producing a somewhat smoother crust, there is less area for conceptacle production. Although "normal" grazing intensities are not enough to completely remove the conceptacles, manipulation experiments have shown that under abnormally intense grazing pressure ("2X" grazing), the limpet has the capacity to almost completely denude the surface of the coralline of all its conceptacles. Furthermore, grazing by P. cochlear also reduces the size and even alters the shape of the conceptacles (Table 1, Figs 16 and 20); even the internal dimensions of the conceptacles are smaller when the thallus is heavily grazed (Table 1). Since tetrasporangia in S. yendoi characteristically develop at the extreme periphery of the conceptacles (Chamberlain 1993), any factor reducing the internal conceptacle diameter, invariably also reduces the number of tetrasporangia produced.

Although gut contents of P. cochlear comprise almost solely S. yendoi (Figs 53 and 54), Branch (1980), and Branch and Griffiths (1988) have stated that production and energy content of S. yendoi (as Lithothamnion) is so low that it cannot alone support the energetic needs of P. cochlear. Branch (1980) further stated that the gardens of red algae thus seem vital for the densely packed P. cochlear and although they often form only a small fringe around each animal, their production and energy contents are high. The results of this study show that S. yendoi is as high in its organic content per volume as G. micropterum. It is thus not hard to see why juvenile P. cochlear, and adult limpets lacking gardens, survive almost exclusively on a diet of S. yendoi (G. W. Maneveldt, personal observation). Recent work by M. E. Hay and Q. E. Kappel (Personal communication) have revealed similar results. They have data showing that organic content per volume is high in many corallines relative to fleshy algae. Branch (1980) has however stated that limpets lacking gardens have a higher ash content, lower calorific value, and lower reproductive output compared to limpets with gardens. It may be because S. yendoi is relatively slow growing (compared to fleshy algae), that once P.

cochlear reaches a certain size, the coralline's low production rates cannot support the energy requirements of the limpet any longer. *Spongites yendoi*'s organic matter per bite is certainly high enough and the limpet does have the capacity to effectively graze the coralline. It may even be that the coralline and the garden of fine red algae are fulfilling different energy requirements and that larger *P. cochlear* are indeed maintaining an essentially mixed diet of algae. Other limpets are known to forage and maintain mixed diets of intertidal algae. Kitting (1980), for example, reports individual plate limpets, *Acmaea scutum*, preferentially consuming mixtures of encrusting algae, even when each of these foods is readily available. Furthermore, Kitting (1980) states that adjacent individuals tend to select the same mixture of algae while sharing the same foraging area, without intraspecific partitioning of encrusting algal species.

This examination of the interaction between *P. cochlear* and *S. yendoi*, and of that of other herbivore-coralline associations (Steneck 1982, Steneck and Paine 1986, Steneck et al. 1991, Littler et al. 1995), suggest that the exact nature of their relationship determines the strength of the association between the herbivore and its coralline food. Generally, in "strong" (i.e. where the herbivore and the coralline are most often associated) herbivore-coralline associations (see Table 2), both organisms benefit mutually by the association (see Steneck 1982, Littler et al. 1995). In such associations, although the grazing frequency is high, the grazing intensity is relatively low (Table 2). "Weak" associations (i.e. where the herbivore is associated with a single plant for only a relatively short period) generally involve herbivores which graze less frequently but produce extremely deep wounds (see Steneck and Paine 1986, Steneck et al. 1991) (Table 2). There seems thus to be an inverse relation between the strength of the association and the intensity of grazing and a positive correlation resulting with the frequency of grazing. By reducing the intensity of grazing under conditions of high grazing frequencies, herbivores in strong associations with coralline algae are able to maintain the algae and assure a continued and abundant food supply under these high grazing frequencies, the alga itself to some extent benefitting by the association. One such benefit would be an increase in its productivity (e.g. Littler et al. 1995).

In conclusion, the interaction between Spongites yendoi and Patella cochlear shows characteristics of a facultative mutualistic association. Both organisms clearly benefit from their association. The limpet has an abundant and dependable source of food while the corallines' benefits are two-fold (Fig. 71). Firstly, grazing by P. cochlear reduces the margin and thallus thickness of S. yendoi which then grows faster, increasing the corallines exploitation competitive ability and invariably results in the corallines' dominance of the mid- and lower eulittoral zones. Secondly, thinner crusts are less susceptible to boring by burrowing organisms which results in the thinner crusts having higher attachment strengths than the thicker crusts (Keats et al. 1994b). A stronger attachment possibly also increases a crust's chances of dominance of the shore under conditions of high physical disturbance. Keats et al. (1994b) have also shown experimentally that grazing by P. cochlear is clearly the main factor preventing the surface of S. yendoi from being overgrown by fleshy algae. However, there are also negative aspects to the association between S. yendoi and P. cochlear (Fig. 71). As crust thickness is important in the competition for space, grazing by P. cochlear results in S. yendoi being overgrown by almost all the other encrusting algae with which it comes into contact. There is thus a trade-off of better exploitation competitive ability against weaker interference competitive ability. Grazing also reduces the fecundity since the surface area for conceptacle production is essentially reduced. This presumably results in a lower recruitment ability of the coralline. A more notable effect of grazing is that thin forms of S. yendoi are much less protuberant, this having a direct influence on the fecundity since conceptacles are produced on the protuberances as well. A thinner crust invariably also means less storage space for photosynthates which might otherwise be stored and later used to recover from disturbances. It should be emphasized that P. cochlear often grazes well below the layer of meristematic cells. Spongites yendoi is, however, capable of regenerating a new layer of meristematic cells below the damaged tissue (Keats et al. 1993). It cannot be denied that P. cochlear has a profound effect on the ecology and morphology of S. yendoi and that grazing contributes to the coralline being a very obvious feature on South African South and Southwest coasts.

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Table 1. Comparison of the two forms of encrusting coralline algae with those of South African species of Spongites Kützing. All measurements are in μm; characters in bold are particularly distinctive; na = not applicable.

FEATURE	S. discoideus (Chamberlain, 1994)	S. impar (Chamberlain, 1994)	S. yendoi (Chamberlain, 1993)	S. yendoi (Holbaaipunt-thin)	Thick coralline (Port Nolloth)
Habit	Epilithic	Epilithic\epizoic	Epilithic\epizoic	Epilithic\epizoic	Epilithic\epizoic
General physiognomy	Flat, developing orbicular protrusions	**Flat, becoming crested\convoluted**	Flat to warty	Flat to warty	Warty to highly protuberant
Thallus construction	Dimerous\monomerous	Monomerous	Monomerous	Monomerous	Monomerous
BASAL FILAMENT CELLS					
Length	14-16	na	na	na	na
Diameter	5-16	na	na	na	na
ERECT FILAMENT CELLS					
Length	4-17	na	na	na	na
Diameter	4-11	na	na	na	na

MEDULLARY CELLS					
Length	na	5-25	10-27	10-37	12-34
Diameter	na	3-6	3-7	3-9	5-8
CORTICAL CELLS					
Length	4-17	2.5-10	5-10	5.5-12	6-10
Diameter	4-11	3-5	3-7	3-10	3-10
EPITHALLIAL CELLS					
Maximum number	4	6	**1**	**1**	**1**
length	2-3	2.5-4	2-5	2-5	2-7
Diameter	4-6	3-6	3-8	3-8	3-10
Trichochytes	Rare	Absent	**Common**	**Common**	**Common**
MALE CONCEPTACLE CHAMBER					
Height	17-31	35-40	**52-60**	**48-61**	**47-62**
Diameter	52-91	150-200	117-169	120-172	122-260
Roof thickness	18-52	35-50	33-39	30-40	29-62

CARPOSPORANGIAL CONCEPTACLE CHAMBER					
Height	52-65	-	52-109	-	-
Diameter	146-200	-	138-234	-	-
Roof thickness	**91-100**	-	**39-78**	-	-
maximum no. cells in gonimoblast filament	7	-	7	-	-
TETRASPORANGIAL CONCEPTACLE CHAMBER					
Height	**52-65**	70-104	62-117	63-120	63-158
Diameter	169-190	180-247	147-207	136-211	142-303
Roof thickness	35-100	39-50	26-65	30-43	37-56
Pore canal cells	Short papillae	Long, very thin filaments	Papillae to long filaments	Papillae to long filaments	Papillae to long filaments
TETRASPORANGIUM					
Length	35-50	55-119	43-78	29-78	58-115
Diameter	13-26	36-38	15-47	15-45	16-74
OLD TERTASPORANGIAL CONCEPTACLES BECOMING BURIED IN THE THALLUS	Yes	No	No	No	No

Table 2. Comparison of the intensity (bite depth) of grazing on corallines by various herbivores, in relation to the strength of their assocation with the corallines. "Strong" = most often associated, "Moderate" = commonly associated and "Weak" = associated with a single plant for a relatively short period (Adapted, with permission, from R. S. Steneck and G. M. Branch, unpublished manuscript).

Coralline-Herbivore Association	Herbivore species	Mean length (mm)	Coralline species	intensity (μm)	REGION
Strong[1]	C. lata	23	Po. pachydermum	±10	W. North Atlantic
Strong[2]	P. cochlear	42.9	S. yendoi	15.4	W & SW South Atlantic
Strong[3]	T. testudinalis	15.4	C. circumscriptum	17.4	W. North Atlantic
Moderate[4]	L. pelta	22.5	L. impressum	32	E. North Pacific
Moderate[4]	T. scutum	22.5	L. impressum	32	E. North Pacific
Weak[2]	I. textilis	30	S. yendoi	45.5	W. South Atlantic
Weak[4,5]	A. mitra	21	Ps. whidbeyense	213.7	E. North Pacific

Key to Herbivore genera: C. Choneplax, A. Acmaea, I. Ischnochiton, L. Lottia, P. Patella, T. Tectura

Key to coralline genera: Po. Porolithon, C. Clathromorphum, L. Lithophyllum, Ps. Pseudolithophyllum, S. Spongites

Key to references: 1 - Littler et al. 1995, 2 - This study, 3 - Steneck 1982, 4 - Steneck et al. 1991, 5 - Steneck & Paine 1986

FIGURE CAPTIONS

Figure 1. The pear limpet Patella cochlear dominates the lower eulittoral zone along with the encrusting coralline alga, Spongites yendoi. Territories of adjacent limpets are known to touch but apparently do not overlap, as indicated by narrow strips (A) between territories, ungrazed by P. cochlear.

Figure 2. The geographical distribution patterns of P. cochlear, P. argenvillei and Spongites yendoi and the location of study sites (1 = Port Nolloth; 2 = Groenriviermond; 3 = Holbaaipunt).

Figure 3. Map of the locations of study areas.

Figure 4. Diagrammatic model of overgrowth competition in encrusting algae. (A) A thicker than B and therefore overgrows B. (B) A thicker than B, but B has a raised margin which is raised above the thickness of A and therefore B overgrows A. (C) A and B of equal thickness and thus reach a competitive standoff. (D) A thicker than B, but B retaliates by regenerating thallus margins.

Figure 5. The method of using tagged and untagged screws to measure lateral margin extension in encrusting algae.

Figure 6. The method for manipulating limpets. Side (A) of the screws effectively represents the "0" grazing portion while side (B) of the screws represents the "2X" grazing portion.

Figures 7-10. Three of the four features diagnostic of Spongites Kützing.

Figure 7. A spermatangial conceptacle.

Figure 8. Spermatangial initials (arrow) each bearing two elongated spermatangia that round off when released.

Figure 9. Roof of tetrasporangial conceptacle (arrowheads) beginning to grow in from the periphery. The tetrasporangial initials (shaded), and the old thallus layer still covering the conceptacle (arrow) are visible.

Figure 10. A mature tetrasporangial conceptacle. Note that the pore filaments are orientated more-or-less parallel to the surface of the conceptacle.

Figure 11. The habit of the thin form of S. yendoi from Holbaaipunt.

Figures 12-17. Thallus features of the thin form of S. yendoi.

Figure 12. Surface of the S. yendoi.

Figure 13. The margin of the thallus showing the medulla (M) and the cortex (C).

Figure 14. Surface of S. yendoi showing tetrasporangial conceptacles (arrows). Note the grazing scars and concavity left by a shed conceptacle (arrowhead).

Figure 15. Vertical fracture of the outer cortex showing epithallial cells (arrowheads) , subepithallial initials (i), and cell fusions (F).

Figure 16. A tetrasporangial conceptacle of S. yendoi.

Figure 17. Vertical fracture of the medulla and lower cortex showing terminal initials (T) and cell fusions (F).

Figures 18-20. Thallus features of the thin form of S. yendoi.

Figure 18. Vertical fracture of a tetrasporangial conceptacle showing the pore canal (P) and tetraspores (T).

Figure 19. Vertical fracture of a spermatangial conceptacle showing the pore canal (P).

Figure 20. The grazer damaged surface of S. yendoi. Note the flattened conceptacle (K).

Figure 21. The habit of the thick form of S. yendoi from Port Nolloth.

Figure 22-26. Thallus features of the thick form of S. yendoi.

Figure 22. Surface of S. yendoi showing a trichocyte (T).

Figure 23. The margin of the thallus showing the medulla (M) and the cortex (C).

Figure 24. Vertical fracture of the outer cortex showing epithallial cells (arrowheads), subepithallial initials (i), and cell fusions (F).

Figure 25. Vertical fracture of the medulla and inner cortex showing cell fusions (F).

Figure 26. Vertical fracture of the thallus of S. yendoi showing the medulla (M) and the cortex (C).

Figures 27-31. Surface of the thick form of S. yendoi showing the protuberance and conceptacle detail.

Figure 27. Surface of S. yendoi showing tetrasporangial conceptacles.

Figure 28. A tetrasporangial conceptacle. Note the superficial grazing scars (arrows).

Figure 29. Vertical fracture of a tetrasporangial conceptacle showing the pore (P) and a tetraspore (T).

Figure 30. Conceptacles (arrowheads) may occur on the tops of protuberances, on the sides of the protuberances, at the base of the protuberances, or even on areas lacking protuberances.

Figure 31. The thallus of the thick form of S. yendoi is extremely protuberant and may often reach thicknesses of 15mm.

Figure 32. The radula and hypothesized grazing trace of P. cochlear. Shading shows the relative amounts of hardening agents. Numbers indicate the number of grazing traces made by the "dominant" teeth. The homologous teeth of each species are labelled as follows: ct, central tooth; lt, lateral teeth; mt, marginal teeth.

Figures 33-37. Grazing scars and radula of P. cochlear. Numbers indicate the number of grazing traces corresponding to those of Figure 32.

Figure 33. Simulated grazing trace of P. cochlear.

Figure 34. Actual grazing scar made by P. cochlear.

Figure 35. Vertical fracture of S. yendoi showing P. cochlear graze marks.

Figure 36. Radula of P. cochlear as seen under the scanning electron microscope.

Figure 37. Radula of P. cochlear as seen under the light microscope. Note the different

amounts of hardening agents.

Figure 38. The radula and hypothesized grazing trace of P. granularis. Shading shows the relative amounts of hardening agents. Numbers indicate the number of grazing traces made by the " dominant" teeth. The homologous teeth of each species are labelled as follows: ct, central tooth; lt, lateral teeth; mt, marginal teeth.

Figures 39-43. Grazing scars and radula of P. granularis. Numbers indicate the number of grazing traces corresponding to those of Figure 38.

Figure 39. Simulated grazing trace of P. granularis.

Figure 40. Actual grazing scar made by P. granularis.

Figure 41. Vertical fracture of S. yendoi showing P. granularis graze marks.

Figure 42. Radula of P. granularis as seen under the scanning electron microscope.

Figure 43. Radula of P. granularis as seen under the light microscope. Note the different amounts of hardening agents.

Figure 44. The radula and hypothesized grazing trace of P. argenvillei. Shading shows the relative amounts of hardening agents. Numbers indicate the number of grazing traces made by the " dominant" teeth. The homologous teeth of each species are labelled as follows: ct, central tooth; lt, lateral teeth; mt, marginal teeth.

Figures 45-47. Grazing scars and radula of P. argenvillei. Numbers indicate the number of grazing traces corresponding to those of Figure 44.

Figure 45. Simulated grazing trace of P. argenvillei.

Figure 46. Radula of P. argenvillei as seen under the light microscope. Note the different amounts of hardening agents.

Figure 47. Radula of P. argenvillei as seen under the scanning electron microscope.

Figure 48. The radula and hypothesized grazing trace of Acanthochiton garnoti. Shading shows the relative amounts of hardening agents. Numbers indicate the number of grazing traces made by the " dominant" teeth. The homologous teeth of each species are labelled as follows: ct, central tooth; lt, lateral teeth; mt, marginal teeth.

Figures 49-52. Grazing scars and radula of A. garnoti. Numbers indicate the number of grazing traces corresponding to those of Figure 48.

Figure 49. Simulated grazing trace of A. garnoti.

Figure 50. Vertical fracture of S. yendoi showing A. garnoti graze marks.

Figure 51. Radula of A. garnoti as seen under the scanning electron microscope.

Figure 52. Radula of A. garnoti as seen under the light microscope. Note the different amounts of hardening agents.

Figure 53. The radulae and grazing details of the various herbivorous molluscs commonly found associated with S. yendoi (N = 20 individuals for each species).

Figure 54. The percentage of the various food types found in the four herbivores commonly found on *S. yendoi* (A = *P. cochlear*, *P* < . 001, ANOVA; B = *P. granularis*, *P* = .063, TWOSAMPLE 'T'test; C = *P. argenvillei*; D = *A. garnoti*, *P* < .0001, TWOSAMPLE 'T' test, Means with the same letters are not significantly different).

Figure 55. The percentage of the surface area of *S. yendoi* grazed over two days at the three sites (Means with the same letters are not significantly different).

Figure 56. The grazing frequency experienced by *S. yendoi* over two days at the three sites (Means with the same letters are not significantly different).

Figure.57. The intensity of grazing experienced by *S. yendoi* at the three sites (*P* < .001, ANOVA, Means with the same letters are not significantly different - Individual 95 percent [PCT] confidence index's [CI's] for means based on pooled standard deviation [STDEV]).

Figure 58. The margin (A) and thallus thickness measurements (B, *P* < .001 for thick forms, ANOVA; *P* = .64 for thin forms, TWOSAMPLE 'T'test) of the two forms of *S. yendoi* at the three sites, as well as the margin and thallus thickness measurements (C) under limpet manipulated conditions (Means with the same letters are not significantly different - Individual 95 PCT CI's for means based on pooled STDEV).

Figure 59. The marginal extension rates of the two forms of *S. yendoi* at all sites.

Figure 60. The relationship between the thickness of the thallus away from the margin and the lateral margin extension rate.

Figure 61. Protuberance data from all sites under natural conditions (A-D), and under limpet manipulated conditions (E) (Means with the same letters are not significantly different - Individual 95 PCT CI's for means based on pooled STDEV).

Figure 62. The nature of the thallus at and away from the margins in the two forms of S. yendoi at (A) Holbaaipunt, and (B) Port Nolloth.

Figure 63. Mean number of conceptacles at the surface of S. yendoi at all sites under natural conditions (A), and under limpet manipulated conditions (B) (Means with the same letters are not significantly different - Individual 95 PCT CI's for means based on pooled STDEV).

Figure 64. Marginal extension rates of S. yendoi under limpet manipulated conditions.

Figure 65. Coralline and herbivore abundance throughout the mid- and lower eulittoral zones at all sites.

Figure 66. Percentage overgrowth interactions among intertidal encrusting algae from all sites (MESO = Mesophyllum engelhartii; SPIKEY = Synarthrophyton sp.; FERO = Leptophytum ferox; YEND = Spongites yendoi; RALF = Ralfsia verrucosa; HILD =

Hildenbrandia lecannellieri; PEYS = Peyssonnelia sp.; FOVE = Leptophytum foveatum) and their rank within the competitive hierarchy (1 ranks lowest; 5 ranks highest). The algae separated by the "/" sign have received equal ranking because they do not compete; it could not be determined which of these algae was the superior overgrowth competitor.

Figure 67. The relationship between thallus thickness and overgrowth ranking for the intertidal encrusting corallines at all sites.

Figure 68. S. yendoi's (Y) cover in the lower eulittoral zone at Groenriviermond is somewhat patchy, much of the primary substratum being occupied by L. foveatum.

Figure 69. Much of the primary substratum within the lower eulittoral zone along the West coast is occupied by L. foveatum with strips of S. impar (S) occurring between limpet territories. From the central to the northern West coast, S. yendoi's cover becomes increasingly patchy, much of the coralline being restricted to the shells of limpets.

Figure 70. The nutrient status of the two forms of S. yendoi and G. micropterum (Means with the same letters are not significantly different - Individual 95 PCT CI's for means based on pooled STDEV).

Figure 71. Schematic diagram of the positive and negative effects of grazing by P. cochlear on S. yendoi.

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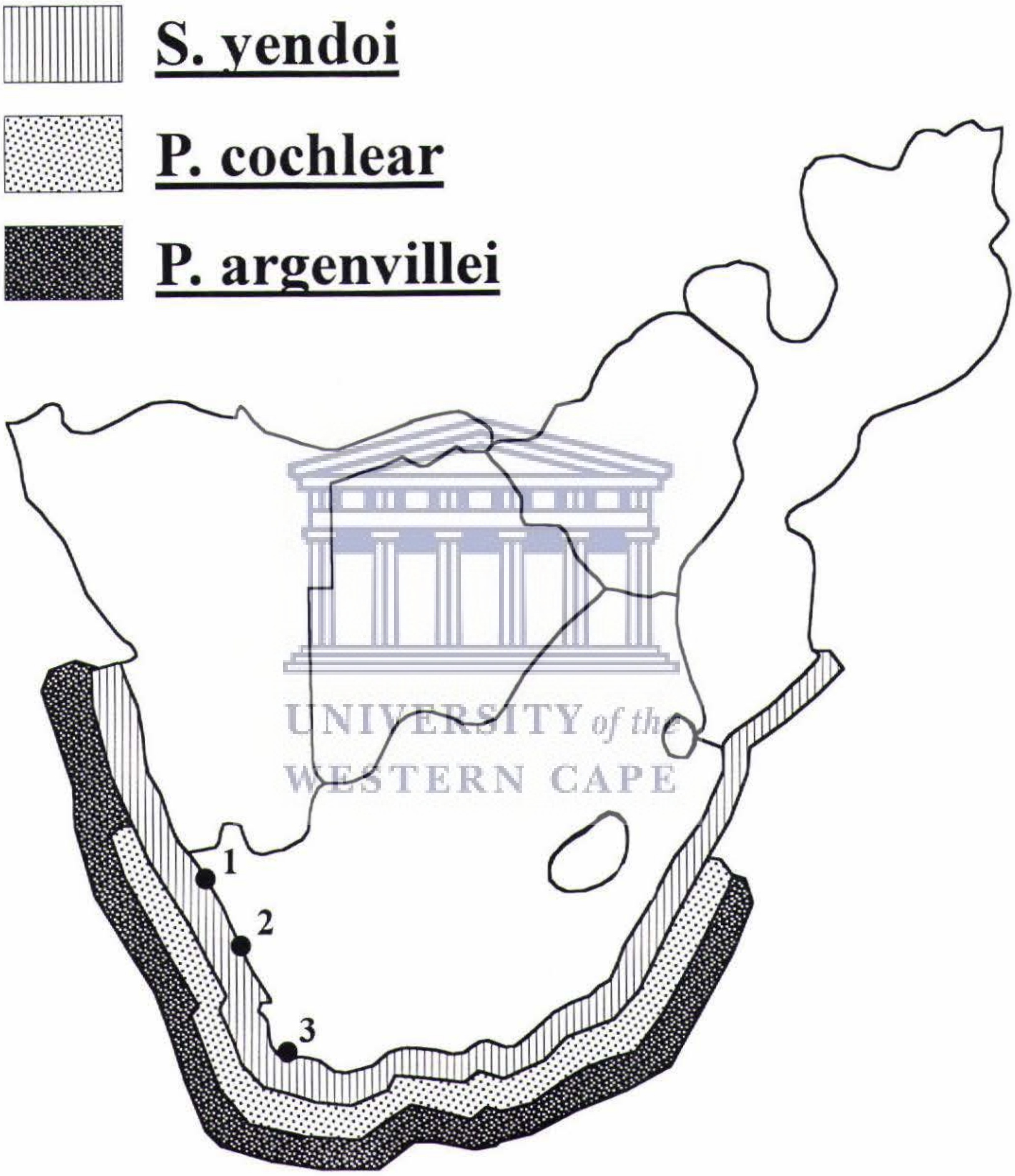

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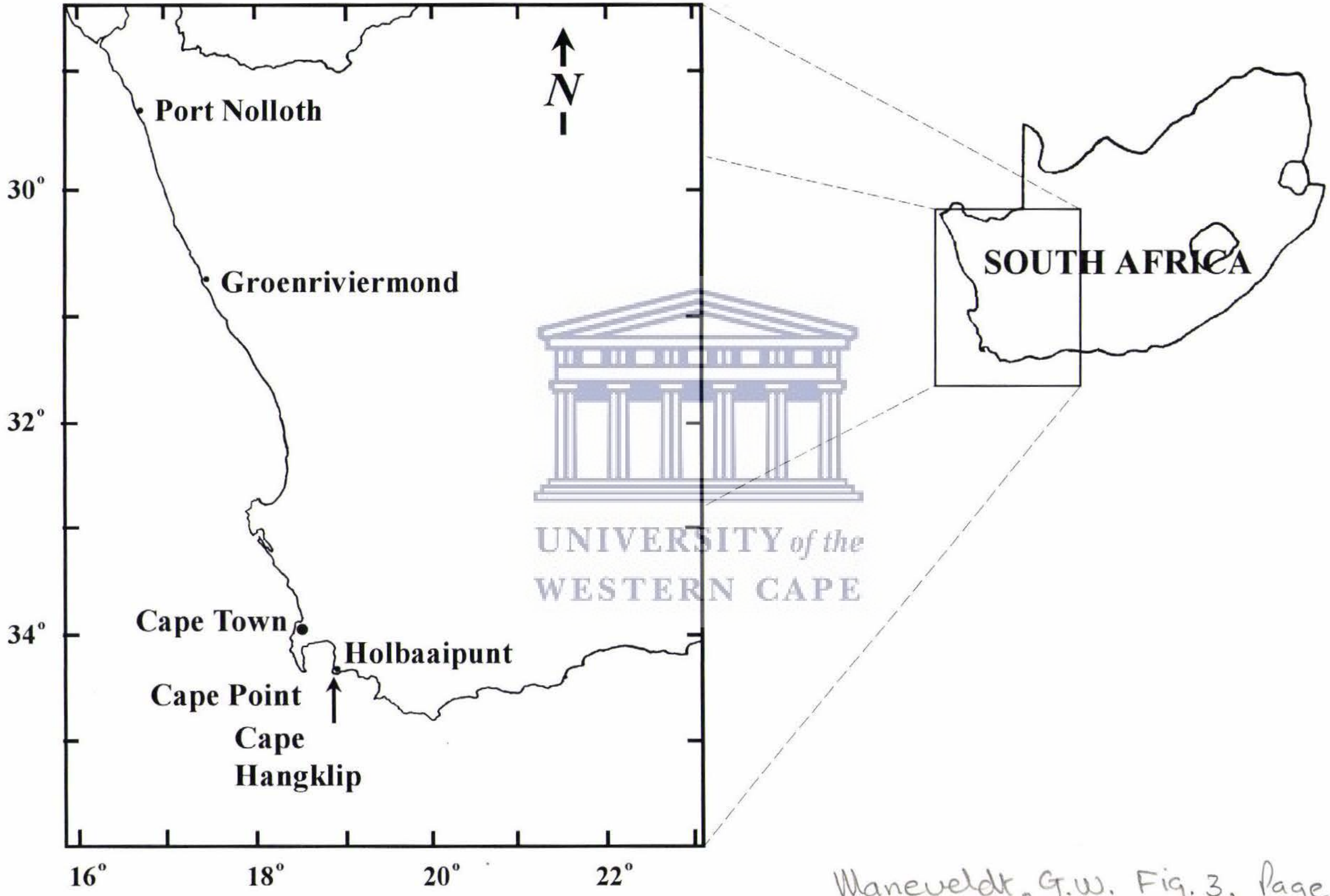
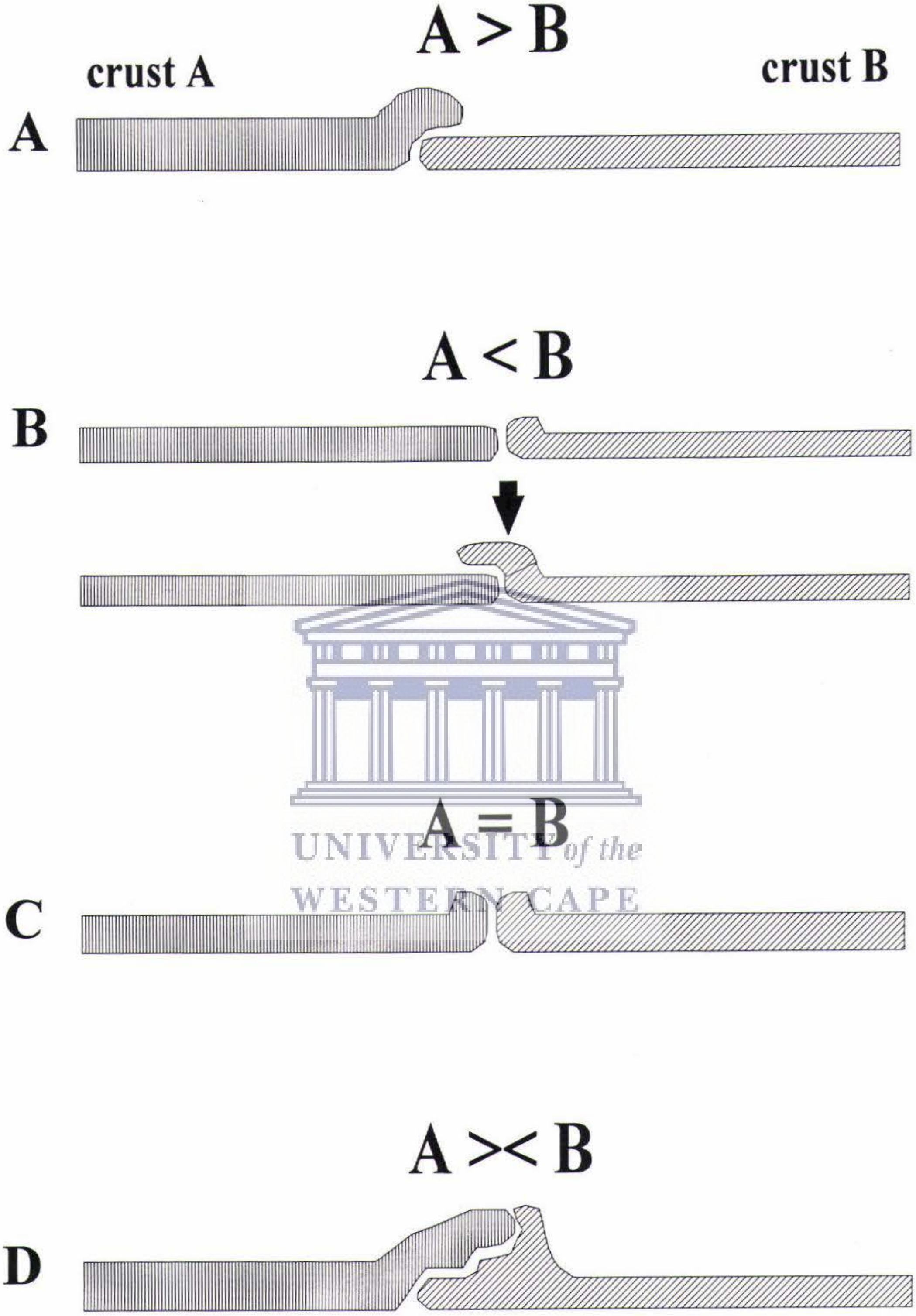


Maneveldt, G.W. Fig. 3, Page 80



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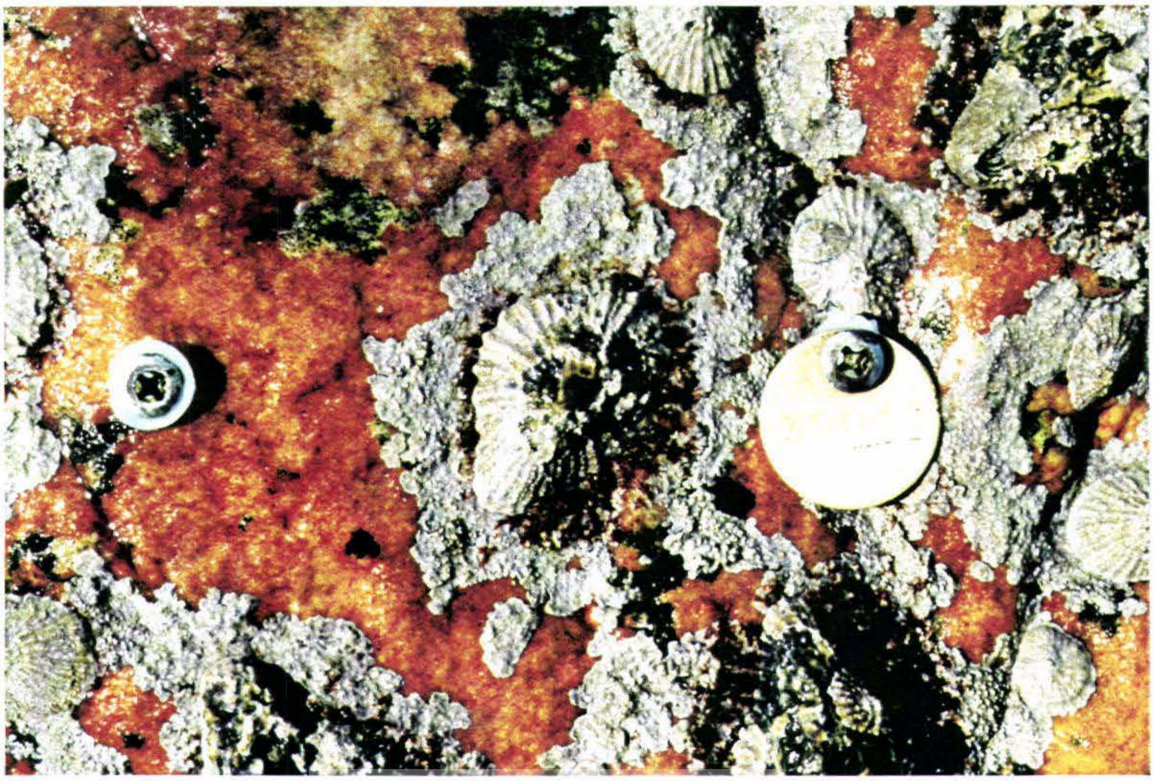
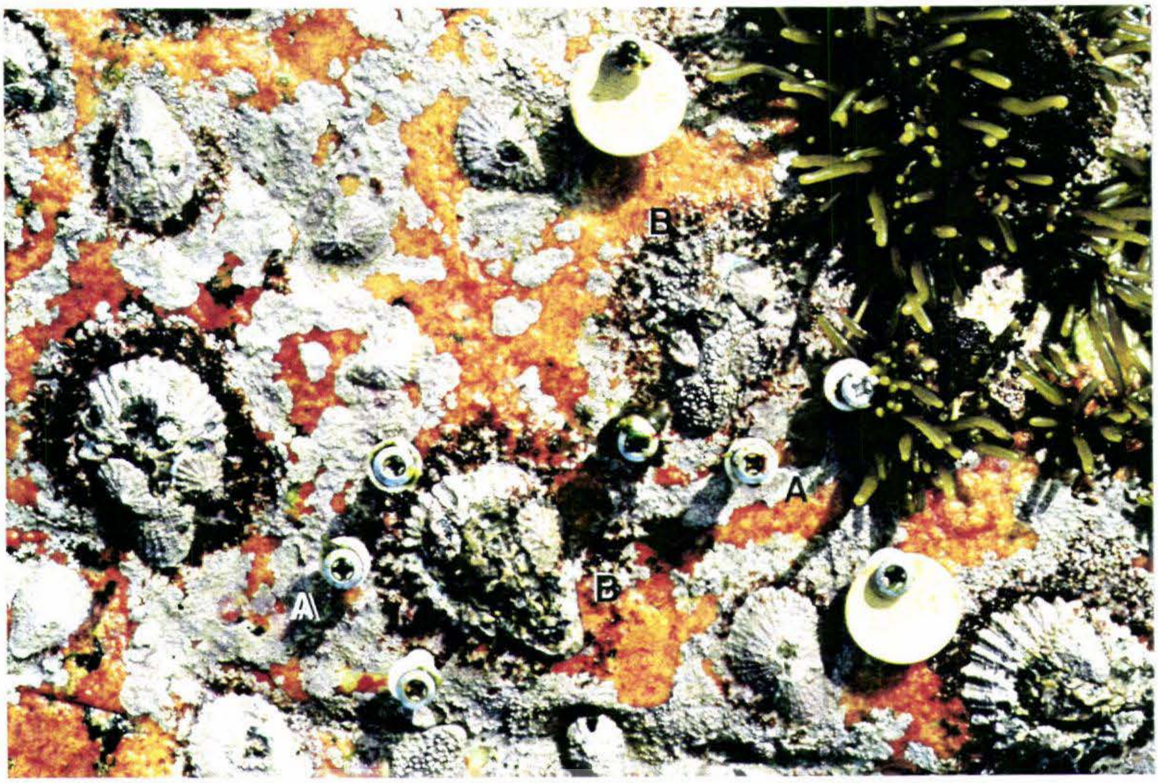


Maneveldt, G.W. Fig 5, Page 82



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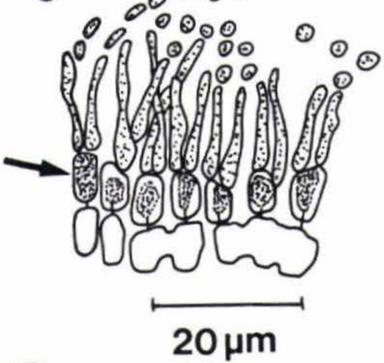

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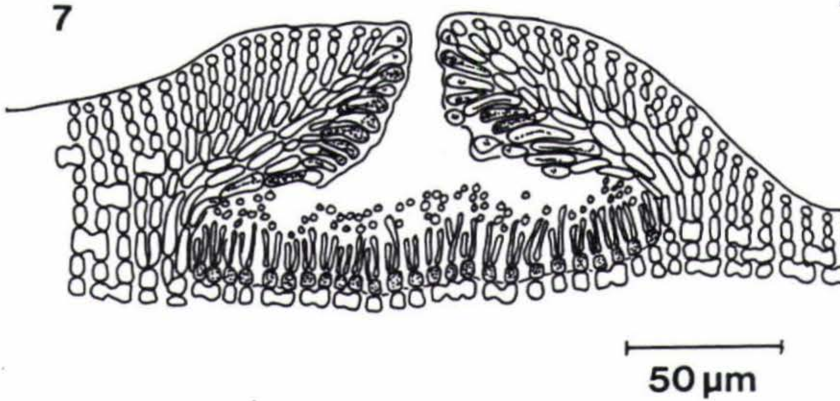

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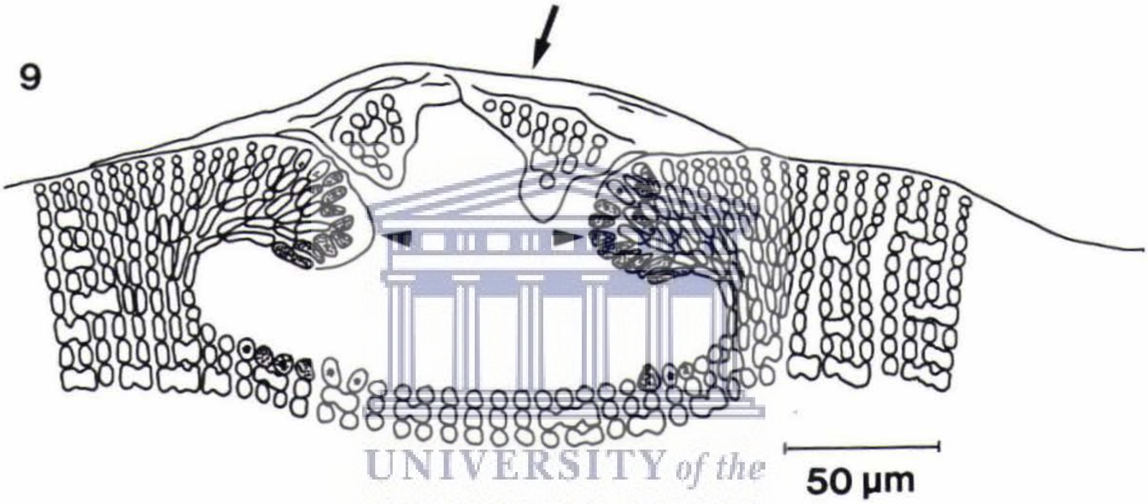

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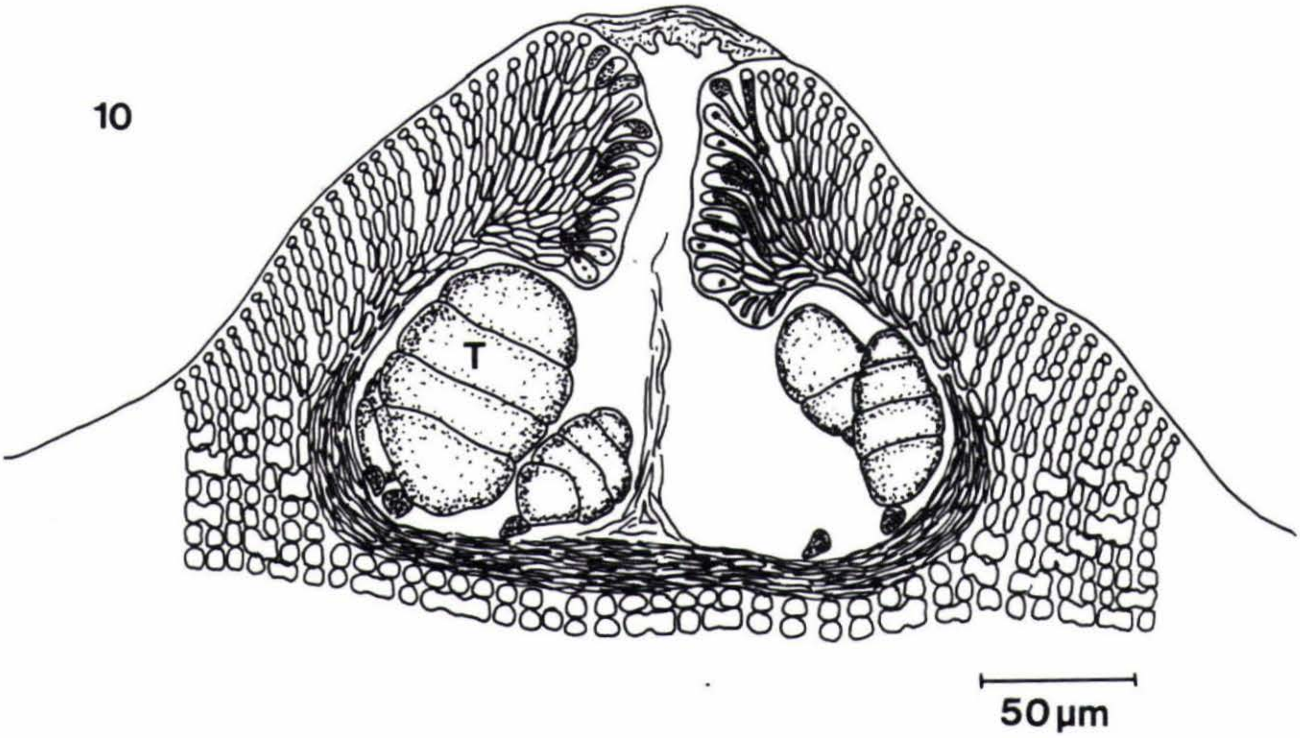

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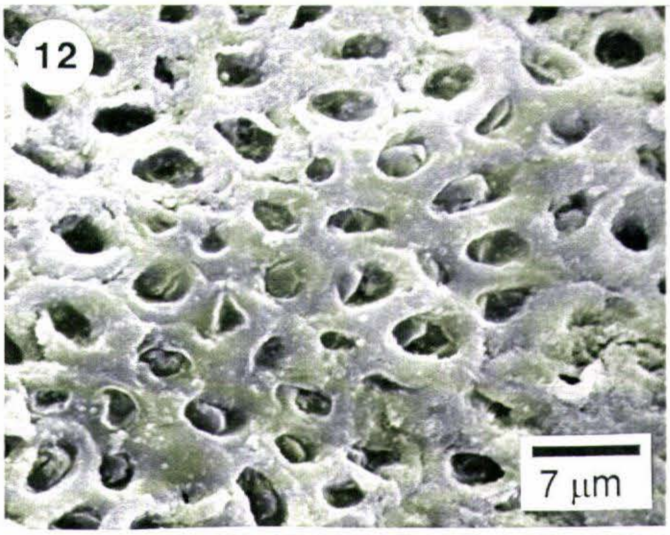
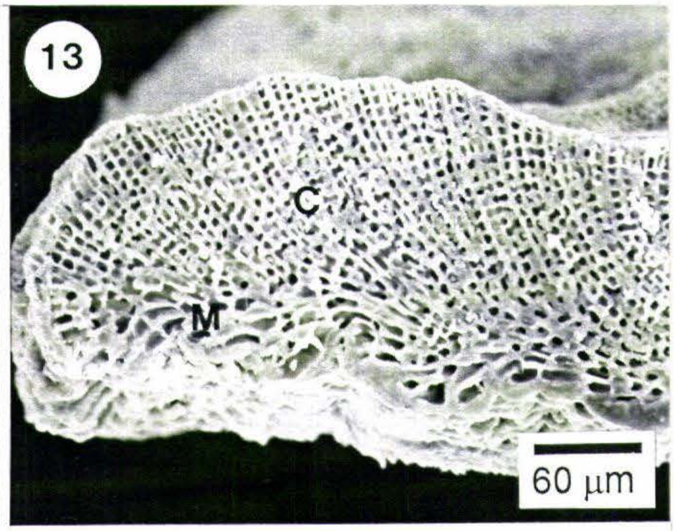
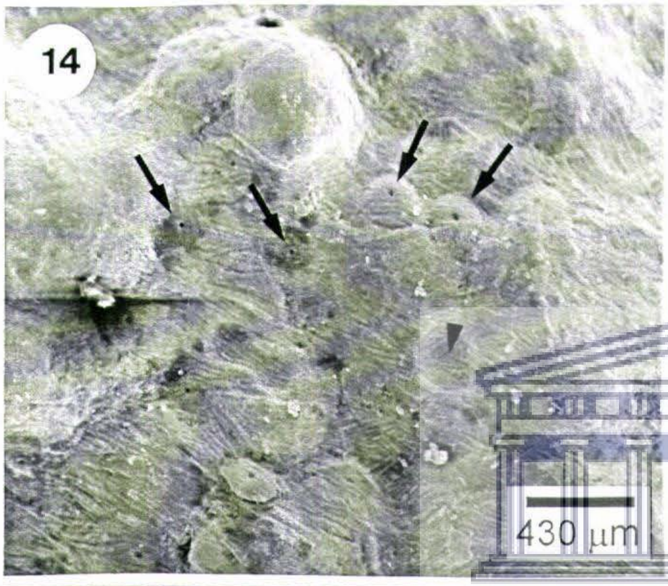
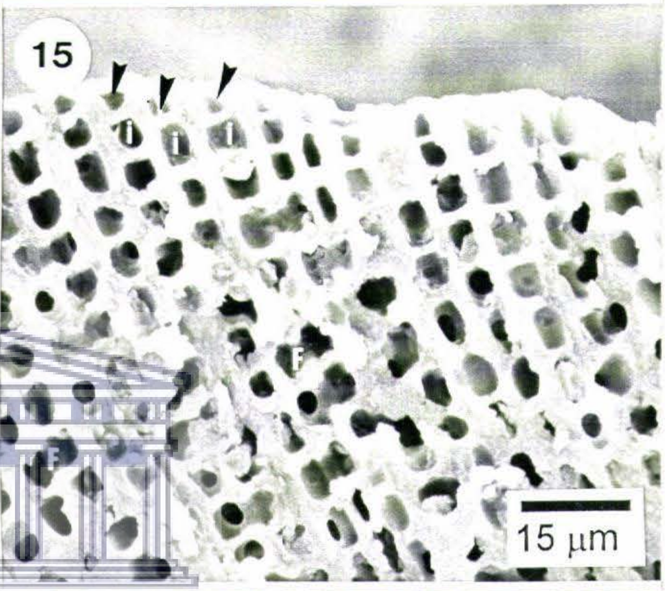
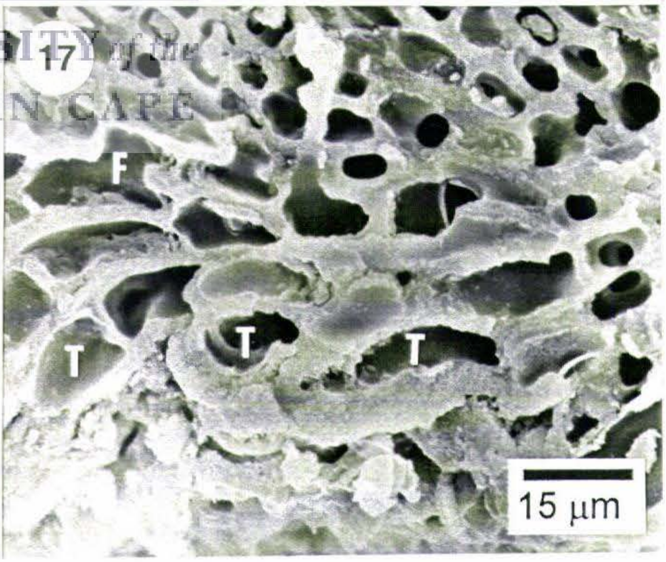
Maneveldt, G.W. Fig 11, Page 85











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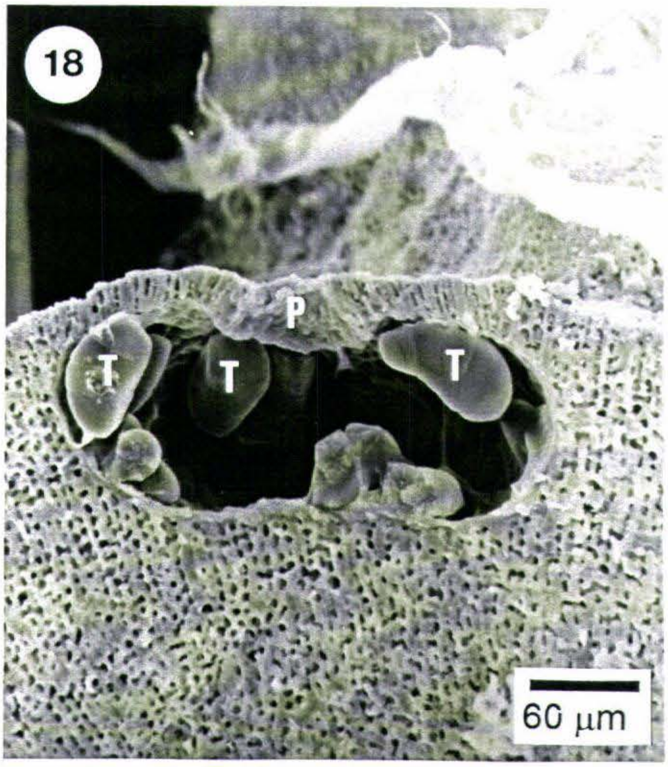

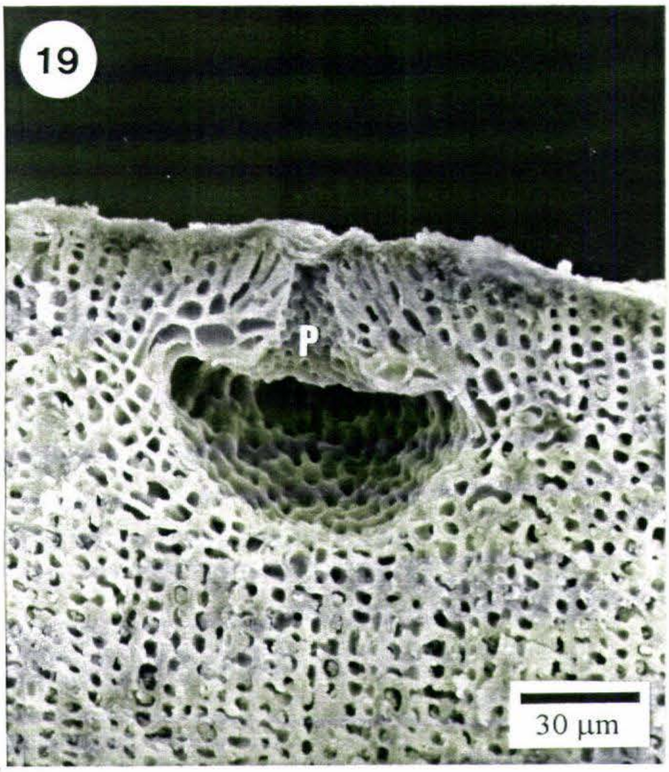

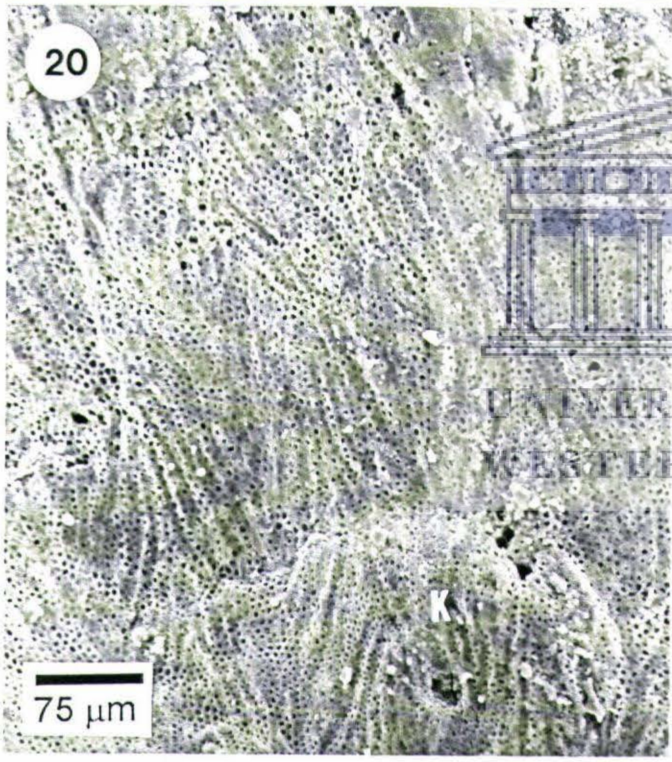

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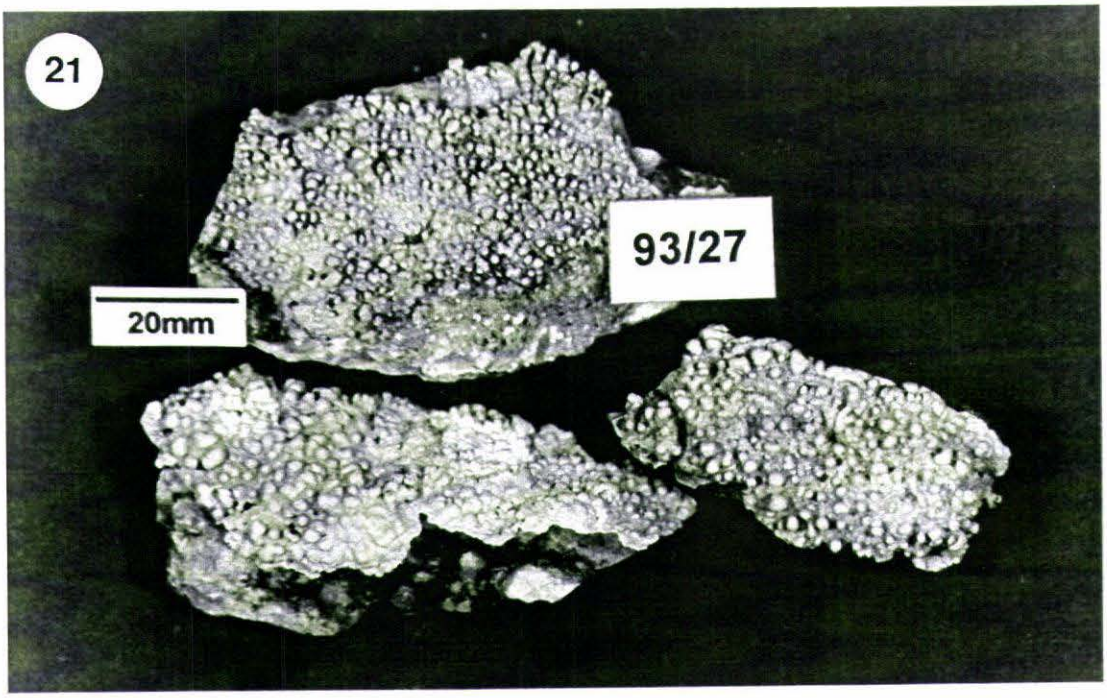

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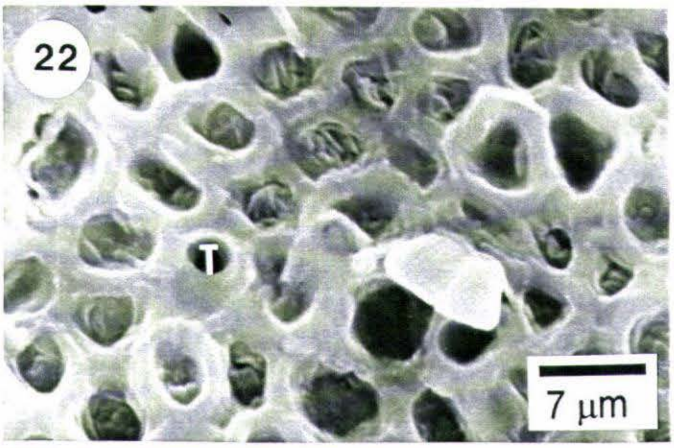

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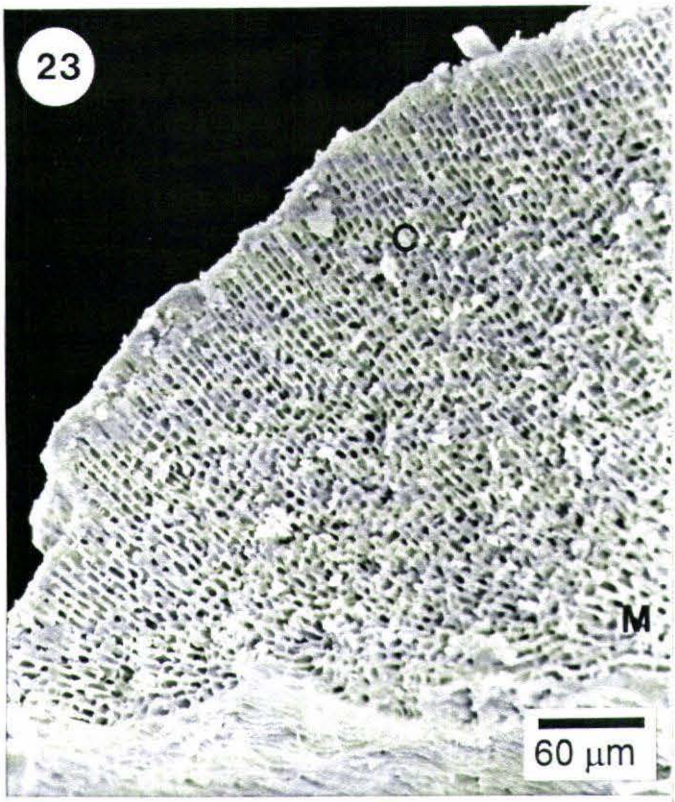

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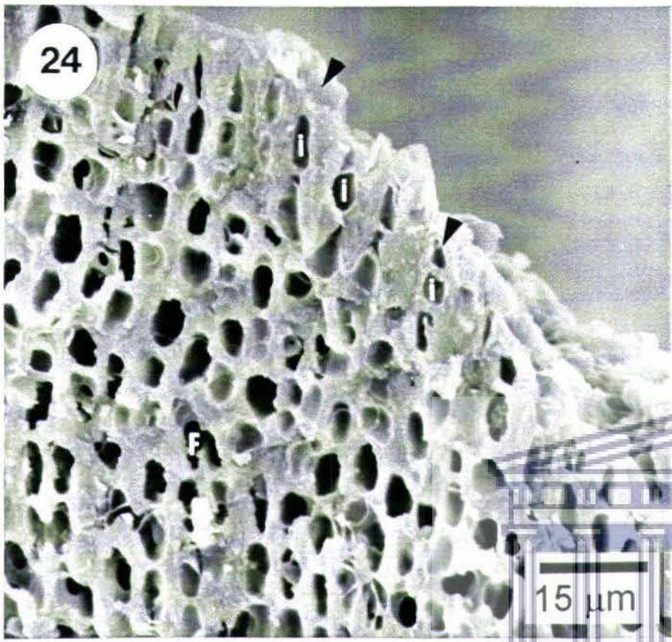

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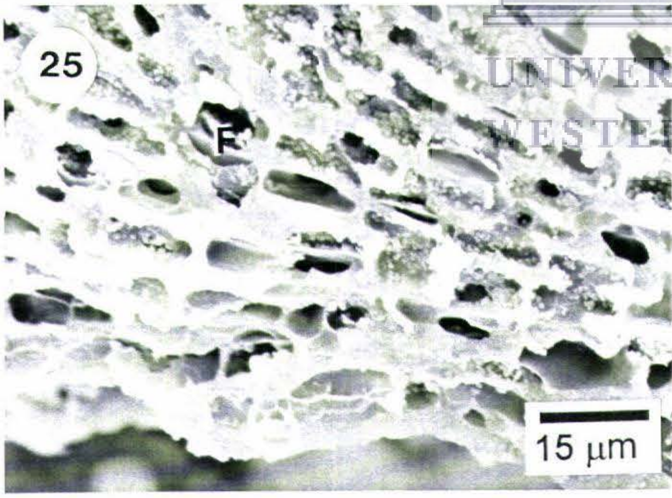

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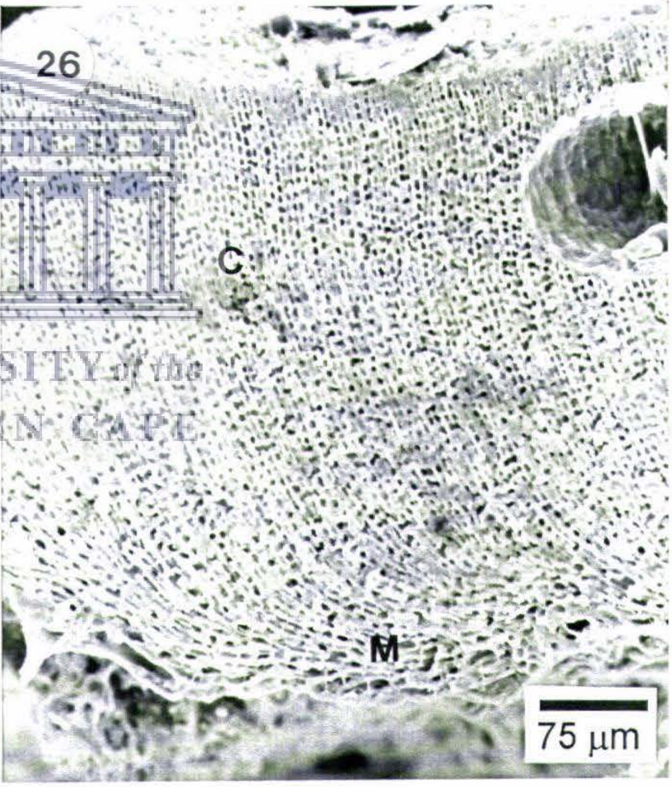

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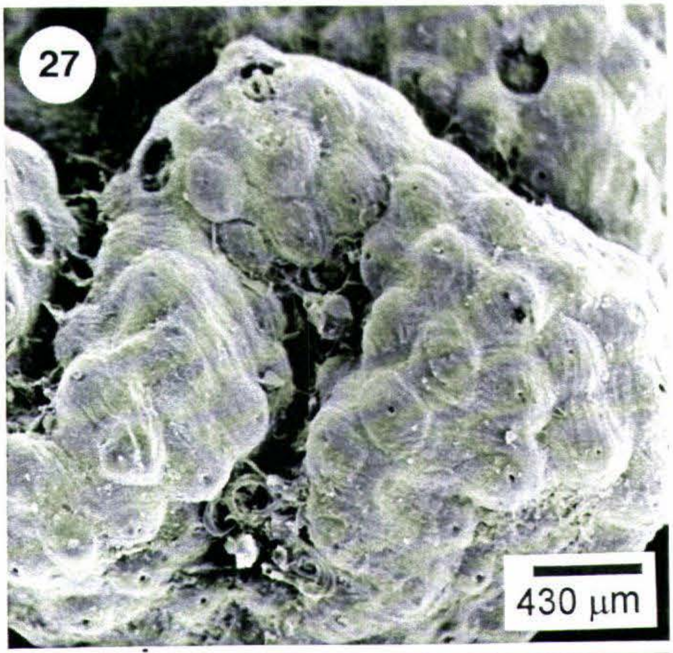
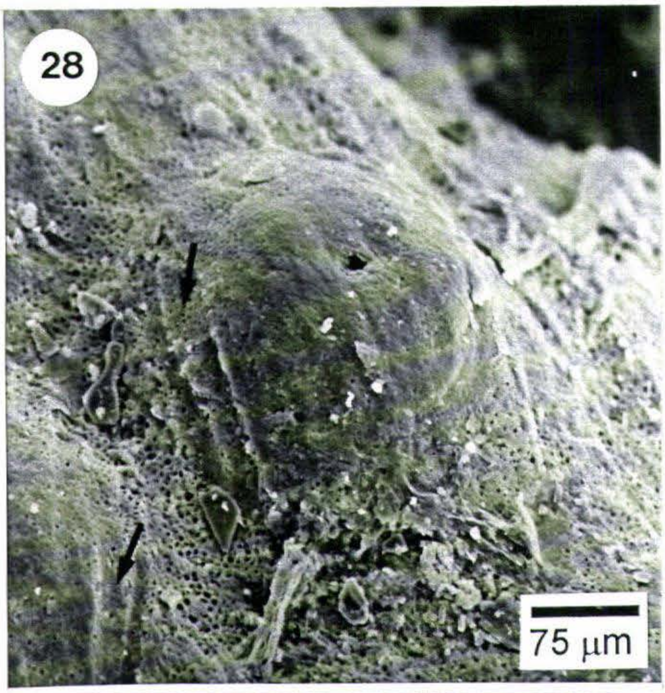
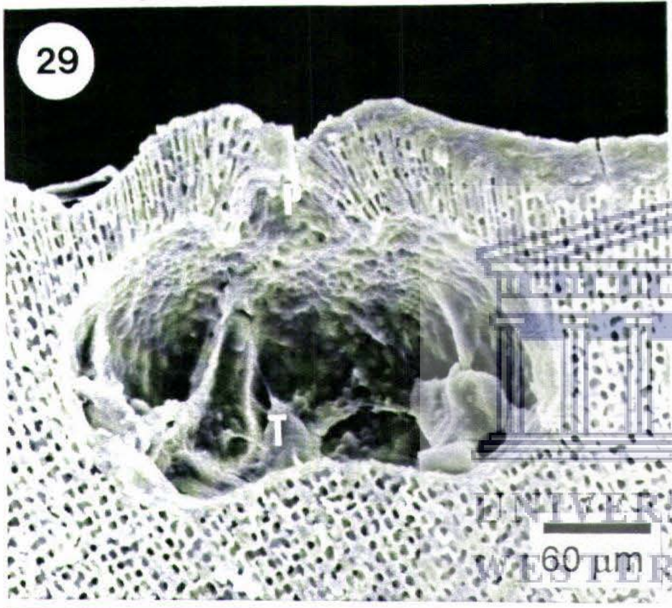
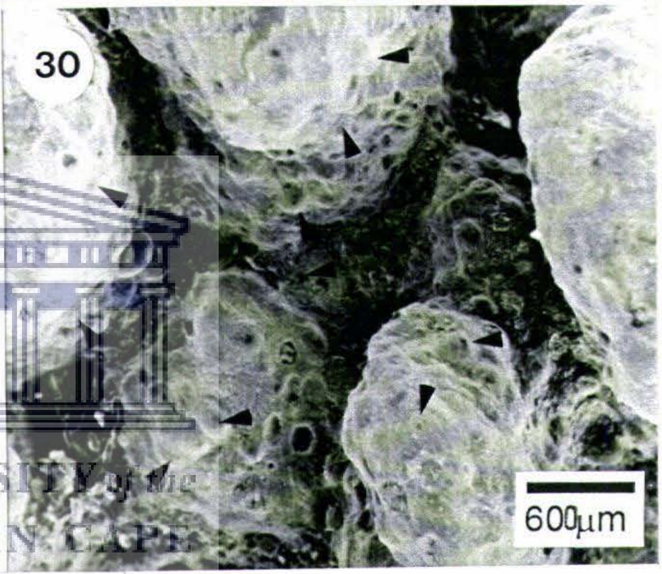
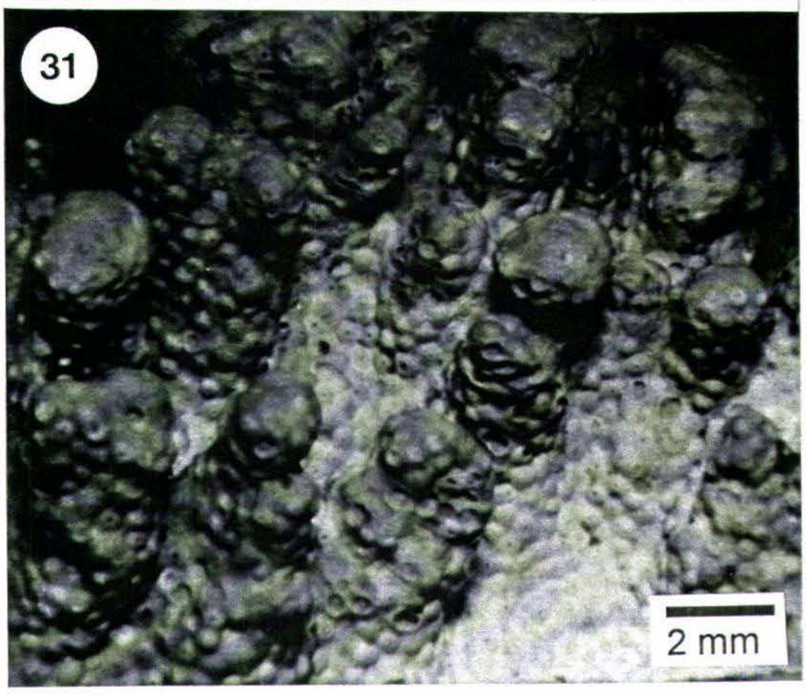


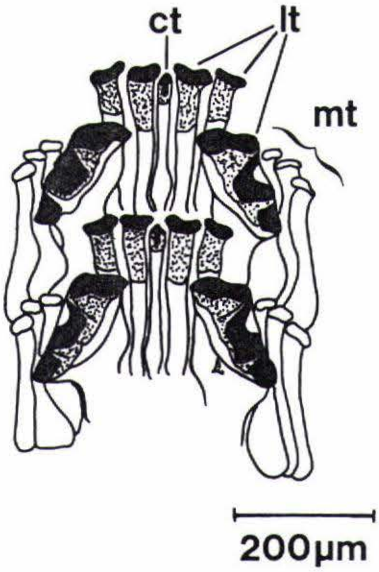


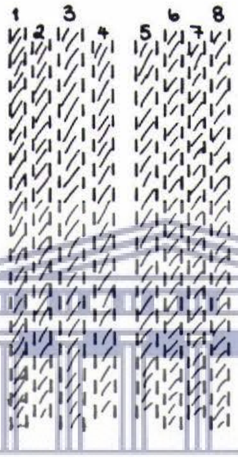




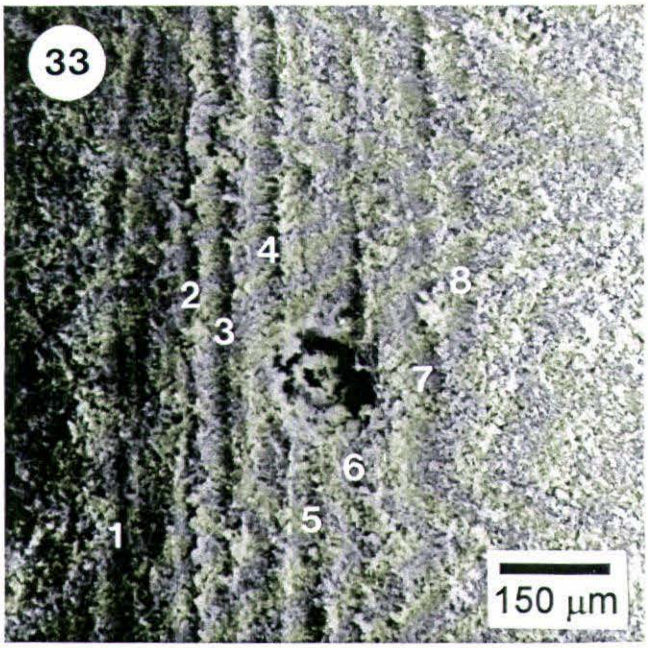


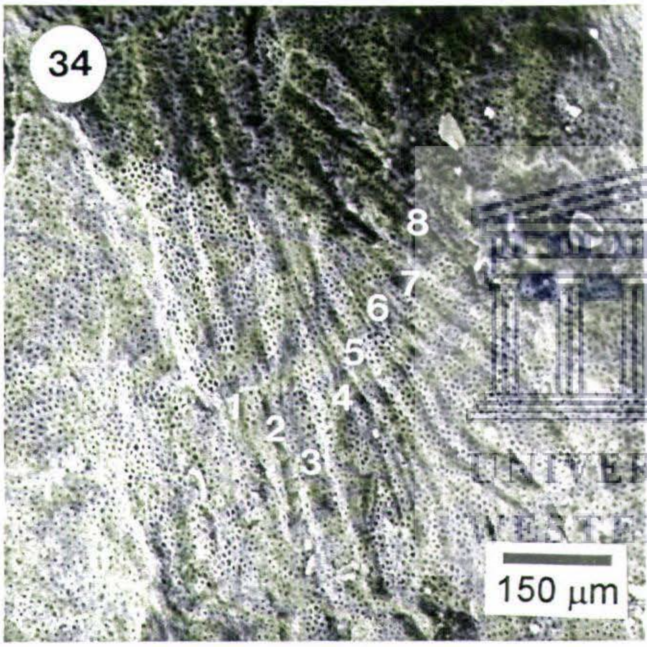
Maneveldt, G.W. Figs 27-31, Page 90

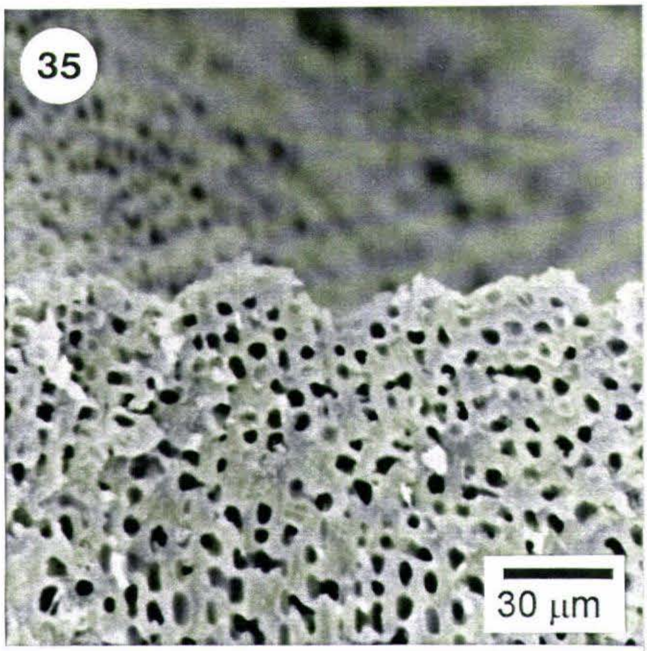


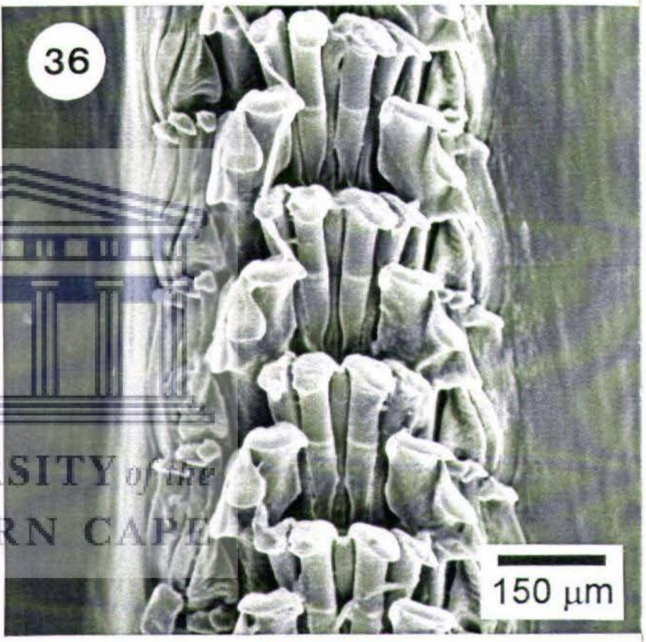


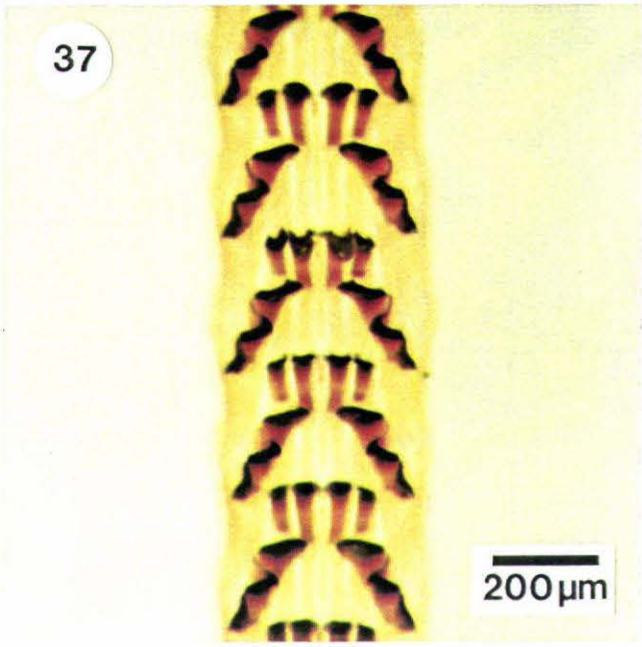
Maneveldt, G.W. Fig. 32, Page 91



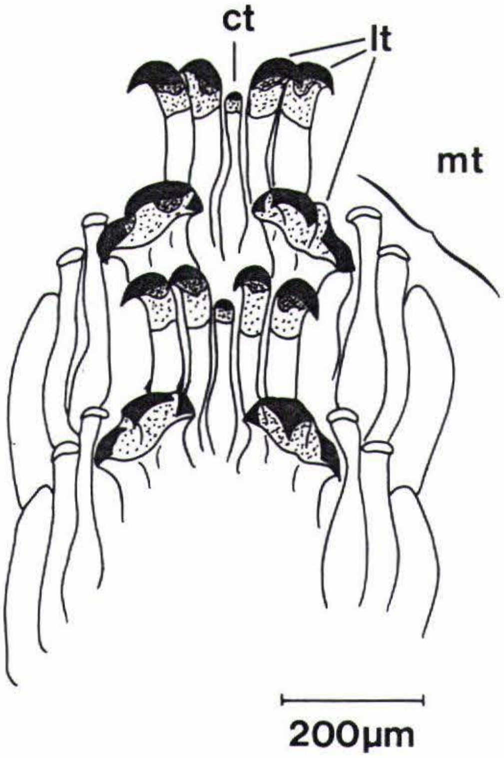


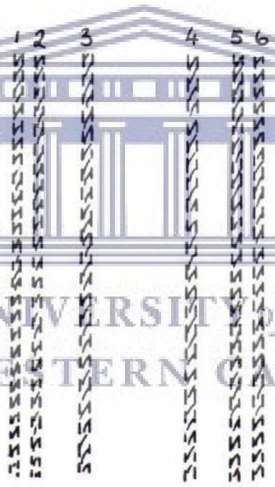






Maneveldt, G.W. Figs 33-37, Page 92





Maneveldt, G.W. Fig. 38, Page 93

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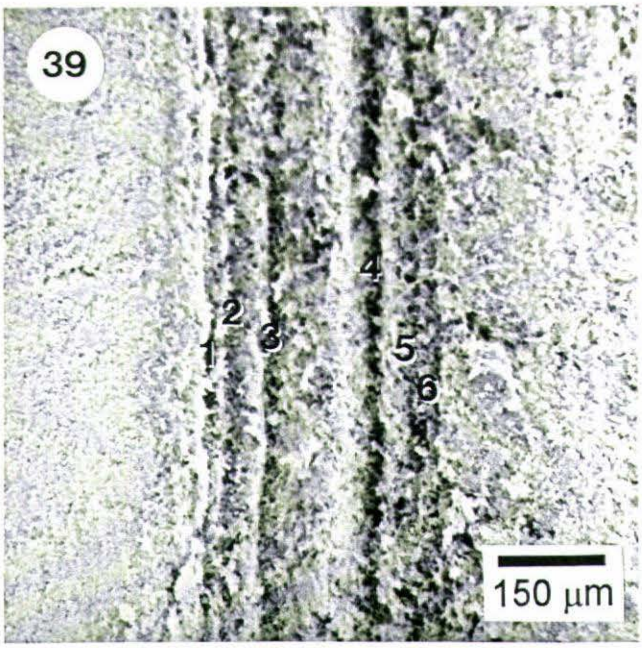

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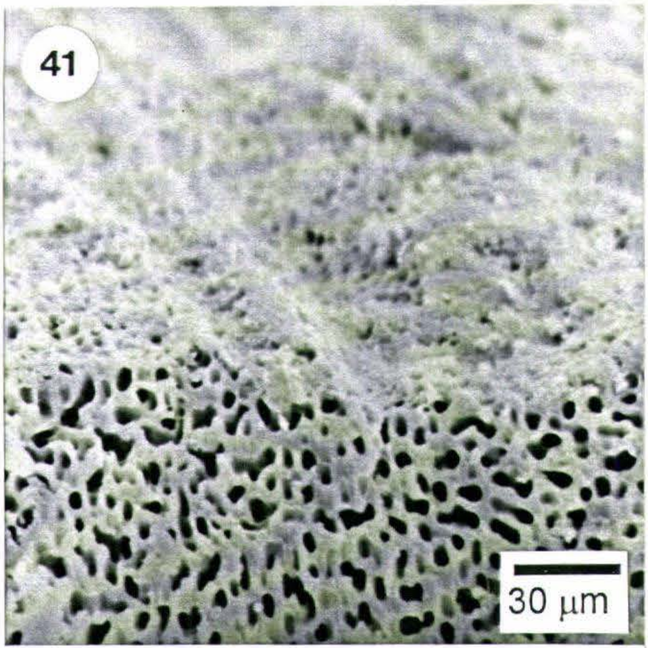

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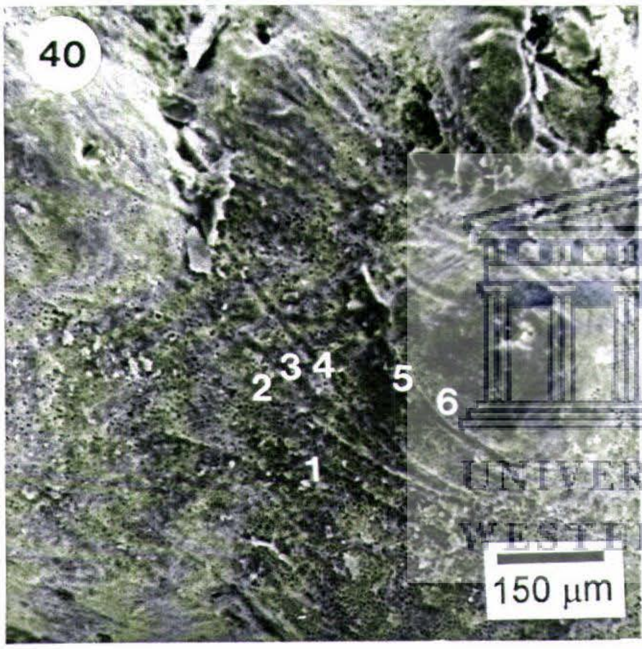

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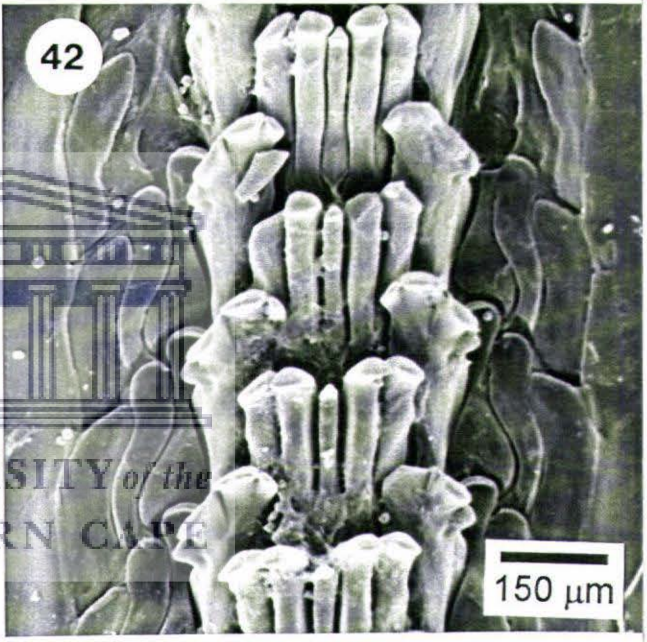

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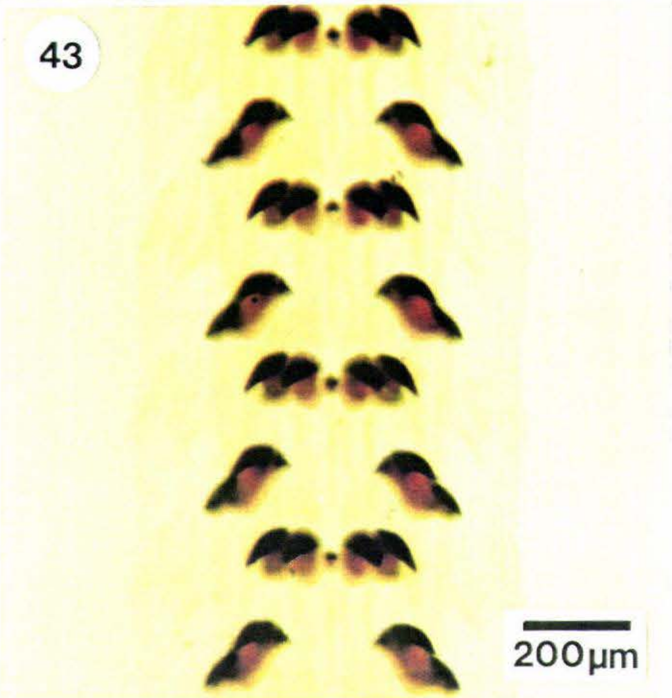
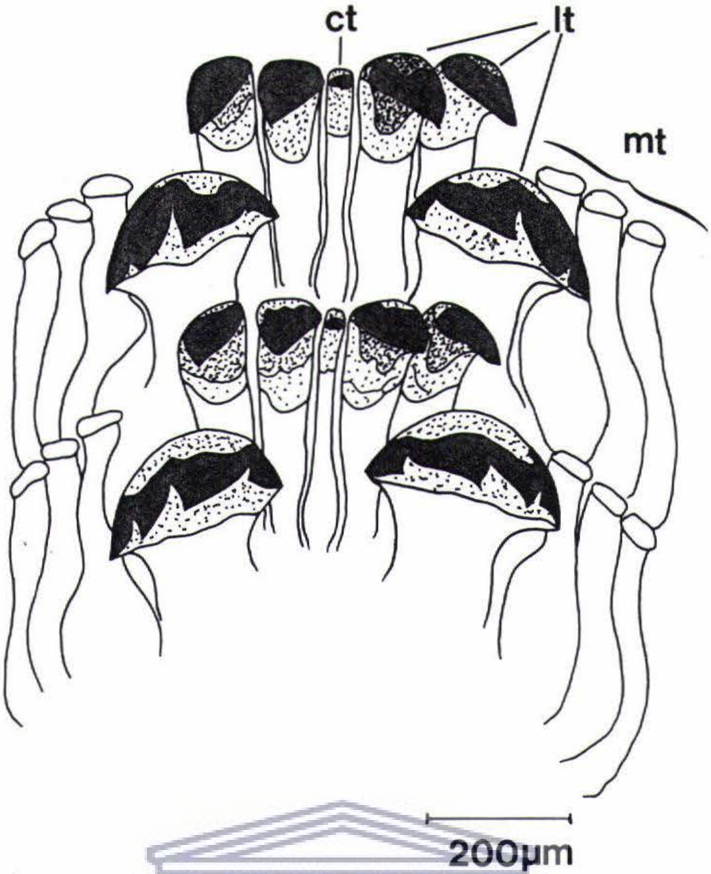
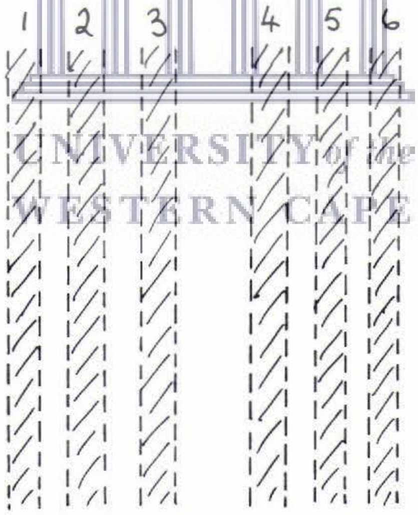
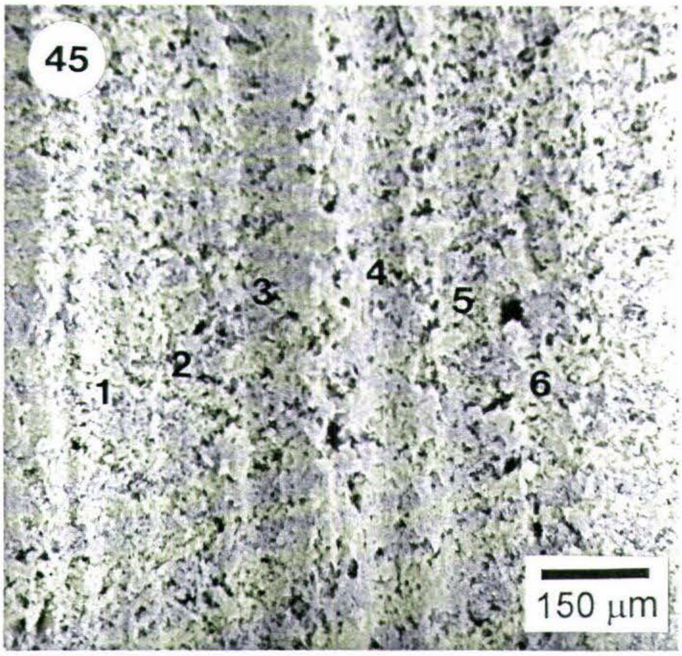


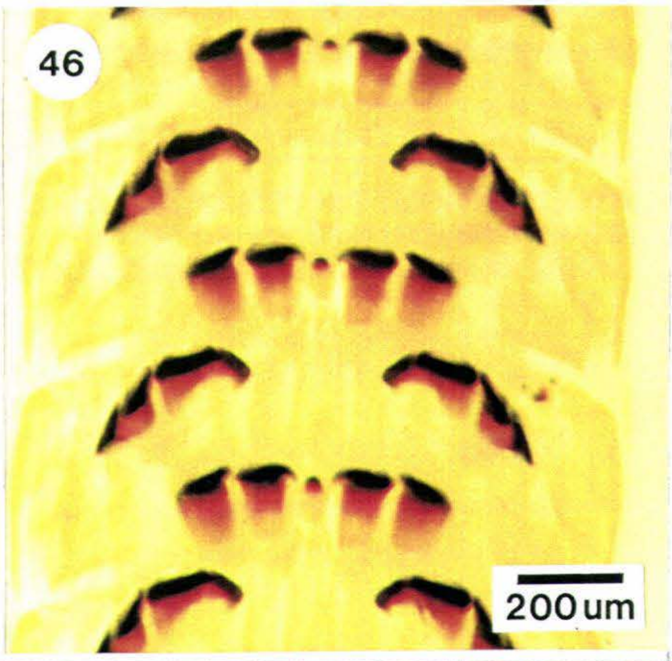
Maneveldt, G.W Figs 39-43, Page 94



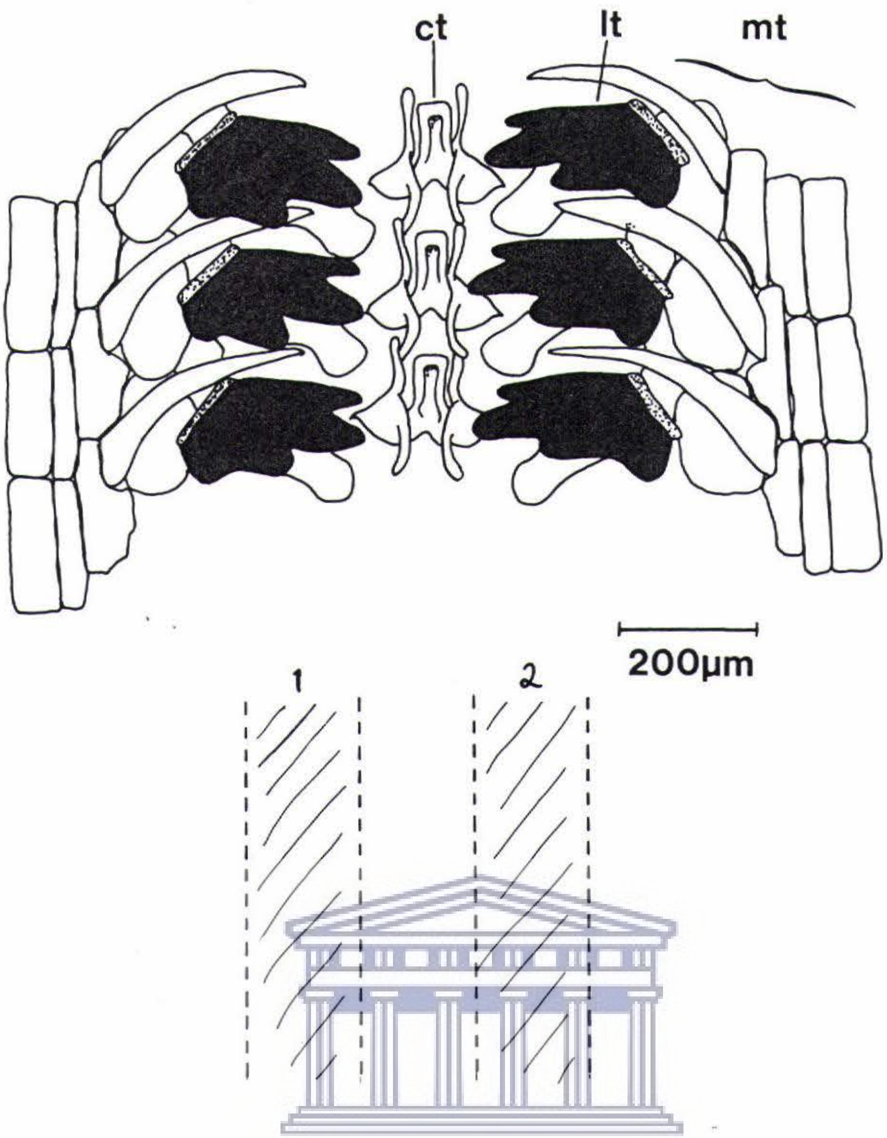


Maneveldt, G.W. Fig. 44, Page 95

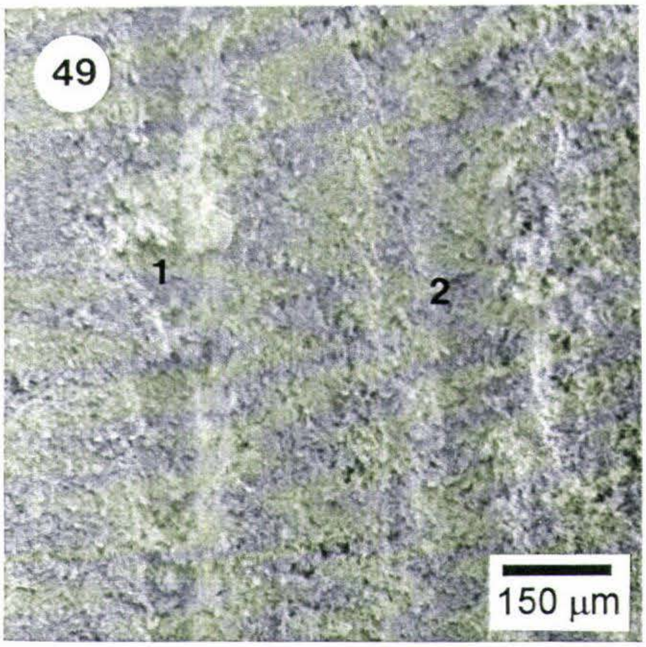


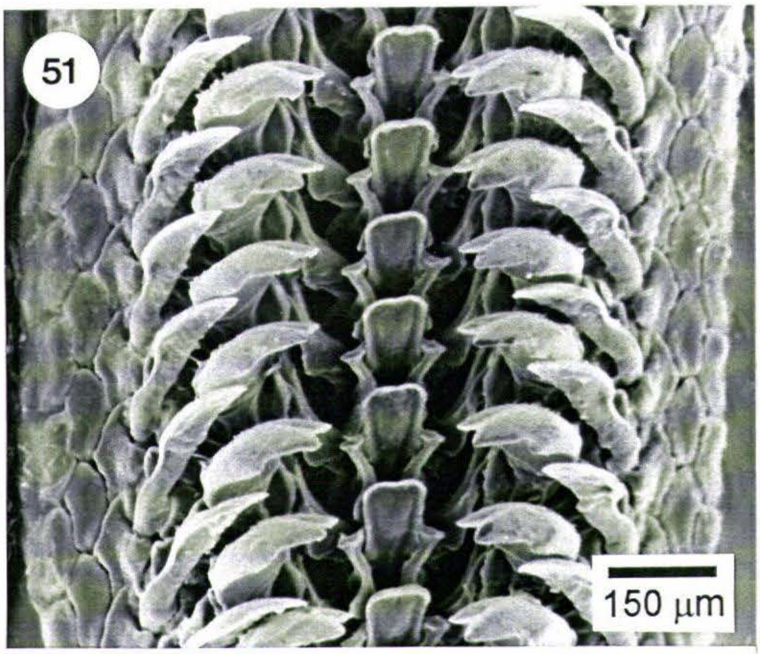


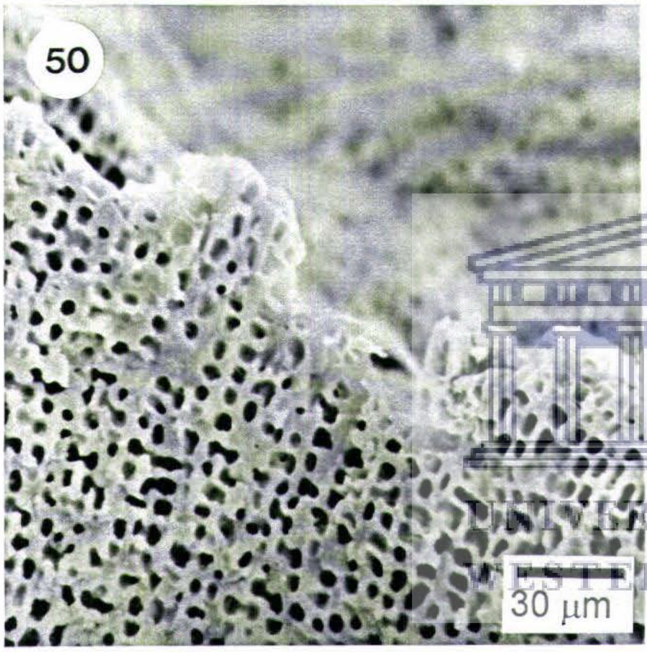
Maneveldt, G.W. Figs 45-47, Page 96

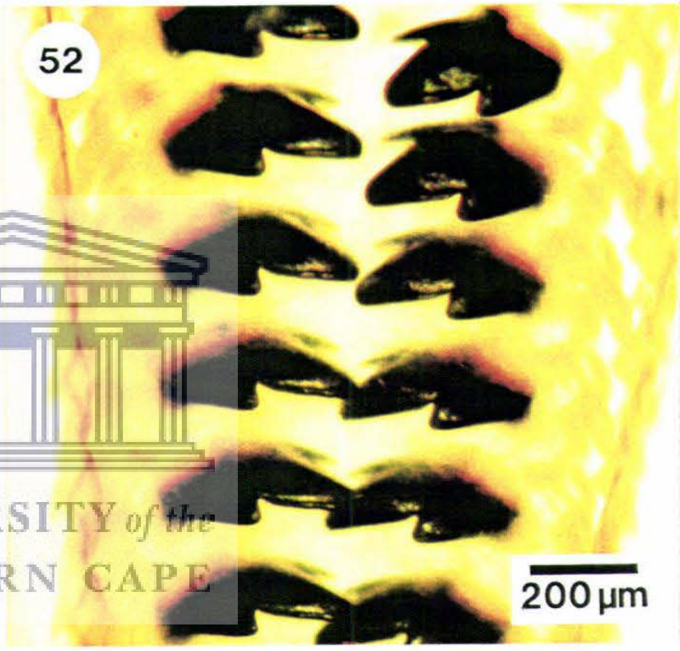


Maneveldt, G.W. Fig. 48, Page 97

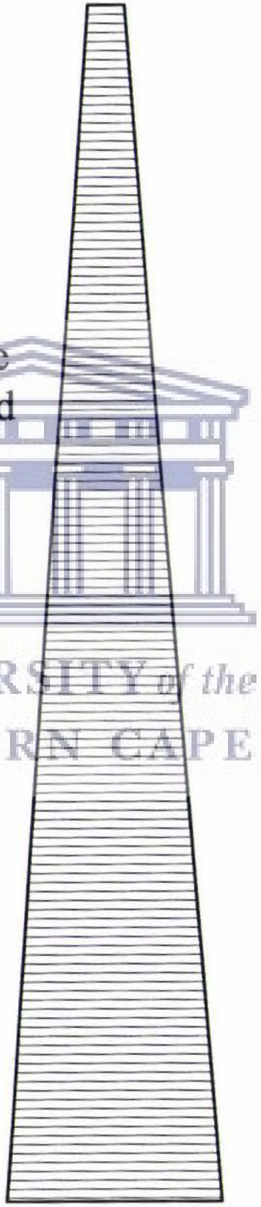
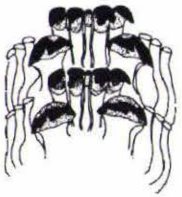
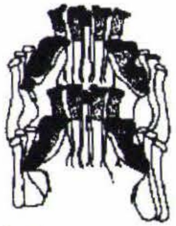
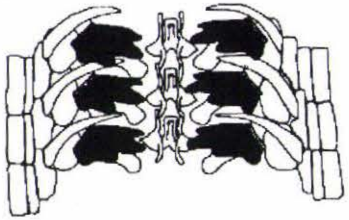




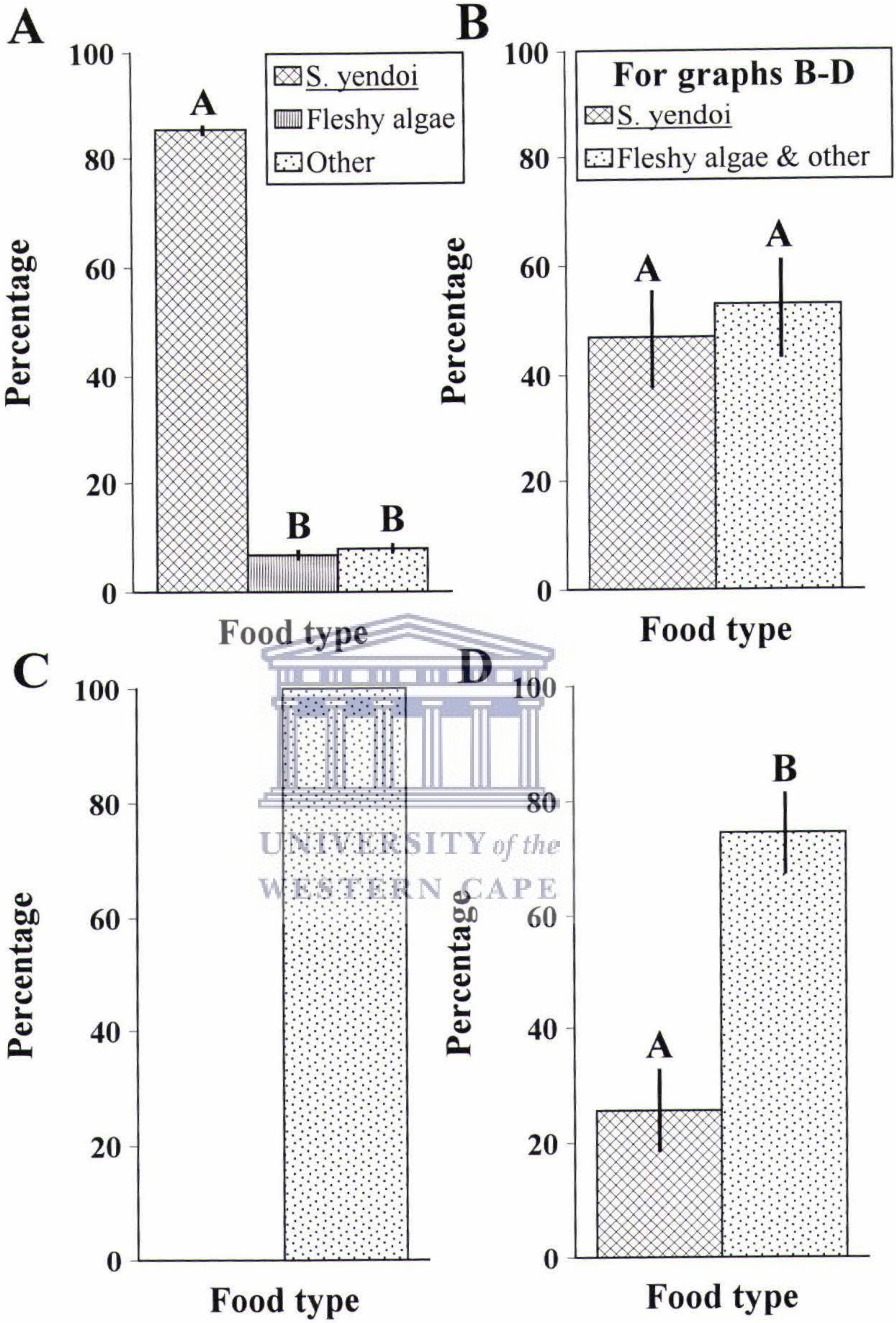




Maneveldt, G.W. Figs 49-52, Page 98

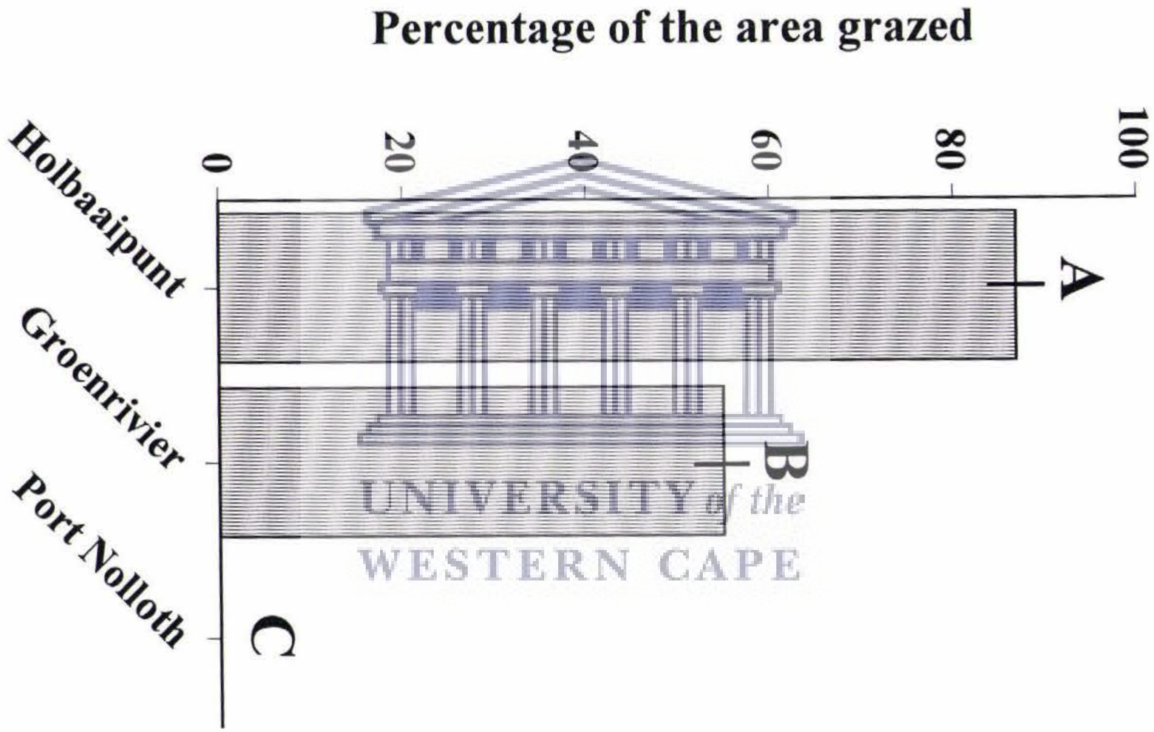
Radula type	Species	Grazing intensity (micrometers)	Excavation ability	Radula-shell/body length ratio	% of gut comprising coralline algae
DOCOGLOSSA					
	1. P. granularis 	7.20 ± 0.42		1.83 ± 0.03	47 ± 8.6
	2. P. argenvillei 	presumably intermediate between P. granularis and P. cochlear		0.95 ± 0.02	0.0
	3. P. cochlear 	15.40 ± 0.97		0.64 ± 0.02	85.4 ± 0.58
POLYPLACOPHORA					
	4. Acanthochiton garnoti 	45.50 ± 1.98		0.44 ± 0.01	25.6 ± 2.08

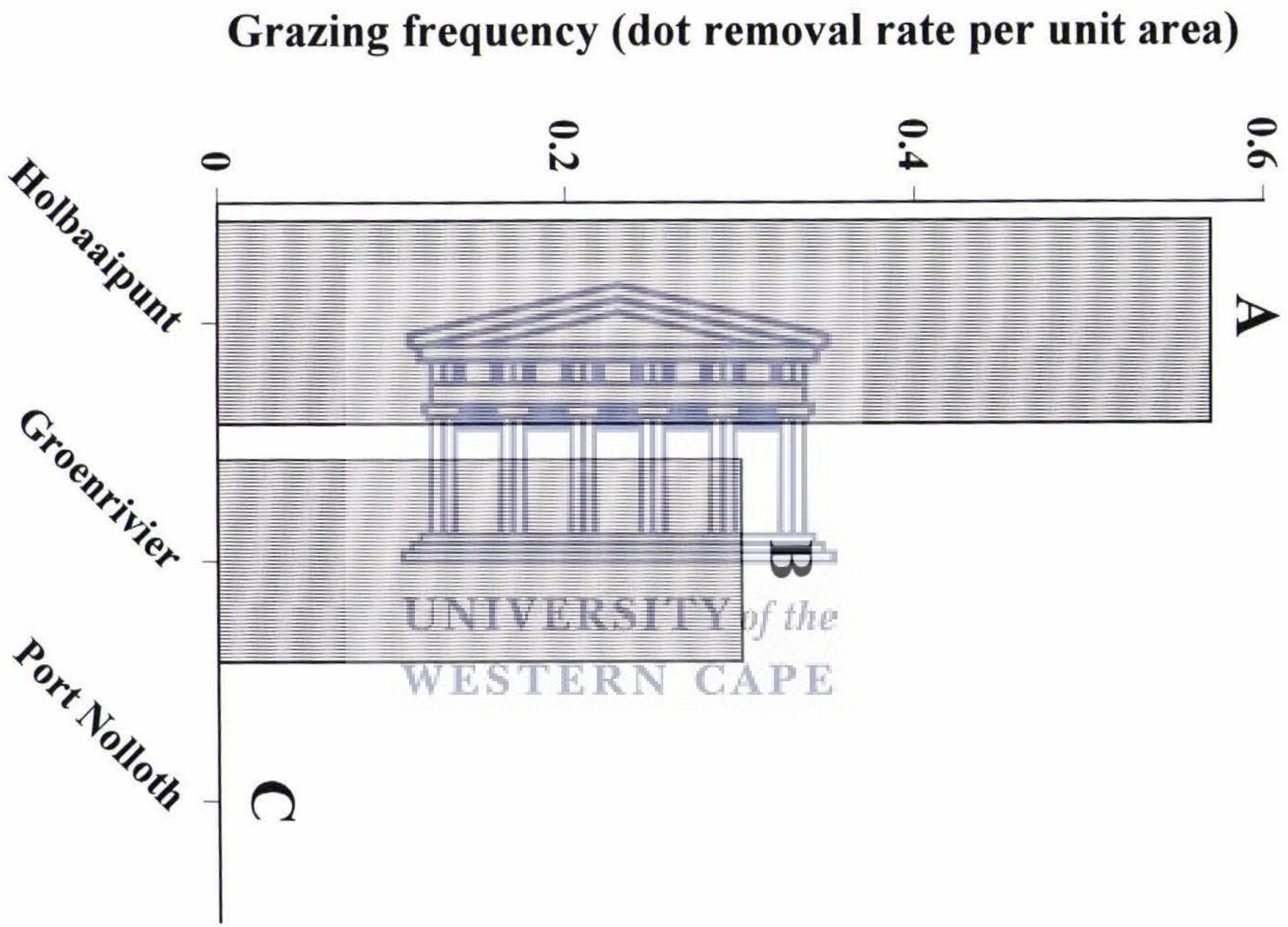
Mancveldt, G.W. Fig 53, Page 99



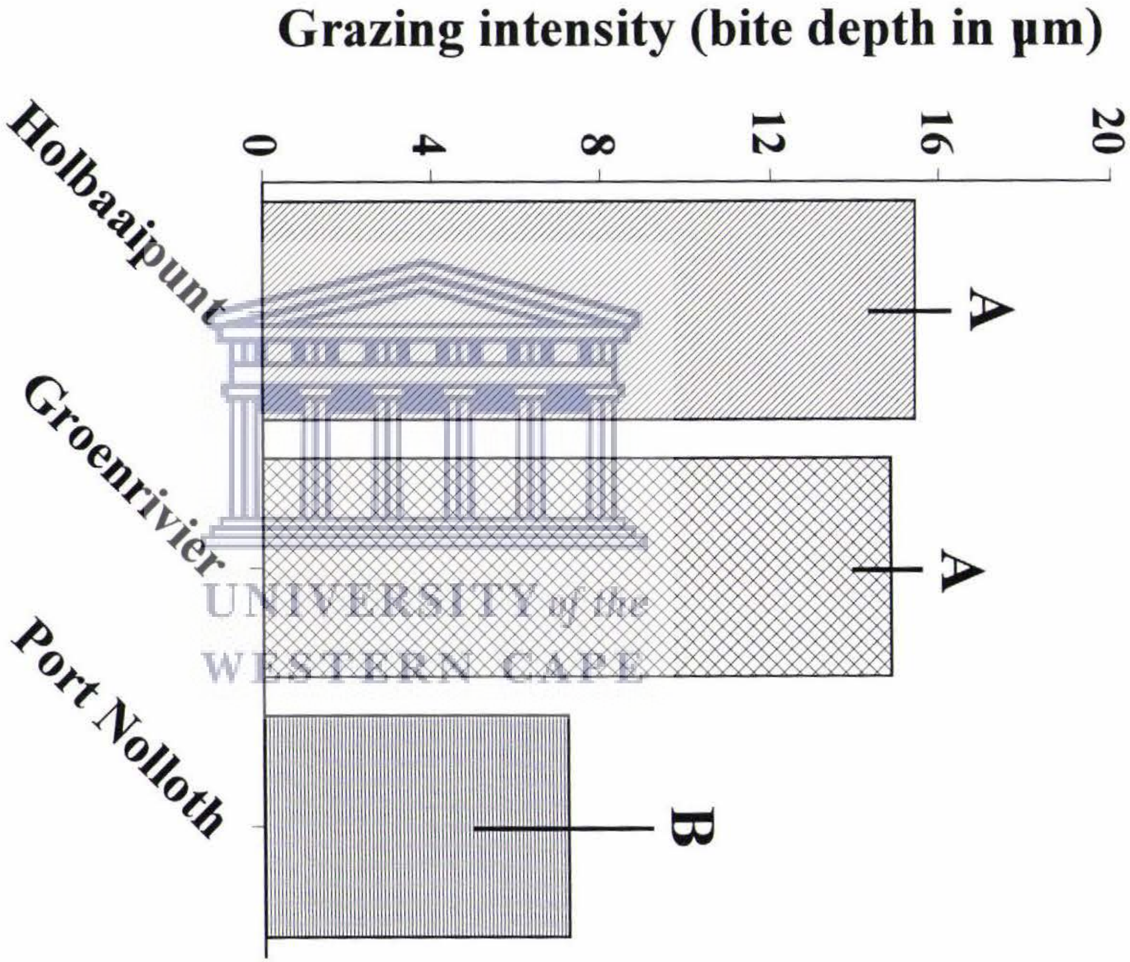
Maneveldt, G.W. Fig. 54, Page 100

Maneveldt, G.W. Fig. 55, Page 101

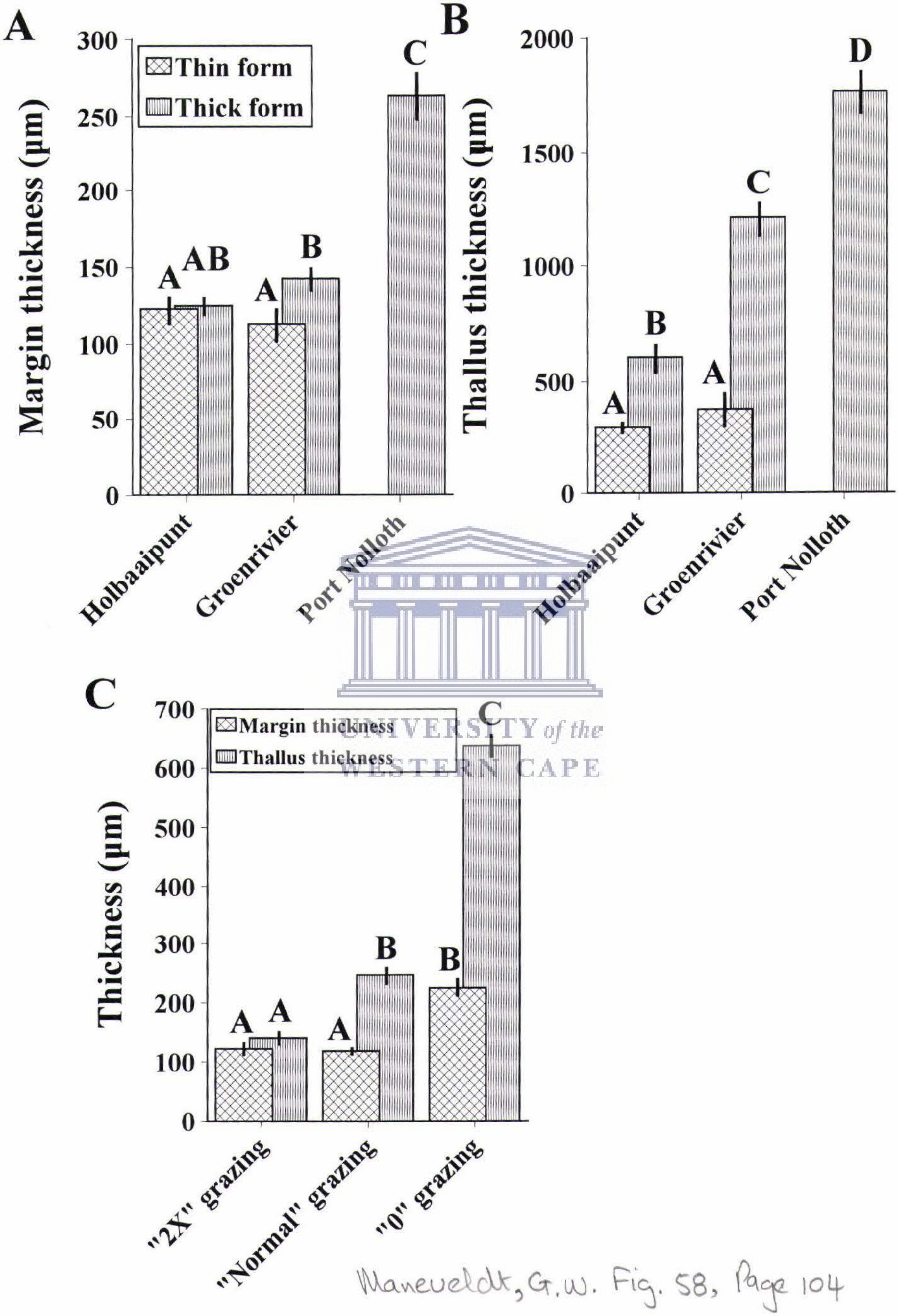




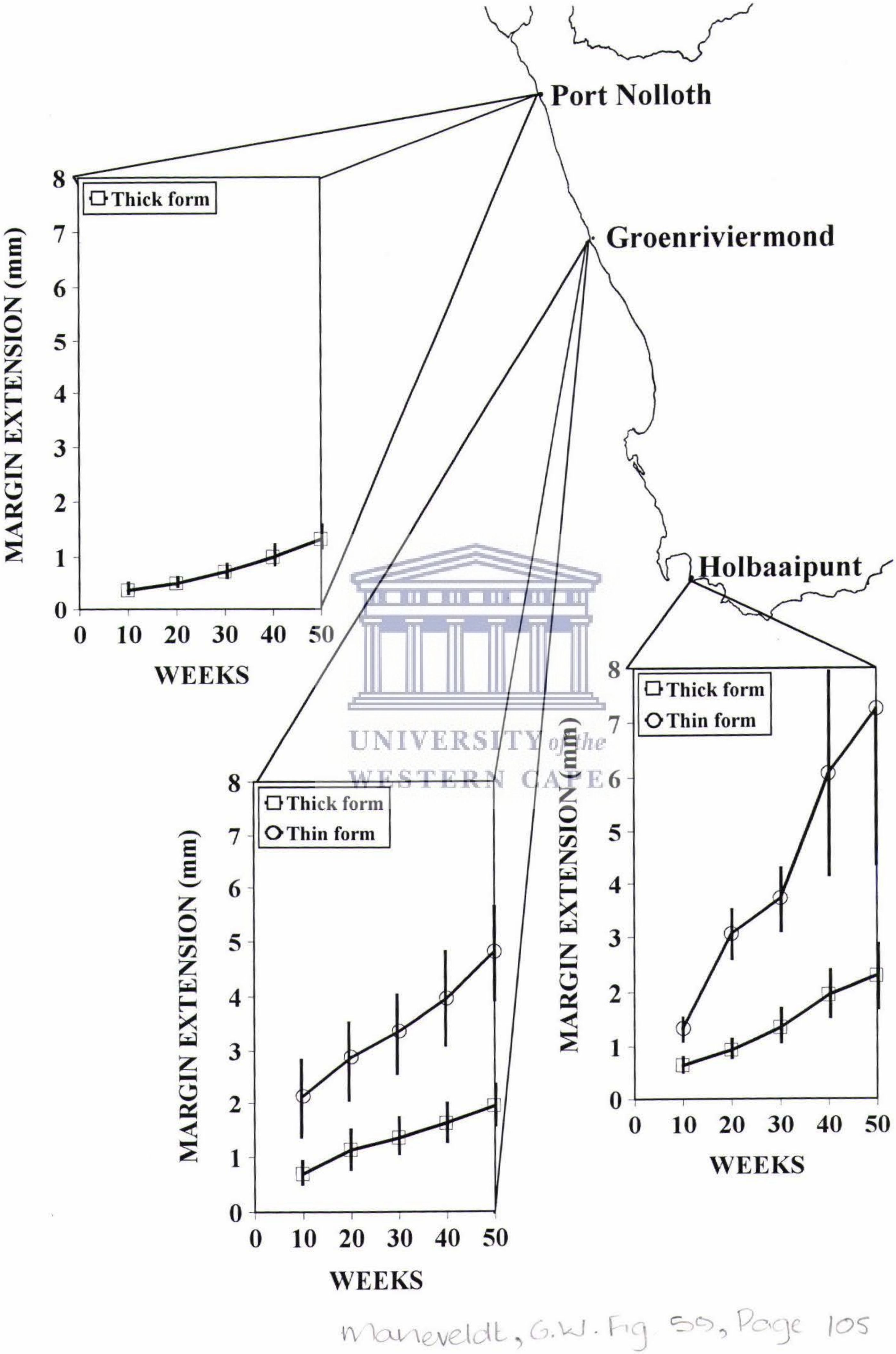
Maneveldt, G.W. Fig. 5b, Page 102



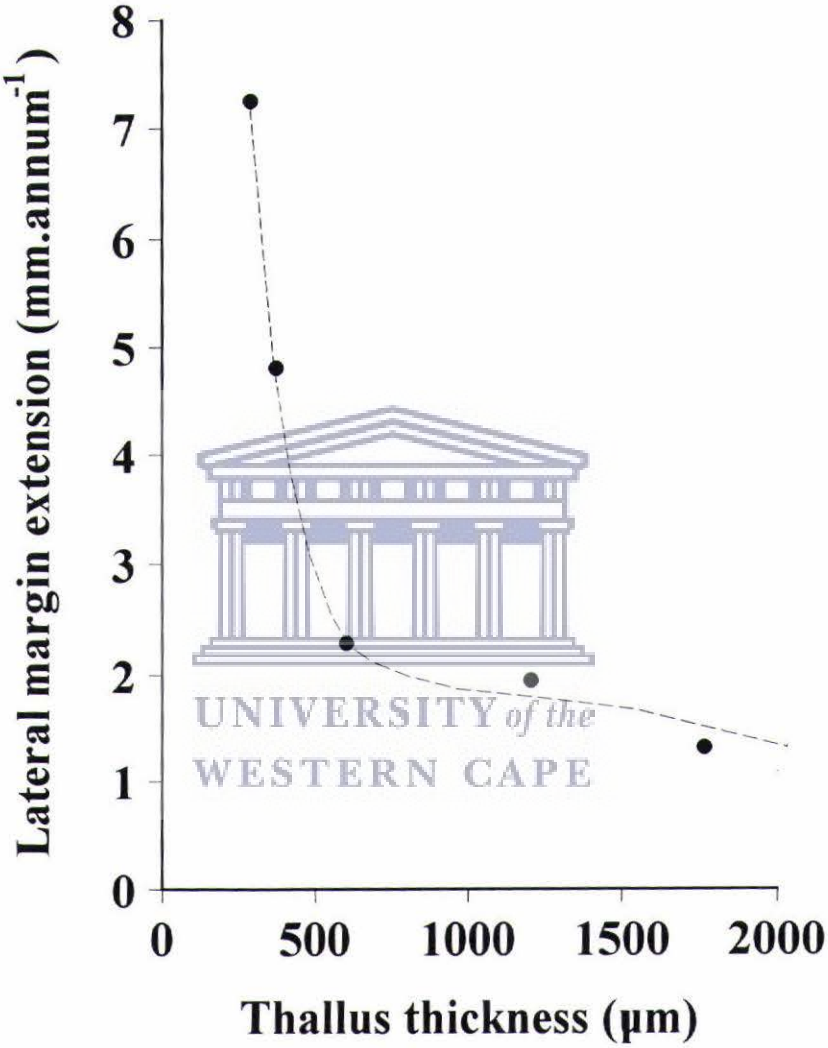
Maneveldt, G.W. Fig. 57, Page 103



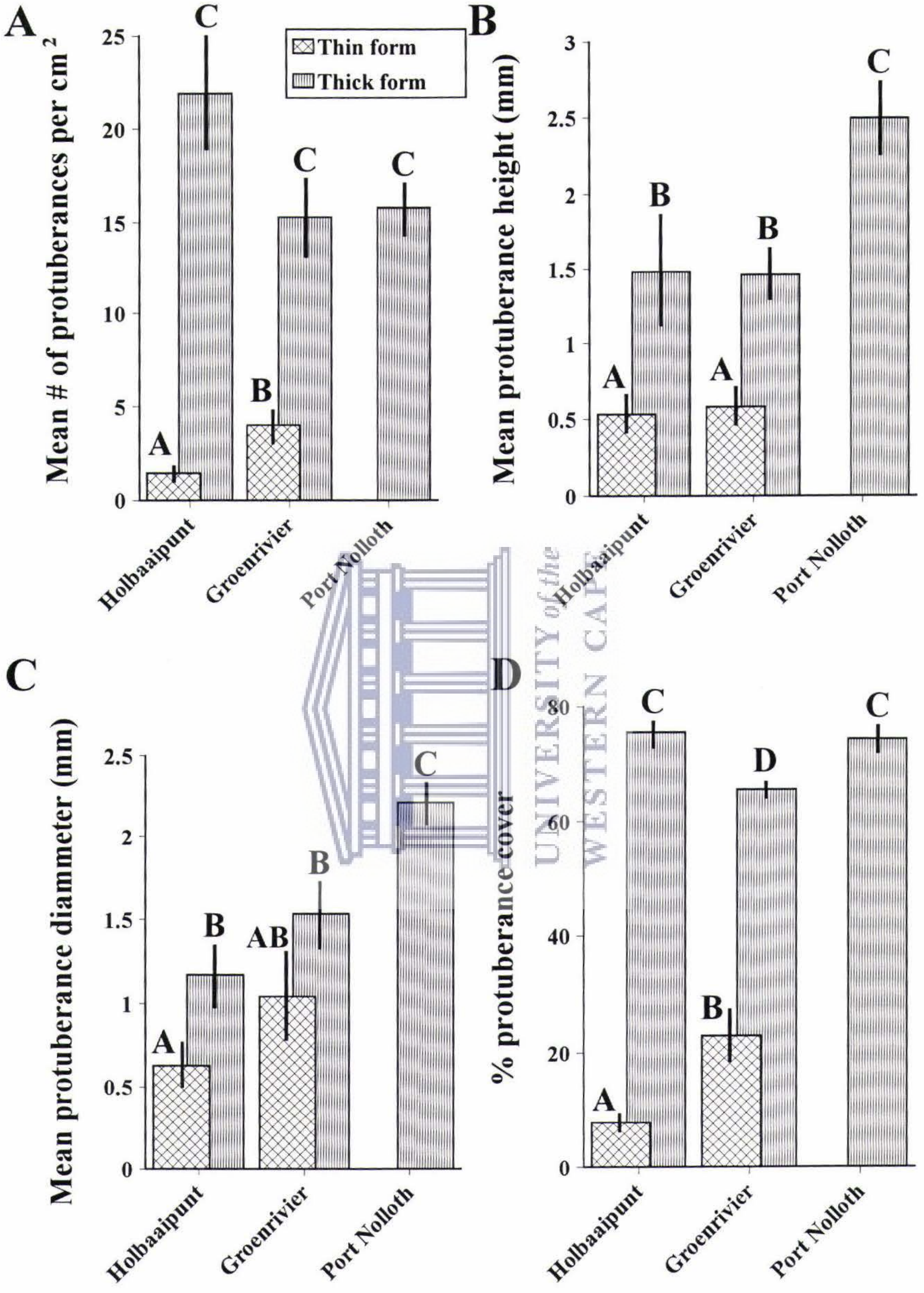
Maneveldt, G.W. Fig. 58, Page 104



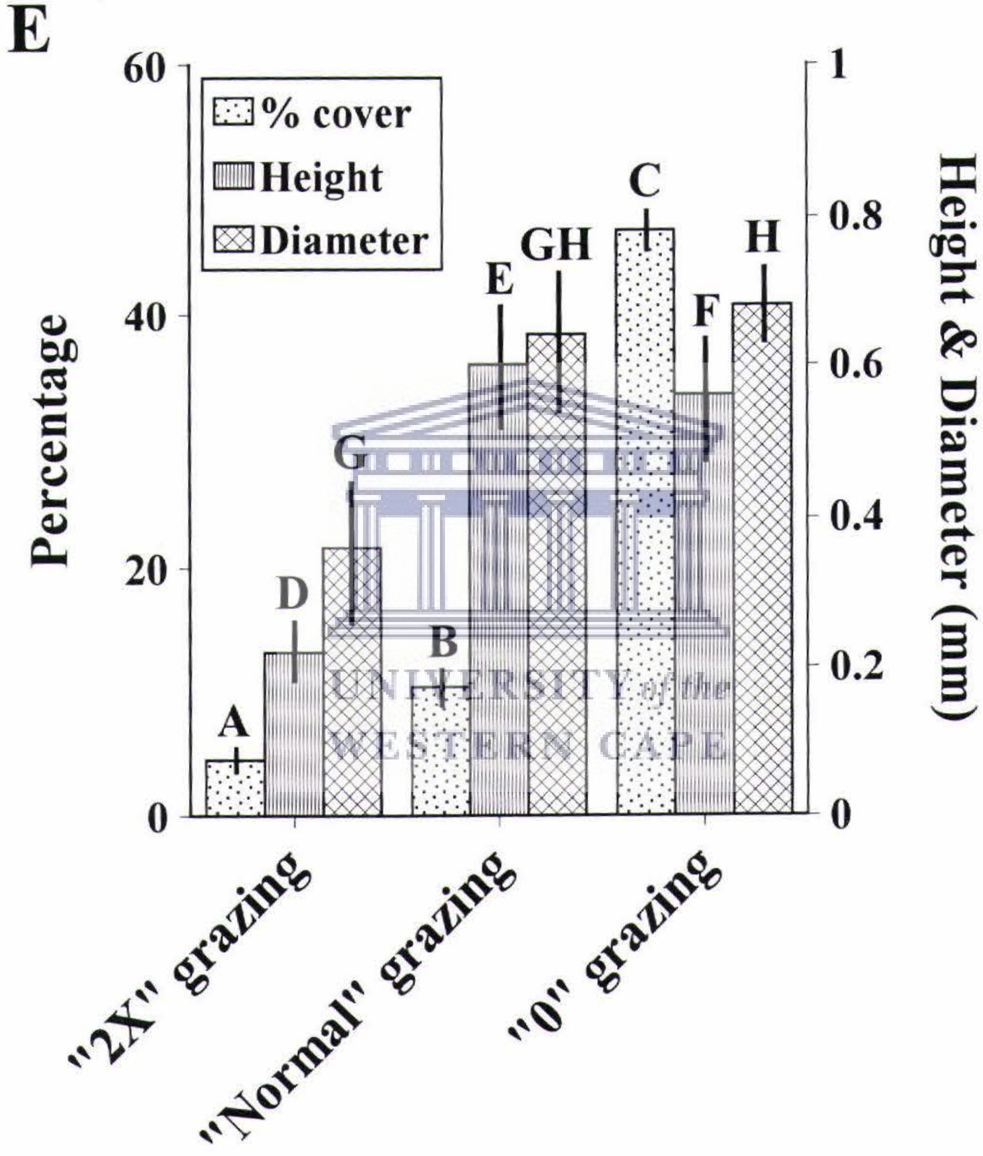
Maneveldt, G.W. Fig. 50, Page 105



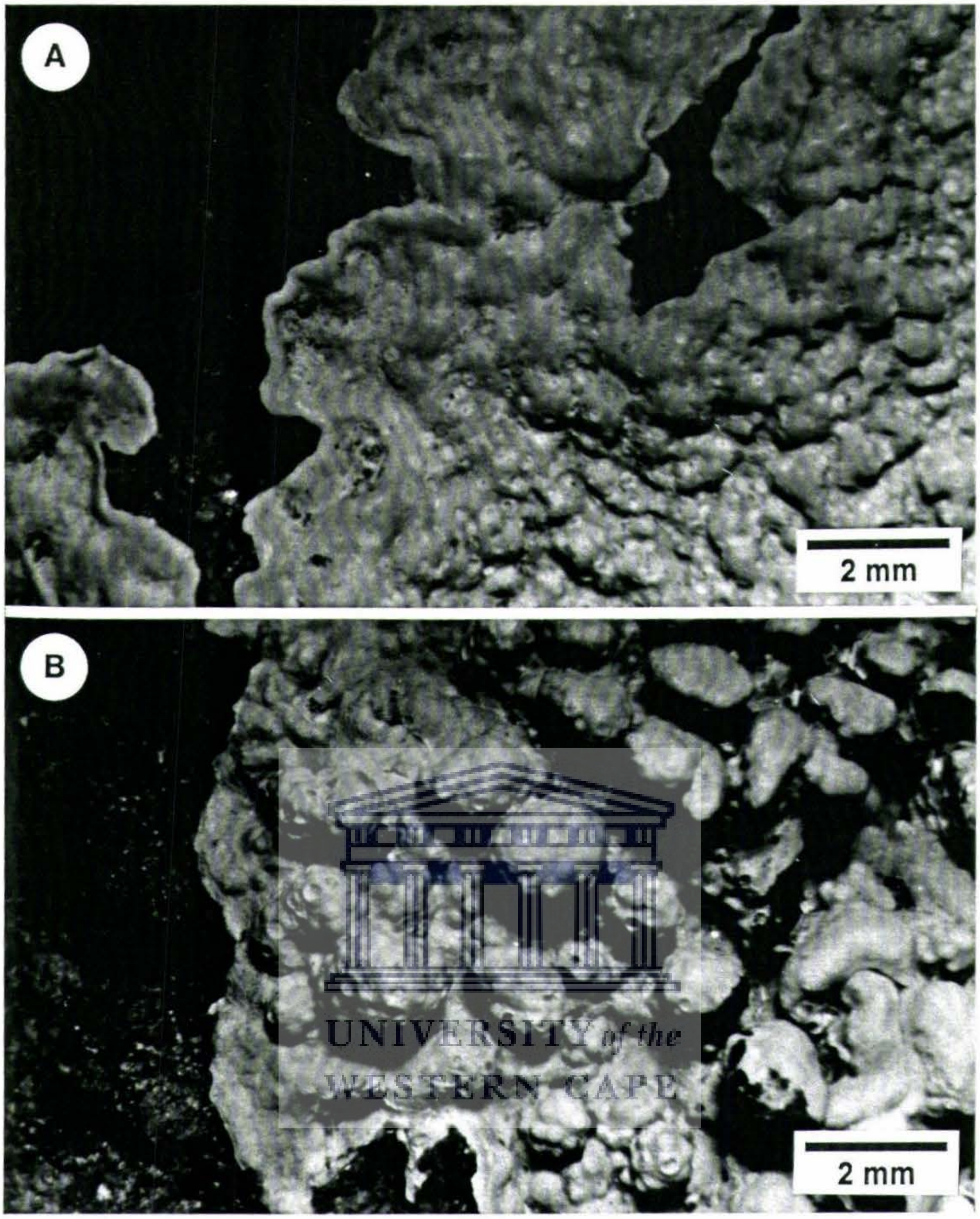
Maneveldt, G.W. Fig. 60, Page 106



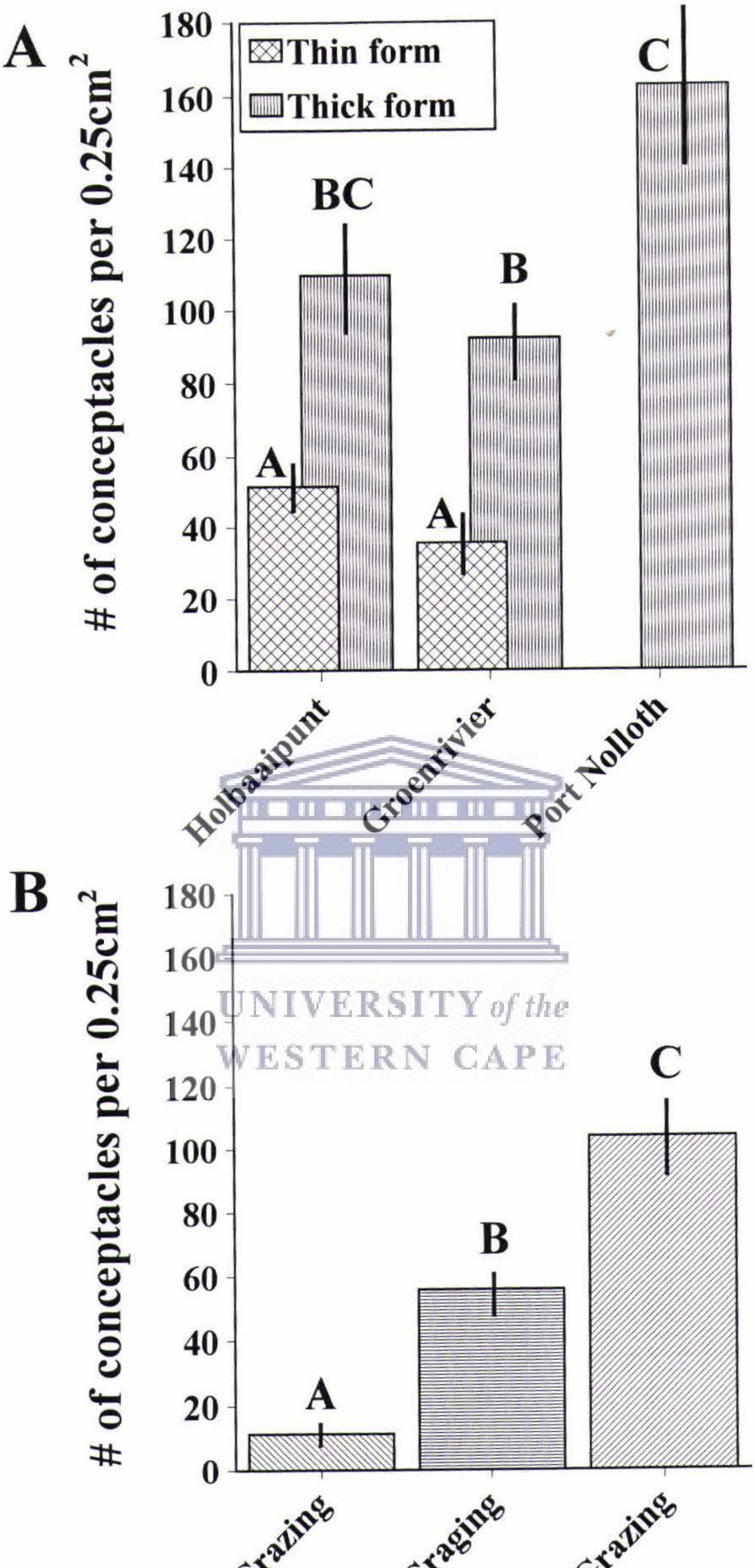
Maneveldt, G.W. Fig. 61, Page 107



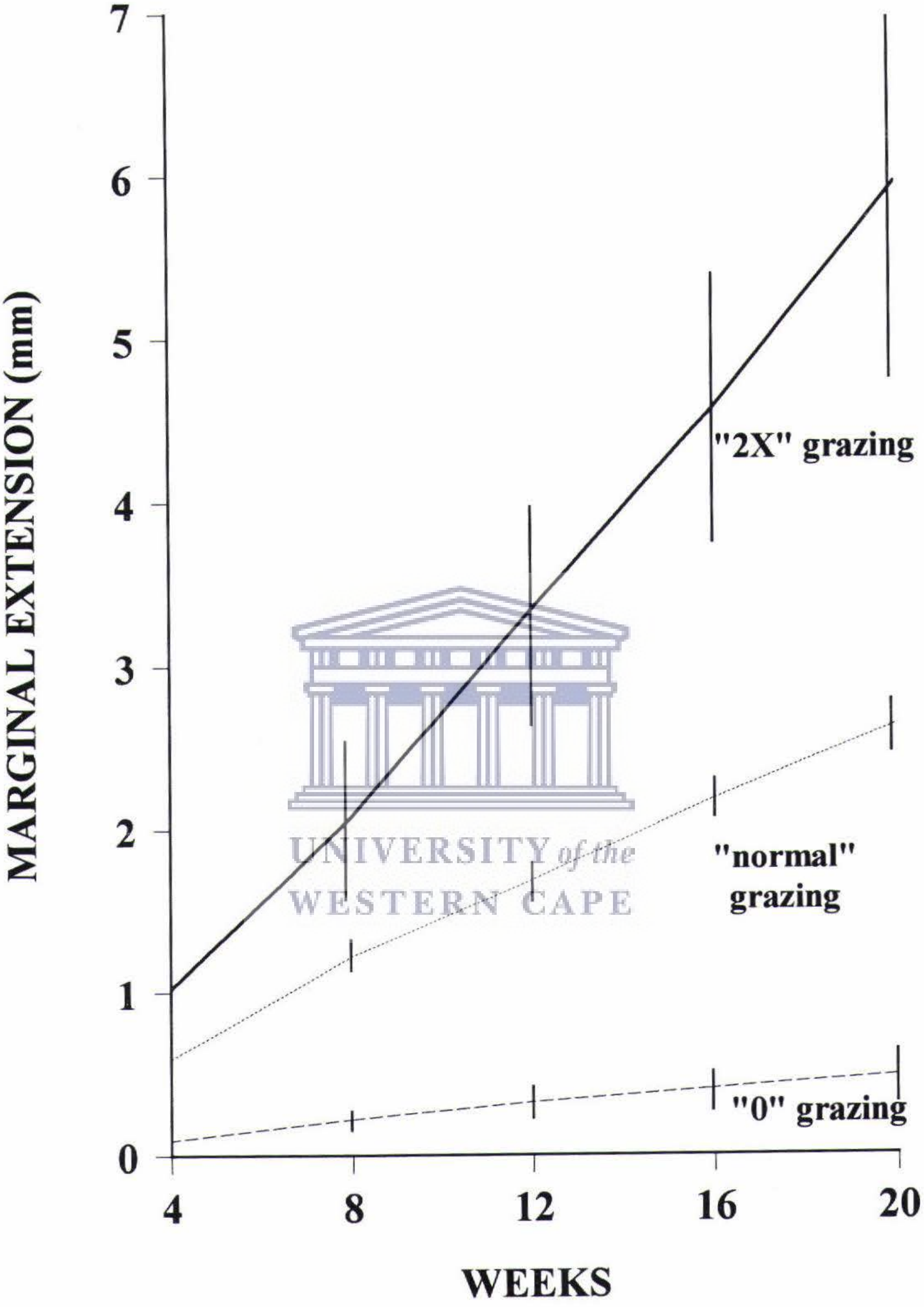
Maneveldt, G.W. Fig. 61, Page 108



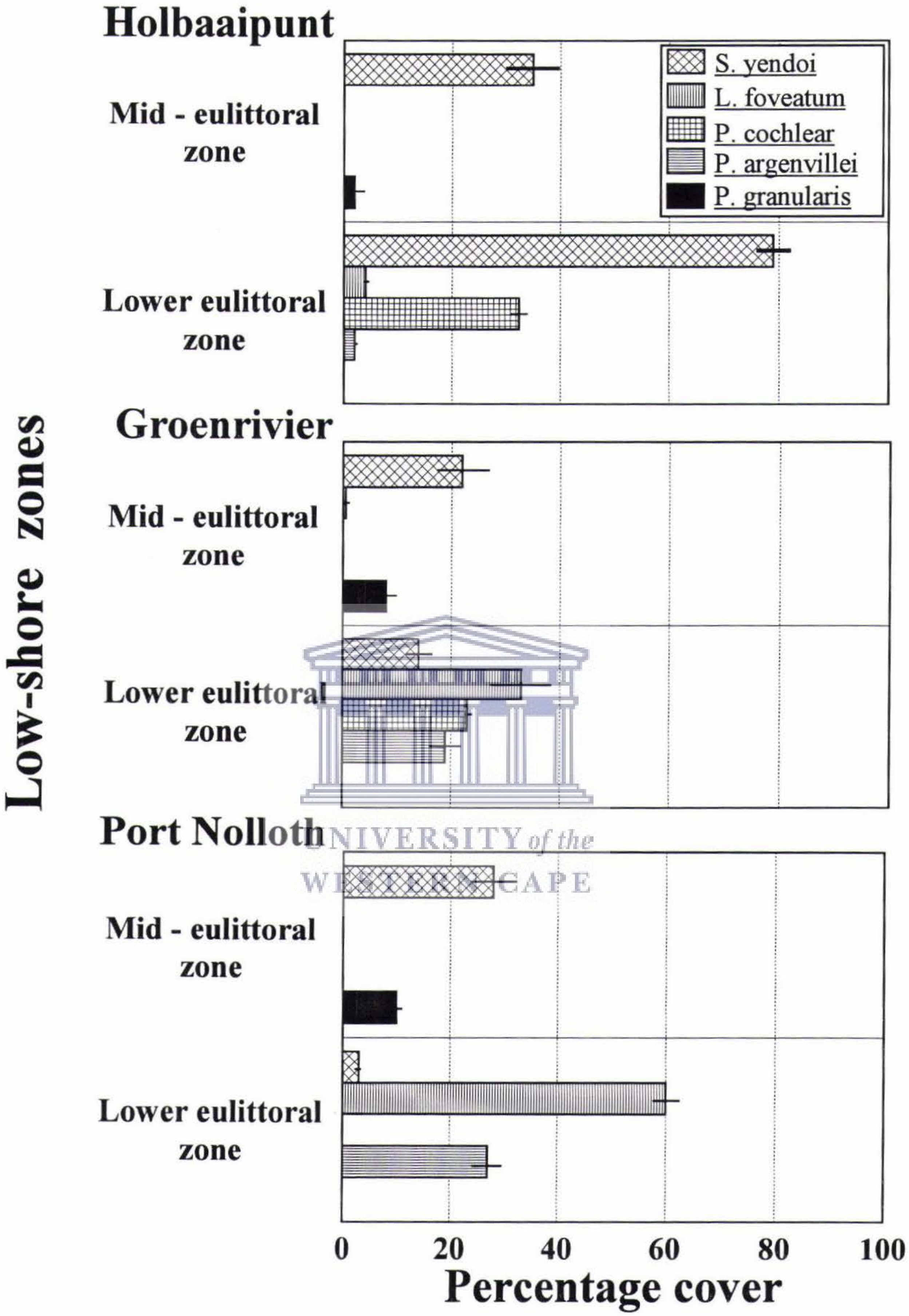
Maneveldt, G.W. Fig. 62, Page 109



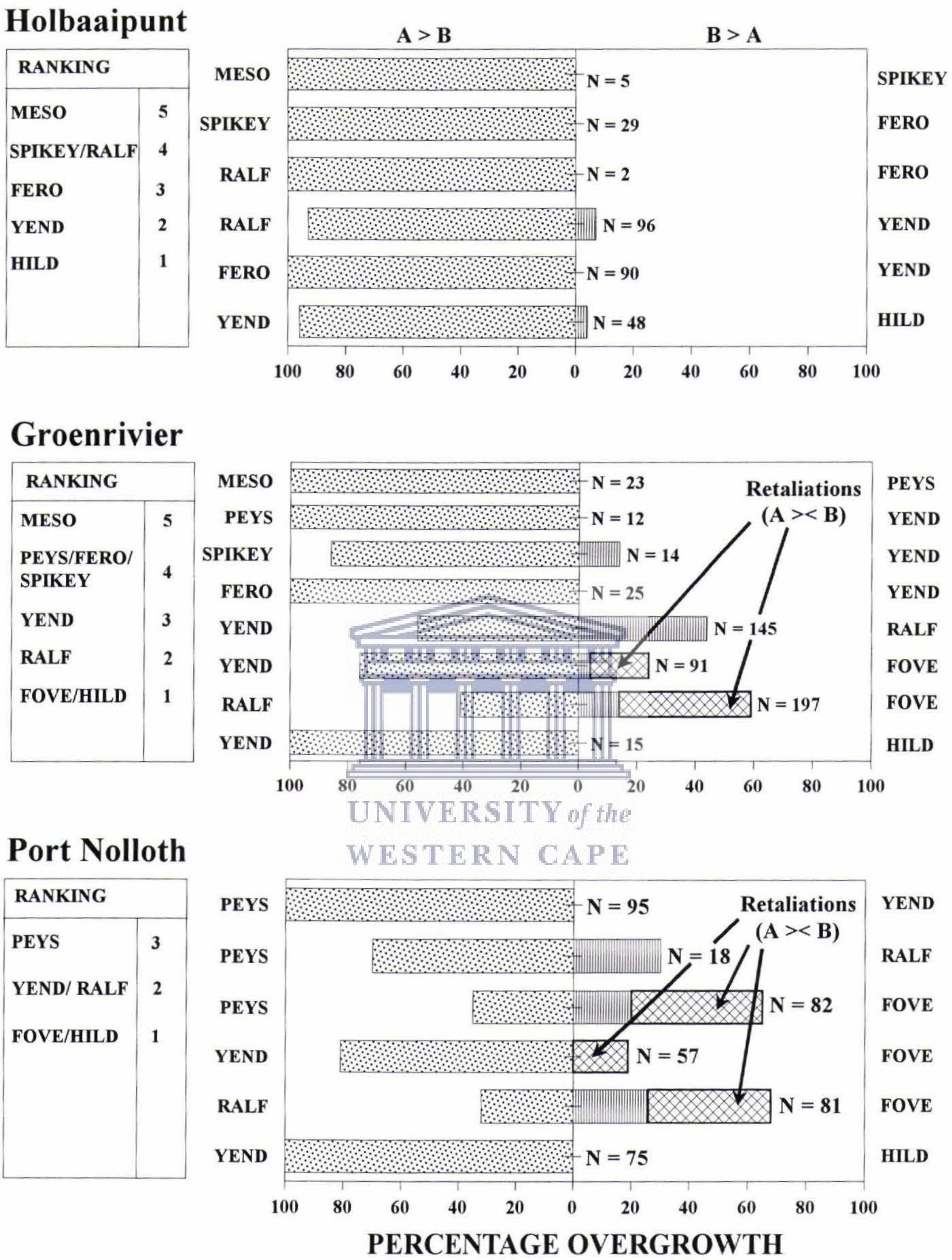
Maneveldt, G.W. Fig. 63, Page 110



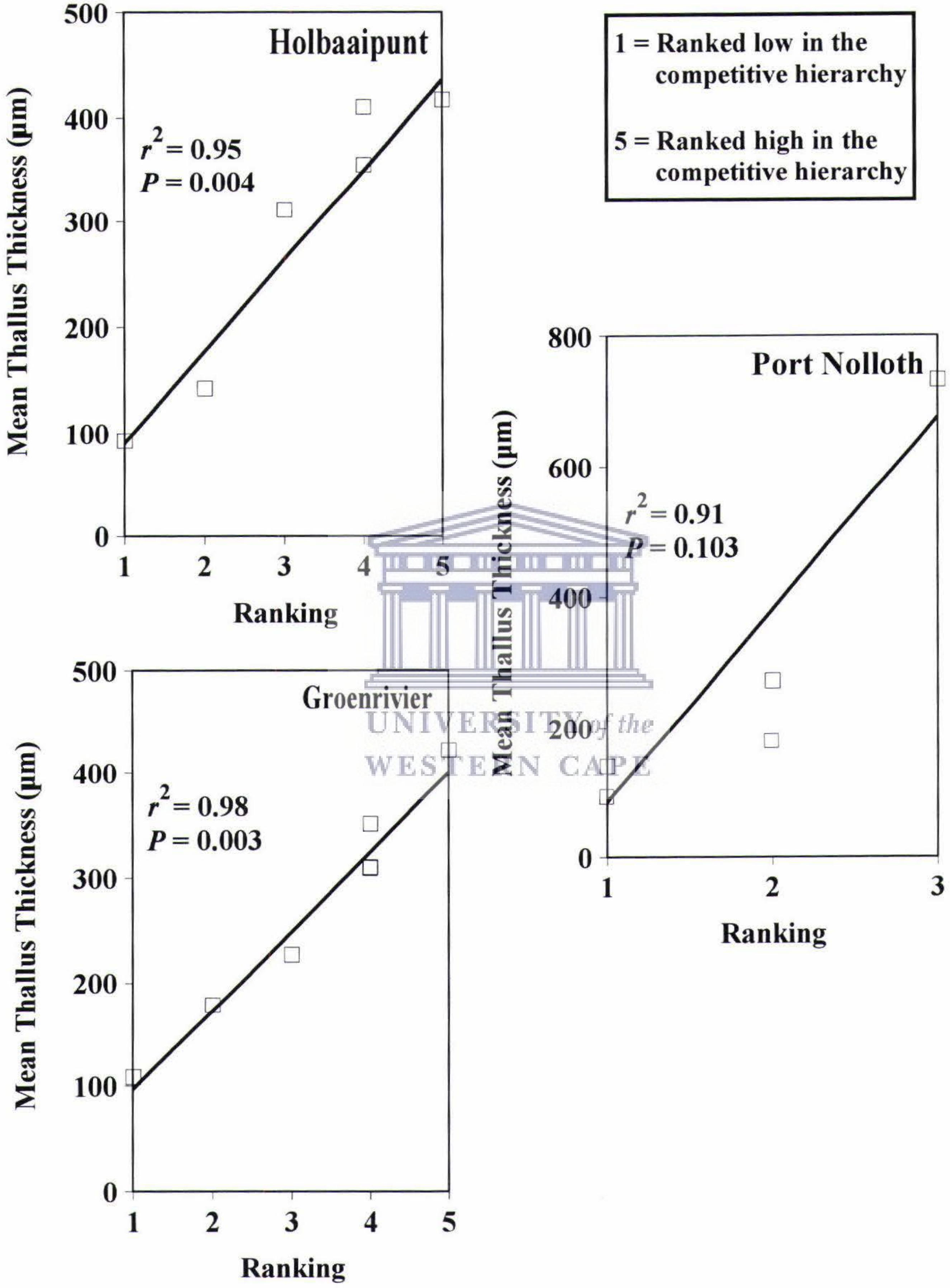
Maneveldt, G.W. Fig. 64, Page 111



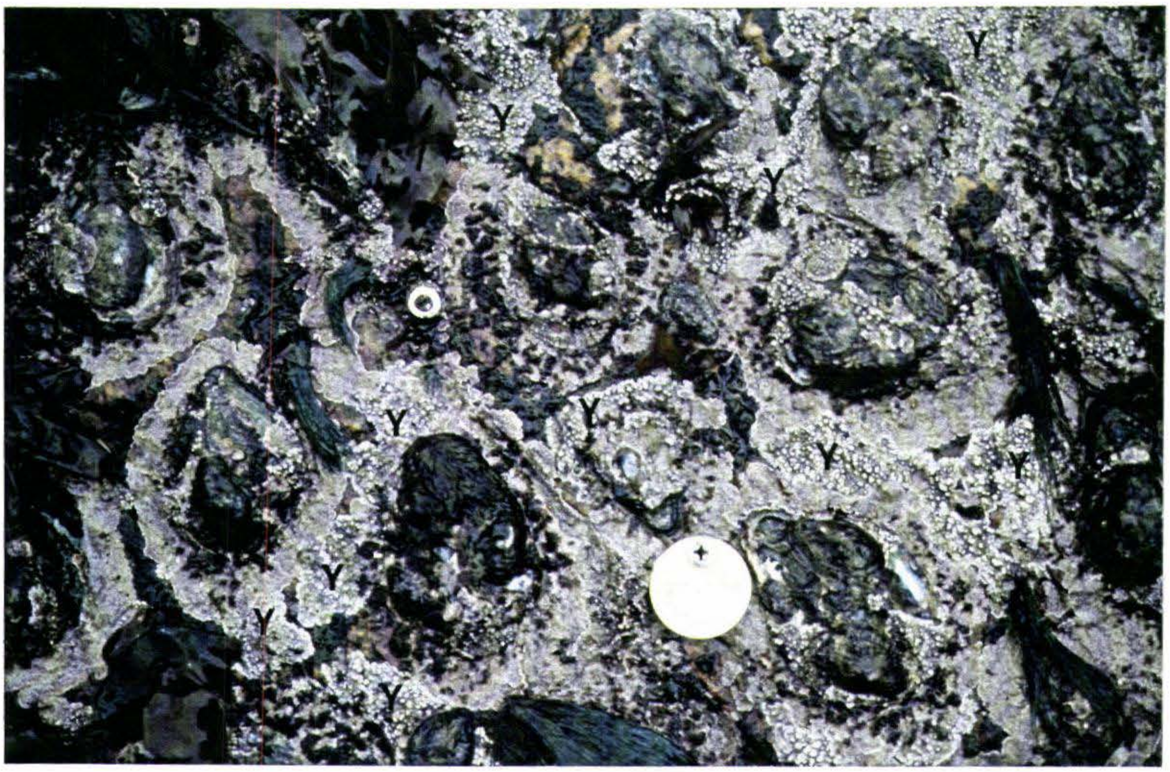
Maneveldt, G.W. Fig. 65, Page 112



Maneveldt, G.W. Fig. 66, Page 113

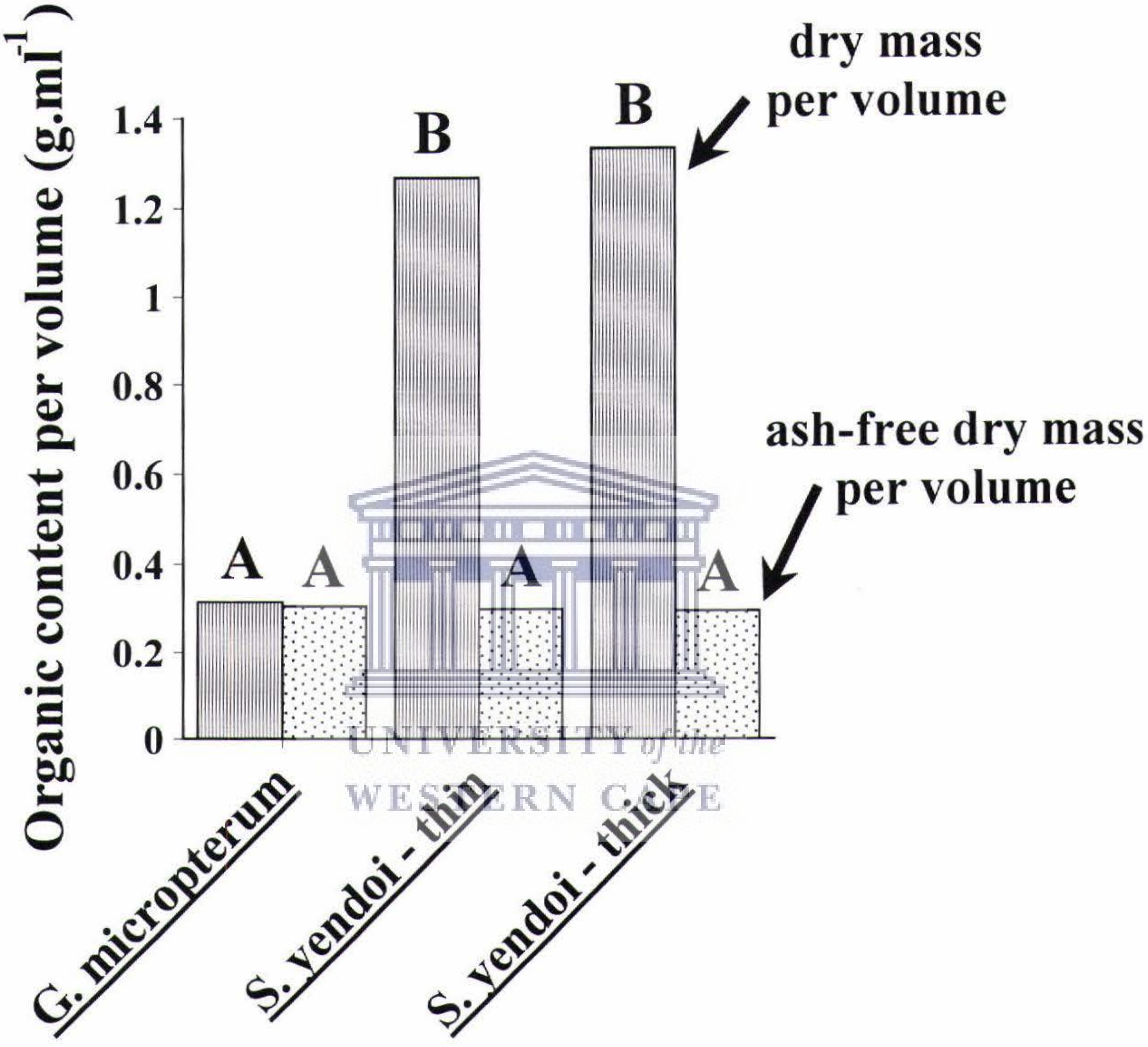


Maneveldt, G.W. Fig. 67, Page 114

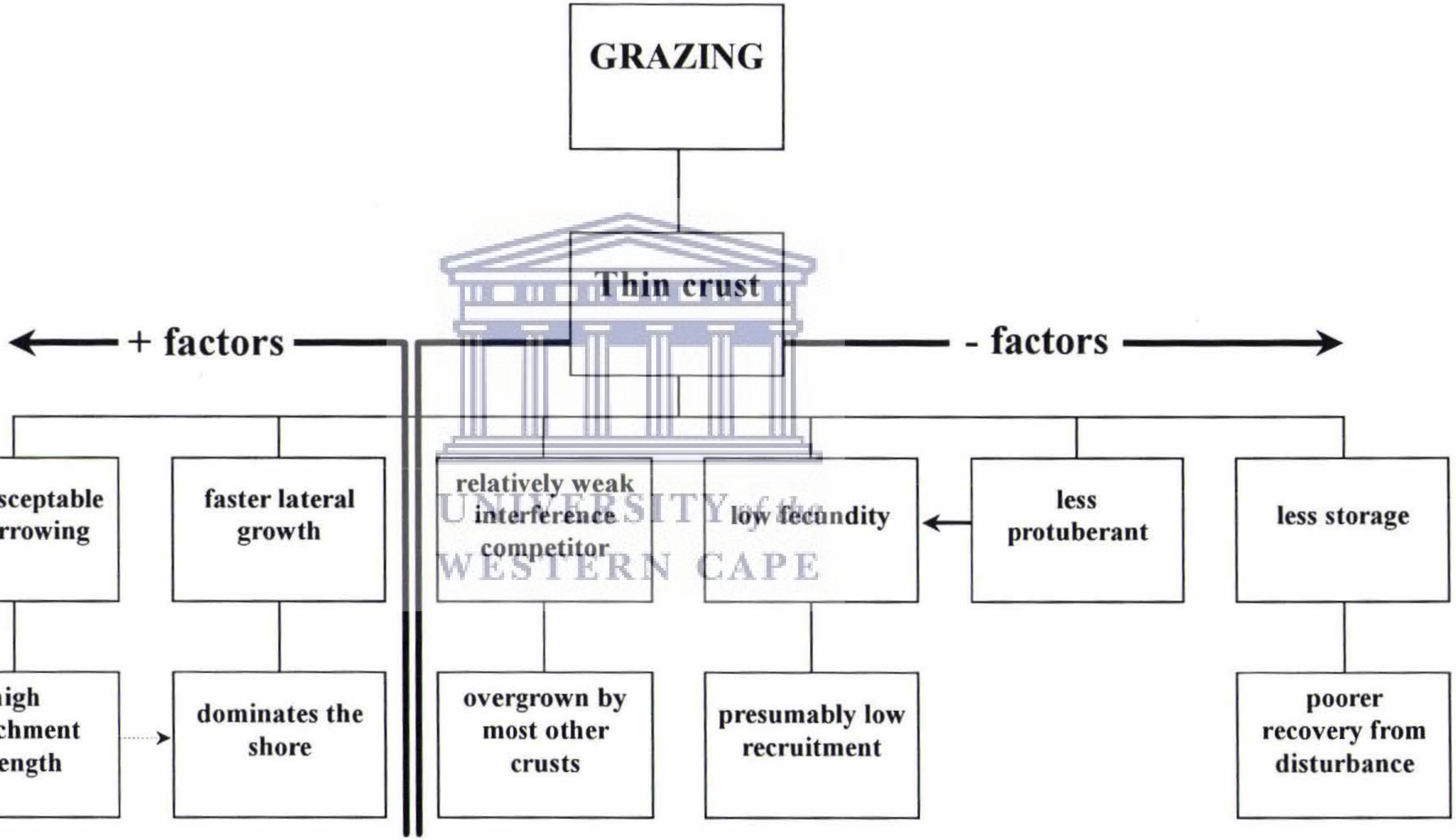


Maneveldt, G.W. Fig. 68, Page 115

Maneveldt, G.W. Fig. 69, Page 116



Maneveldt, G.W. Fig. 70, Page 117



Maneveldt, G.W. Fig. 71, Page 118

GENERAL DISCUSSION

Although the evidence and support of physica l factors determining species boundaries and abundance along geographic gradients are overwhelming (Wilce 1963, unpublished manuscript, Dayton 1971, 1975, Menge 1976, Vermeij 1978, Werger 1978, Pielou 1979, South 1979, 1987, Bush and Weis 1983, Laughlin 1983, Branch 1984, Hay and Gaines 1984, van den Hoek 1984, Hooper and Whittick 1984, Harlin et al. 1985, Keats et al. 1985, Lobban et al. 1985, Bolton 1986, Bolton and Anderson 1987, 1990, Bolton and Levitt 1987, Bolton and Stegenga 1987, Breeman 1988, Anderson and Bolton 1989, Kooistra et al. 1989, Lüning 1990, Zimmeman and Rechenik 1991, McClanahan 1992, Chen and Chen 1993, Breeman et al. 1993, Coutinho and Zingmark 1993, Péres-Lloréns et al. 1993, Peters and Breeman 1993, Gierdien 1994), there has recently however been an accumulation of evidence supporting the biological control of species boundaries and abundance along geographic gradients (Lubchenco 1980, Hay 1981, Sousa et al. 1981, Whethey 1983, Brenchley and Carlton 1983, Hay and Gaines 1984). After an examination of all this work, it seems reasonable to conclude that general delimitations are controlled by the physical environment, while the finer, actual species delimitations are biologically controlled. It is thus possible to recognize patterns in marine biogeography, more specifically, primary and secondary patterns.

I refer to primary patterns as that existing when groupings of distinct species may be recognised. This type of biogeographic pattern would consider only species absence or presence. More specifically, primary patterns would be controlled by physical factors of which sea water temperature has been shown to be extremely important.

Secondary patterns describe the relative abundance of a species within its geographic range, the species richness within a single geographic location, species dominance, how much endemism exists, the productivity, biomass, etc. It is at this lower level that biological factors such as predation and competition may play integral parts in the dynamics of the species niche. Although Spongites yendoi occurs beyond the geographic range of Patella cochlear, it is at this lower level that the limpet has controlled the abundance of the encrusting coralline alga within its geographic range.

This study has shown that within the study area, there is a positive correlation between the abundance of the limpet and that of the coralline. Outside of the study area, the trend is also consistent with these findings. Y. Chamberlain (personal communication) reports that beyond the eastern boundary of the limpet, S. yendoi, although still being present, is extremely rare, having a discontinuous, extremely patchy distribution. At Port Nolloth and beyond, S. yendoi's abundance also decreases dramatically, the coralline having the lowest abundance of all intertidal encrusting algae found at Port Nolloth (G.W. Maneveldt, personal observation). At Swakopmund in Namibia however, S. yendoi is again the most abundant intertidal coralline (G.W. Maneveldt, personal observation). Spongites yendoi's high abundance is no doubt due to the corallines extremely thin thallus which grows fast laterally; S. yendoi's thallus is thin because the coralline experiences severe sand blasting along the Namibian West coast (G.W. Maneveldt, personal observation).

This and other studies (Sousa et al. 1981, Whethey 1983, Brenchley and Carlton 1983, Hay and Gaines 1984) are but a few that have shown experimentally that biological factors can control species abundance and distribution along geographic gradients. There are no doubt however, many other biological interactions which have not yet been examined and which will in time prove to strengthen the idea of the biological control of species abundance and distribution along geographic gradients.

One such an interaction, which surprisingly has not been examined experimentally, is that between seaweeds and their host specific epiphytes; certainly such associations lend themselves to the concept of the biological control of species distributions (A.K. Peters, personal communication). The encrusting coralline alga Pneophyllum keatsii Chamberlain for example, occurs only on the seaweed Ecklonia maxima (Osbeck) Papenfuss (Chamberlain 1994). Other than the Western Cape Province, South Africa, the distribution of this epiphyte elsewhere is unknown (Chamberlain 1994). Along the South African coast however, E. maxima appears to control the distibution of P. keatsii. Three other species of red algae epiphytic on E. maxima namely Carpoblepharis flaccida (C. Agardh) Kuetzing, Polysiphonia virgata (C. Agardh) Sprengel, and Suhria vittata (Linnaeus) J. Agardh have geographical distribution patterns identical to E. maxima (Branch et al. 1994). Ecklonia maxima has however been reported from St. Paul Island in the southern ocean and since this island has a number of other seaweed species in common with South Africa (Papenfuss 1942), it seems likely that some, if not all, of these epiphytes could coexist there in association with E. maxima.

Similarly the encrusting coralline alga, Clathromorphum tubiforme Y. Chamberlain, R. Norris, D. Keats et G. Maneveldt, has been found to occur epiphytically on the fronds of three species of Amphiroa (Chamberlain et al. 1995). It may well be that epiphytes like C. tubiforme and P. keatsii, being newly described species which are ecologically little known, have geographic ranges which do not coincide with their algal host. Certainly epiphytes such as C. flaccida, P. virgata and S. vittata however, which have geographic ranges which coincide exactly with their algal host, lend themselves to the concept of the biological control of species geographic distributions.

Host specific species occuring epizoically have also received similar attention. The whelk, Nucella squamosa (Lamarck) is the chosen habitat of the hydroid Hydractinia altispina Millard and grows nowhere else (Richards and Thorpe 1988). The bryozoan Alcyonidium nodosum O'Donoghue lives exclusively on shells of the whelk, Burnupena papyracea (Bruguière) and has a geographic range almost identical to that of the whelk (see Branch et al. 1994). Rio and Cabioch (1988) have even postulated that oysters are the vectors of transport of the seaweed Caulacanthus ustulatus (Turner) Kuetzing to its new northern limit near Roscoff on the north coast of western Brittany (northern France); two years earlier, the seaweeds northern limit was Biarritz on the southern west coast of France.

It is thus plain to see that there are many other symbiotic associations which clearly favour the biological control of species geographic distributions. In fact, the concept of the species niche (or 'realized niche') is based almost entirely on the control of species boundaries by biological factors such as competition and predation. If biological factors can control the vertical boundaries of species, why not their geographic boundaries.

The regulation of community structure by herbivores is a well documented phenomenon in both aquatic and terrestrial environments. Marine herbivores, for example, have consistently been shown to control the vertical distribution, abundance, diversity, composition and biomass of algal communities (Dayton 1975, Lubchenco and Gaines 1981, Steneck 1983, Branch 1971, 1975a, 1981, Branch and Griffiths 1988, Keats 1991, Eekhout et al. 1992, Littler et al 1995). However, not all marine herbivores have negative impacts on the seaweeds they graze; many have been shown to increase the abundance (Adey and Macintyre 1973, Steneck 1982, 1985), diversity (Dayton 1975, Lubchenco 1978, Hay 1981, Breitberg 1984), and productivity or biomass (Branch 1971, 1975a, 1981, Steneck 1982, Littler et al. 1995) of their algal food. By grazing its coralline food, Patella cochlear reduces the alga's thallus thickness enabling it to grow faster (increasing its productivity) and thereby increasing the corallines abundance. Productivity in Spongites yendoi is thus also grazer dependent. Grazers increasing productivity is poorly documented for the marine environment and only two other known cases exist of herbivores increasing the primary productivity of their coralline food (see Steneck 1982, Littler et al. 1995). In contrast, grazing as a regulator of primary productivity is well documented for the terrestrial environment. Grassland ecosystems, for example, are highly productive ecosystems under continual herbivory (McNaughton 1979, 1985, McNaughton et al. 1988, Seagle et al. 1992). More recently, Van der Heyden and Stock (1995) have even documented an increase in productivity in non-succulent shrubs under low grazing frequencies.

The effects of grazing on the gross morphology of plants are also well documented for the terrestrial environment. While the presence of some insects produce plant galls (beside physical protection, galls often provide a higher quality food than the plant would ordinarily offer), and the harvesting activities of leaf-cutting ants are often capable of denuding trees of all their leaves (Edwards and Wratten 1980), the grazing activities of mega-herbivores such as elephants, are particularly well documented (e.g. Jachman and Croes 1991). Recently for example, the impact of elephant and in particular goat grazing on succulent thicket, has received considerable attention (see Stuart-Hill 1992, Moolman and Cowling 1994). Elephant grazing tends to result in relatively low growing shrubs since these herbivores browse from the "top downwards". Goat grazing, by contrast, result in shrubs taking on an umbrella shape due to the "bottom up" grazing behaviour of goats (Stuart-Hill 1992).

In order to successfully understand certain ecological processes, we have to realize that we need to expand our ideas and our studies beyond the small "within ecosystem" scale. Many authors (Foster 1990, Underwood and Kennelly 1990, Kennelly and Underwood 1993) have already expressed the need to do this and expand our observations to experimental testing of observed trends. The present study, and several others (Sousa et al. 1981, Dethier and Duggins 1988, Keats 1991, Eekhout et al. 1992, Kennelly and Underwood, 1993, Bustamante 1995) have, without doubt, greatly enhanced our knowledge of ecological processes within and more importantly, between ecosystems. Since most generally accepted ecological theory have been based on small-scale "within ecosystem" studies, and since it has been shown that similar communities can behave quite differently depending on their geographic locations (Dethier and Duggins 1988), the need for large-scale, geographic studies has become apparent. How else can we successfully evaluate our understanding of ecosystem assemblage structure.

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APPENDIX I

Instructions to Authors

SUBJECT MATTER

The pages of *Ecology* and *Ecological Monographs* are open to research and discussion papers that develop or test ecological theory with data from field and laboratory experiments, observations, or simulations. New methodologies with a potential for broad use in ecology are also of interest. Papers that are well grounded in ecological theory and that have broad implications for environmental policy or resource management are welcome in *Ecological Applications* as well as in *Ecology* or *Ecological Monographs.*

Each paper should report original research or a reanalysis of published research that results in new insights. Treatment of the research topic should lead to generalizations that are potentially applicable to other species, populations, communities, or ecosystems.

SCOPE

We invite contributions from scientists working on the full spectrum of ecological problems. Included within this spectrum are studies of the physiological responses of individual organisms to their abiotic and biotic environments, ecological genetics and evolution, the structure and dynamics of populations, interactions among individuals of the same or differing species, the behavior of individuals and groups of organisms, the organization of biological communities, landscape ecology, the processing of energy and matter in ecosystems, historical ecology and paleoecology, and the application of ecological theory to resource management and the solution of environmental problems. Reports of ecological research on all kinds of organisms in all environments are welcome.

LENGTH

Ecology considers papers that will occupy up to 20 printed pages, including illustrations. Notes, Comments, and Replies to Comments may not exceed 4 printed pages. *Ecological Monographs* handles papers that will be longer than 20 printed pages. Assignment of an accepted paper to *Ecology* or *Ecological Monographs* will depend primarily on the length of the paper after it is set in type. Three pages of typescript equal approximately one printed page. *Ecological Applications* considers papers of any length. Illustrations and tabular material together may constitute up to 20% of the total printed length of the article without extra cost to the author.

SUBMISSION OF MANUSCRIPTS

Manuscripts should be submitted to the Managing Editor, Lee N. Miller, Ecological Society of America, 328 E. State Street, Ithaca, New York 14850-4318. Submit four photocopies of the manuscript; retain the original. **Do not** submit originals or photographic prints of illustrations; photocopies are preferred until the manuscript has been accepted by the subject-matter editor and edited by a technical editor. Include your address and telephone and FAX numbers in your cover letter. An author who moves from the address shown on the manuscript should provide a forwarding address.

At the time of submission authors should provide information describing the extent to which data or text in the manuscript have been used in other papers or books that are published, in press, submitted, or soon to be submitted elewhere.

Authors should adhere to the ESA Code of Ethics, which was adopted by the Society in August 1990. The Code, printed in the *Bulletin of the Ecological Society of America,* Volume **71**(4), December 1990, deals with authorship, plagiarism, fraud, authorized use of data, copyrights, errors, confidentiality, intellectual property, attribution, willful delay of publication, and conflicts of interest, as well as other matters that are not specific to the publication process.

PEER REVIEW PROCESS

Authors will be notified of receipt of the manuscript. A designated subject-matter editor will be responsible for review and acceptance or rejection of the manuscript. Technical correspondence concerning the manuscript may be directed to that editor. The Managing Editor or the subject-matter editor will make an initial appraisal of the manuscript. If the topic and treatment seem appropriate for the journal, the manuscript will then be reviewed by others with expertise in the subject. A decision on the manuscript may generally be expected within 3–4 months of submission; delays in obtaining reviews may prolong this period. If a manuscript is returned for revision, the author should submit a revised manuscript directly to the subject-matter editor within 4 months. Manuscripts undergoing revision for longer than 4 months may (at the editor's discretion) be considered as new submissions. Only ~35% of the manuscripts received can be accepted for publication.

PREPARATION OF MANUSCRIPTS

Write with precision, clarity, and economy; use the active voice and first person whenever appropriate. Use American spellings (e.g., behavior, not behaviour). The *CBE Style Manual,* Fifth Edition, is recommended for details of style. It is available in most university or research libraries, or it can be purchased for $27.95 from the Council of Biology Editors, 111 E. Wacker Drive, Suite 200, Chicago, IL 60601-4298 USA.

SPACING, MARGINS, FONTS

Double-space all material (text, quotations, figure legends, tables, literature cited, etc.) at three lines per inch (12 lines/10 cm). Number the lines of text if a line-numbering option is available in your word processing program. Type on only one side of standard-sized paper, approximately 22 × 28 cm. Leave 2.5-cm margins on all sides of each page. Do not use very thin paper, even when overseas mailing is required. Use a

12-point font (proportionally spaced type) or 10 characters/inch (4 characters/cm) if the letter spacing is uniform.

UNDERLINING

Underlining indicates italicization. Please underline scientific names and the symbols for all variables and constants *except* Greek letters. Symbols should be italic in the illustrations to match the text. Italics should rarely be used for emphasis.

EQUATIONS; STATISTICS

Equations to be set separately from the text will be broken into two or more lines if they exceed the width of one column; mark equations for appropriate breaks. Subscripts and superscripts should be clarified by marginal notes.

State probability values without leading zeroes (e.g., $P < .01$).

FOOTNOTES

Avoid footnotes; most footnote material can be incorporated in the text to the benefit of readers, editors, and printers.

UNITS

Use the International System of Units (SI) for measurements. Consult *Standard Practice for Use of the International System of Units* (ASTM Standard E-380-92) for guidance on unit conversions, style, and usage. (The Standard can be purchased for $23.00 from ASTM, 1916 Race Street, Philadelphia, PA 19103 USA.) When preparing text and figures note in particular that (1) SI requires the use of the terms *mass* or *force* rather than *weight*, (2) when one unit appears in a denominator, use the solidus (e.g., g/m^2); for two or more units in a denominator, use negative exponents (e.g., $g \cdot m^{-2} \cdot d^{-1}$), and (3) you should use the international spelling of metre and litre, and a capital L as the symbol for litre.

IDENTIFYING THE OBJECT OF STUDY

Early in the manuscript, identify the *type(s)* of organism or ecosystem you studied; e.g., "a small deciduous tree," "the ground squirrel *Spermophilus lateralis*," "a bivalve of brackish water." Avoid descriptive terms that may be familiar only to specialists. Provide the scientific names of all organisms. Common names may be used when convenient after stating the scientific names.

TITLE PAGE

Running Head.—A running head not longer than 40 letters and spaces should be provided at the top of the title page.

Title.—The title should tell what the article is about. It should be informative and short—the maximum length is 13 words or 100 characters; longer titles will be shortened by the editor. Do not include the authority for taxonomic names in the title or in the abstract. Titles may not include numerical series designations.

List of Authors.—For each author, state the relevant address—usually the institutional affiliation of the author during the period when all or most of the research was done. The author's present address, if different from this, should appear as a footnote at the bottom of the title page.

ABSTRACT, KEY PHRASES, AND KEY WORDS

An abstract, key phrases, and key words should be provided for all articles, including *Notes, Comments,* and *Special Features.* They are needed for the annual index, whether they appear in the published article or not.

Abstract.—The Abstract should provide a brief summary of the research, including the purpose, methods, results, and major conclusions. Avoid speculation in the abstract; if included, speculation about possible interpretations or applications of your results should play a minor role. Do not include any literature citations in the abstract.

Key Phrases and Key Words.—Following the abstract, list key words and 8–10 key phrases for the annual index. Extract key phrases from topic sentences that tell the main conclusions or "take-home lessons" of your article. Each key phrase should describe a relationship or fact. *Example:* TOPIC SENTENCE: Pollination in a sexually dimorphic species was affected by petal length, nectar, sexual type (hermaphrodite or female), and pollinator visitation rates. KEY PHRASES: Floral characteristics of hermaphrodites vs. females; Pollinator visitation rates vs. flower type; Sexual dimorphism of flowers: effects on pollination. KEY WORDS: nectar, petal length.

The key words should supplement but not duplicate the key phrases. Words from the title of the article may be included in the key words. Each key word or key phrase should be useful as an entry point for a literature search. Key words and key phrases will be listed together in a single annual index; any key word that duplicates the initial word of a key phrase will be deleted. Topic sentences are used only for creating the key phrases; they need not be listed with the key phrases.

BODY OF THE ARTICLE

Organize your article in sections labelled Introduction, Methods, Results, and Discussion. In long articles you may need to add a section of Conclusions. Brief articles usually do not require a label for the Introduction. If the nature of your research requires a different organization, specify the level of each section heading (1st order head, 2nd order head, etc.) in the margin. The motivation or purpose of your research should appear in the introduction, where you state the questions you sought to answer. In the Methods section you should provide sufficient information to allow someone to repeat your work. A clear description of your experimental design, sampling procedures, and statistical procedures is especially important in papers describing field studies, simulations, or experiments. If you list a product (e.g., animal food, analytical device), supply the name and location of the manufacturer. Give the model number for equipment used. Supply complete citations, including author (or editor), title, year, publisher, and version number, for computer software mentioned in your article. Results should be stated concisely and without interpretation. In the Discussion section, carefully differentiate the results of your study from data obtained from other sources. Distinguish factual results from speculation and interpretation.

ACKNOWLEDGMENTS

Acknowledgments or dedications should be placed under an *Acknowledgments* heading just before Literature Cited. Do not include these on the title page.

LITERATURE CITED

The list of Literature Cited must be completely double spaced. Before submitting the manuscript, check each citation in the text against the Literature Cited to see that they match exactly. Delete citations from the list if they are not actually cited in the text of the article. The list should conform in sequencing and punctuation to that in recent issues of the journal. All journal titles should be spelled out completely. In the titles of articles, capitalization of the common names of birds and the spelling of all words should agree exactly with that used in the original publication.

Provide the publisher's name and location when you cite symposia or conference proceedings; distinguish between the conference date and the publication date if both are given. Do not list abstracts or unpublished material in the Literature Cited. They may be listed in the text as *personal observations* (by an author of the present paper), *personal communications* (from others), or *unpublished x*, where *x* = *data, manuscript*, or *report*; provide author names and initials for all unpublished work and abstracts.

TABLES

Double space all parts of tables. Start each table on a separate page. Tables should be numbered in the order in which they are discussed in the text. Provide a short descriptive title at the top of each table; rather than simply repeating the labels on columns and rows of the table, the title should reveal the point of grouping certain data in the table. Statistical and other details should be provided as footnotes rather than appearing in the title. Do not rule tables unless essential to avoid ambiguity. Consult recent issues of the journal for style. Never repeat the same material in figures and tables; when either is equally clear, a figure is preferable. Do not include any class of information in tables that is not discussed in the text of the manuscript.

ILLUSTRATIONS

Each copy of the manuscript should include photocopies of illustrations. Number illustrations in the order in which they are discussed in the text. Group the figure legends in numerical order on one or more pages, separate from the figures.

To avoid extra expense, do not submit photographic prints until they are requested. If important details cannot be distinguished on a photocopy, submit a glossy print of that illustration for review purposes.

Most illustrations will be reduced to single-column width in the journal; symbols and lettering should be clearly legible at that size. Examine each illustration for legibility after it is photo-reduced to an image width of 76 mm. After reduction, all lettering should be at least as large as the smallest type used in the journal (6 points). Uppercase letters are preferred except where SI requires lowercase letters for unit abbreviations. Avoid very large letters and lettering styles in which portions of letters are very thin. *Use italic lettering for variables, constants, and scientific names in illustrations* to make them consistent with the text. Typewritten lettering in figures is not acceptable. Solid black bars in bar graphs tend to overwhelm the adjacent text; use white, shaded, or hatched bars in preference to black ones.

The editor may ask you to modify your illustrations. After the requested modifications have been made, provide either the original drawings or sharply focused photographic prints. Do not submit prints larger than 22 × 28 cm unless asked to do so. Protect the surface of any drawing that includes rub-on lettering or other attachments; include a reference photocopy of each original illustration. Identify each black-and-white figure by number with a label at the top of the reverse side. Color figures should be identified with a label on the top of a photocopy; do not attach *anything* to the back of a color illustration.

SUPPLEMENTS TO THE ARTICLE

Some extensive data sets, mathematical proofs, and other information that will be of interest to a small subset of readers are too costly to publish in the journals. These can be made available to readers as a supplementary publication on paper or computer diskette. In such cases, a footnote giving instructions for obtaining a copy of the supplement from the author or the journal office will be printed in the article.

ASSEMBLY OF MANUSCRIPT COPIES

Assemble the parts of each copy of the manuscript in this order: title page, abstract, key words and phrases, text, acknowledgments, literature cited, appendices, tables, figure legends, figures. Number all pages consecutively.

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After your manuscript is accepted for publication, send the following to the Managing Editor: two copies of the manuscript on paper, one copy on diskette, the name and version of the word processing program used to prepare the diskette, and two photocopies of each illustration. Everything in the manuscript must be double-spaced (3 lines/inch), using a 12-point proportionally spaced font or a 10-character-per-inch uniformly spaced font. A technical editor will contact you if any questions arise during the preparation of your manuscript for typesetting, or if any changes in the figures are required. Proofs and a reprint order form will arrive in 15 weeks or less.