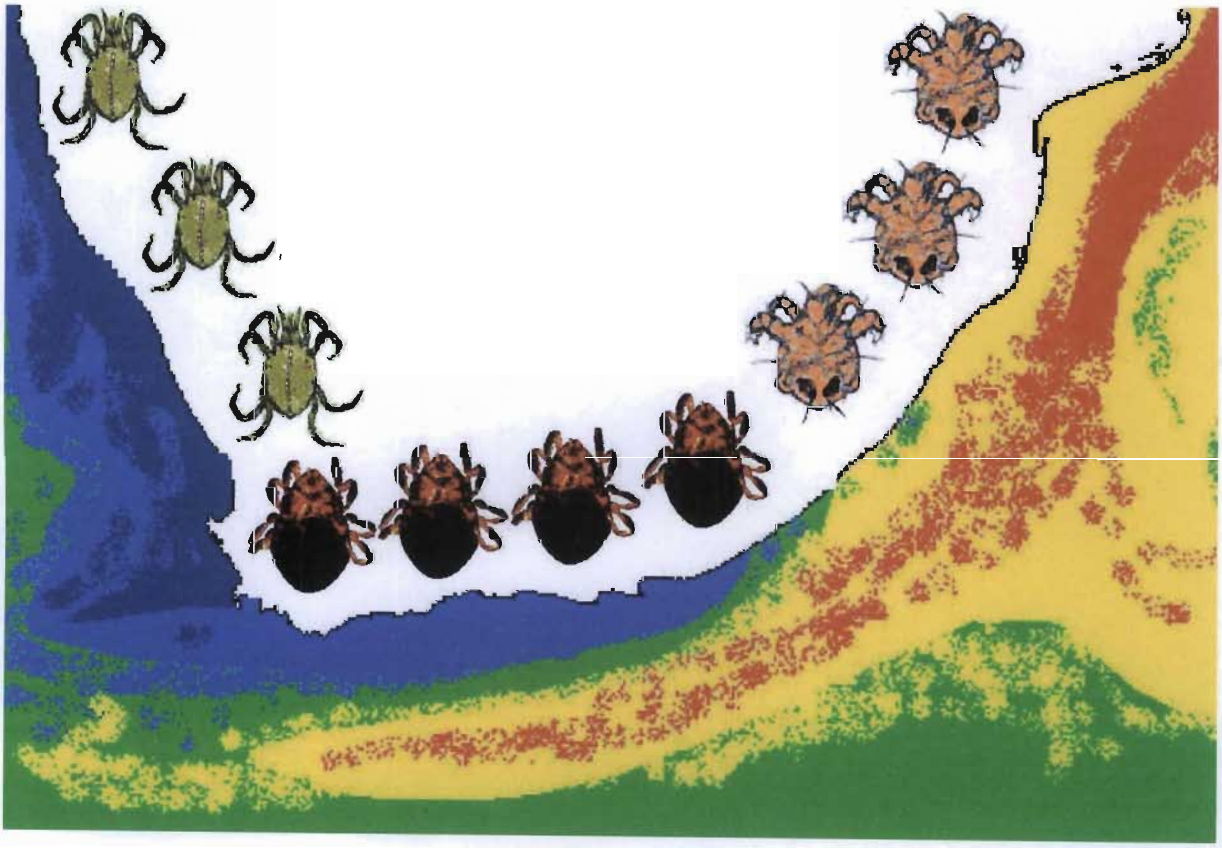
The biogeography and ecology of the secondary marine arthropods of southern Africa

by Şerban Procheş



Submitted in partial fulfillment of the requirements for the degree of
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School of Life and Environmental Sciences
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Promoter: Dr. David J. Marshall

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DECLARATION

The Registrar (Academic)
UNIVERSITY OF DURBAN-WESTVILLE

Dear Sir

I, Mihai Şerban Procheş

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The biogeography and ecology of the secondary marine arthropods of southern Africa

is the result of my own investigation and research and that it has not been submitted in part or full for any other degree or to any other University.

Şerban Procheş

Signature

15 November 2001

Date

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Abstract

Because of their recent terrestrial ancestry, secondary marine organisms usually differ from primary marine organisms in life history and physiological traits. Intuitively, the traits of secondary marine organisms constrain distribution, thus making these organisms interesting subjects for comparative investigation on ecological and biogeographical theory. A primary objective of the studies presented here was to improve our current knowledge and understanding of the generally poorly known secondary marine arthropods (e.g. mites and insects). An additional objective was to outline relationships between ancestry, ecology, and biogeography of small-bodied, benthic marine arthropods.

In establishing a context for the global biogeographical study, the distribution patterns of secondary marine plants and animals were determined by means of a literature survey. These organisms, including mangrove trees and marine tetrapods, form three distinct groupings which relate to northern, tropical and southern latitudinal bands, and, exhibit bimodal species richness in each hemisphere. The exact same patterns were resolved for non-halacarid marine mites and are thought to have arisen from the effects of elevated tropical speciation and high latitude glaciation. Whereas the typically marine Halacaridae show a high degree of radiation in sub-tidal habitats, global distribution patterns and species to genus ratios indicate that the intertidally-restricted Ameronothroidea (Oribatida) and Hyadesiidae (Astigmata), have had long marine associations relative to other non-halcarid mites (Mestostigmata and Prostigmata). The marine mite fauna of southern Africa clusters into three geographical provinces, and the species richness of rocky shore mites peaks in the southern, warm temperate province. In being consistent with the trend for the region's marine fauna in general, the mite biogeography highlights the generality of this faunistic trend, with respect to taxonomic resolution and taxonomic diversity.

Ecological studies focussing on mangrove pneumatophores show that they support a characteristic suite of arthropods (mites, copepods, tanaids, insect larvae), which differs from that of the benthic sediment. Pneumatophore assemblages comprise similar numbers of primary and secondary marine species, although the former group is more abundant by one order of magnitude. Pneumatophore assemblage composition varies between mangrove forests, predominantly in relation to salinity variation. Within mangrove forests differences arise through differential wetting frequency and variable sunlight intensity. Desiccation-limited algal growth and sediment deposition determine the vertical zonation of arthropods along the pneumatophore length, with secondary marine species typically occurring at lower elevations, and primary marine species at higher elevations. The levels of similarity in the composition of arthropod assemblages decreases with spatial scale, the largest differences occurring between estuarine systems.

Despite their recent terrestrial origins, secondary marine arthropods show a high degree of integration into marine ecosystems, and should be consistently considered in marine ecological and biogeographical studies.

Key Terms: Acari, ecological transitions, intertidal, mangroves, mites, southern Africa

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Publications

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Procheş Ş, Marshall DJ. 2001. Diversity and biogeography of southern African marine Acari. *Journal of Biogeography*, submitted.

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Chapter I

Introduction

Primary and secondary marine organisms

The two realms making up the Earth's biosphere, terrestrial and marine, are so different that in many ways meaningful ecological comparisons between them are not yet possible. Rough quantitative comparisons of productivity, species richness, and other simple ecological indicators are available, however, integrating the information about the underlying processes often proves difficult (May, 1992, 1994; Angel, 1994; Briggs, 1994; Gray 1997). Despite these differences, animals and plants have crossed the land/sea barrier repeatedly. While the entire variety of terrestrial life, as seen today, originated, at some point, in the sea (for reviews, see Little, 1983; 1990), few marine organisms have a terrestrial ancestry (Vermeij & Dudley, 2000). The organisms arising from land-to-sea transitions, are the focus of this thesis, and will further be referred to as secondary marine (as opposed to primary marine organisms which have spent their entire evolutionary history in the marine environment). The diversity of secondary marine life is briefly reviewed below.

Among the angiosperms, there are two distinct growth forms associated with marine habitats: the mangrove trees and sea grasses. Tree species from at least fifteen families are strictly limited to coastal waters, and are described under the common name of mangroves (Tomlinson 1987). Although extremely heterogeneous, these trees are characterized by three common adaptations, attained to various degrees in different taxonomic groups: viviparity, breathing roots, and resistance to high salinity. Sea grasses, resembling algae in many superficial ways, represent at least three different invasions of the sea by basal monocots (Les & Cleland, 1997).

No recent species of moss, fern, or gymnosperm can be considered truly marine. Defining secondary marine groups in higher algae and unicellular organisms is rather problematic, because little is known about their transitions between terrestrial, freshwater and marine environments. Among the fungi, at least two secondary invasions of the sea have been documented for the Ascomycota (see Spatafora et al., 1998), and numerous other groups, including lichens, are generally accepted to be only secondarily marine.

Among the vertebrates, the reptiles have had a long history of past associations with the sea. When considering recent taxa, however, marine reptiles are scarce. There is only one, apparently monophyletic group of marine chelonians (Schaffer et al., 1997), one species of sea crocodile, two distinct groups of sea snakes (Keogh, 1998), and one species of truly marine lizard (see Rassman, 1997). Best known among secondary marine organisms are the seabirds, where adaptations to marine life appeared on numerous occasions (at least once each in Sphenisciformes, Procellariiformes, Pelecaniformes and Lariformes; see Cracraft, 1981), and the mammals, with four distinct recent marine groups (Sirenia, Cetacea, Pinnipedia, and the genus *Enhydra* in Fissipedia; see Reeves et al., 1992).

Secondary marine arthropods

Arthropods, like all animal phyla, originated in the sea. One of the major arthropod groups, the Crustacea, has been predominantly marine throughout its evolutionary history. Two other groups, which are largely terrestrial, re-colonized the marine environment to various extents, in multiple invasions: these are the Acari (mites) and the Hexapoda (springtails and insects).

Numerous families of mesostigmatid, prostigmatid, oribatid and astigmatid mites have marine representation. However, most of the marine mites are strictly intertidal, with only one family, the Halacaridae (Prostigmata), extending into subtidal habitats. Halacarid mites represent more than half the total diversity of marine mites worldwide. Bartsch (1989) indicates a total of 700 species described to date, while Otto (2000a; that is, only eleven years later) suggests this figure might have already reached 1000. Two weeks of collections in tiny Rottnest Island off the coast of Western Australia yielded 80 species (Otto, 1999), while extensive collections in the Great Barrier Reef returned almost 300 (Otto, personal communication). Habitat specialization in halacarid mites is obvious at genus level. Some genera, such as *Acarochelopodia* and *Actacarus* are interstitial, inhabiting sandy deposits (Otto 2000b), while others, like *Agauopsis* (Bartsch, 1986) are characteristic for rocky shores. Still others, like *Bathyhalacarus*, inhabit the ocean floor thousands of meters below sea level (Bartsch, 1982), making the Halacaridae the only secondary marine organisms that complete their life cycle on the ocean floor. This makes halacarid mites ecologically closer to primary marine organisms, and it can be explained only by considering their long evolutionary history in the marine environment (see Bartsch 1996).

The degree of adaptation to the marine environment varies less amongst hexapods, with most species being intertidal, and this applies to both collembolans and insects. Only one group of insects, the water-skaters, has adapted to an entirely marine existence on ocean surfaces, and certain parasitic insects can be found in the open sea, together with their hosts.

All marine Colembola are intertidal air-breathers. Invasions of the marine environment happened independently in five families from two orders: Isotomidae, Entomobryidae (Entomobryomorpha) Hypogastruridae, Onychiuridae and Neanuridae (Poduromorpha) (see Greenslade, 1986; Christiansen & Bellinger, 1988; Greenslade & van Klinken, 1994).

Numerous insects (Diptera: Canacidae, Ceratopogonidae, Chironomidae, Coelopidae, Culicidae, Dolichopodidae, Ephydridae, Tipulidae, Trichoptera: Chathamiidae) live in intertidal environments as aquatic larvae, but lead a supralittoral, air-breathing existence as adults. The Canacidae, Coelopidae and Chathamiidae are predominantly marine, as are a few genera in Ceratopogonidae and Chironomidae (midges) (Morley & Ring 1972; Cheng, 1976; Neumann, 1976; Kronberg, 1988; Cheng & Frank, 1993). Midge larval and pupal development is well correlated with tidal rhythms (Neumann, 1976; Robles, 1984; Saigusa & Akiyama, 1995). Two weevil genera, *Bothrometopus* and *Palirhoeus* (Coleoptera: Curculionidae), live (both as adults and larvae) in the supralittoral and intertidal zones of sub-Antarctic islands, heavily exposed to salt spray (Chown & van Drimmelen, 1992). Other groups of insects (Coleoptera: Dytiscidae, Gyrinidae, Dryopidae, and Heteroptera: Corixidae) are known to tolerate brackish and even salt water, but typically live in freshwater.

In water-skaters (Heteroptera: Gerridae, Veliidae, Hermatobatidae), all life stages live on the sea surface (mostly in sheltered mangrove habitats, but in some cases on coral reefs, and even in the open ocean; see Cheng, 1985). This group has radiated extensively in marine habitats; around 170 species are known, most of them in the Indo-Pacific region (Andersen, 1999). However, no known insect spends its entire existence submerged in seawater, reproduction happening most often above the water surface. Even seal lice (from the orders Mallophaga and Anoplura), although staying submerged for entire seasons, only reproduce when their mammalian hosts are on land (Cheng & Frank, 1993).

Present state of knowledge for southern Africa

Our knowledge of the southern African secondary marine arthropods is largely based on taxonomic descriptions and species lists. Recently, numerous mite species have been described, a few of them in papers included in this thesis. Four species of marine spider are known from the region (Lamoral, 1968). Although a single species of collembolan (*Anurida maritima*) is mentioned from the rocky shores of southern Africa (Branch & Branch, 1981), numerous other species have been observed and collected.

Numerous insect families have been reported from sandy beaches (Dermaptera: Labiduridae, Orthoptera: Stenopelmatidae, Coleoptera: Cicindelidae), stranded kelp

(Coleoptera: Carabidae, Cicindellidae, Tenebrionidae, Diptera: Chironomidae, Anthomyiidae), and brackish estuarine waters (Heteroptera: Saldidae, Corixidae, Coleoptera: Dytiscidae, Hydraenidae, Staphilinidae, Heterroceridae, Trichoptera: Ecnomidae, Diptera: Ephydridae) (Hesse, 1934; Branch & Grindley, 1979; Stenton-Dozey & Griffiths, 1980; Branch & Branch, 1981; Scholtz & Holm, 1985; Rebelo, 1987). On rocky shores, several taxa (Coleoptera: Staphilinidae, Diptera: Chironomidae) have been found living in conditions of temporary or permanent submersion (Hesse, 1934; Scholtz & Holm, 1985). One species of water strider (*Halobates micans*) has been recorded along the eastern coast of southern Africa (Scholtz & Holm, 1985). It is however worth noting, that many of the taxa listed above are not normally considered as marine (Cheng, 1976).

Previous to the current series of investigations, there has been a dearth of information concerning the ecology and biogeography of secondary marine arthropods in general. The objectives of this thesis were to 1) describe distribution patterns of secondary marine arthropods at global, regional (southern Africa) and local scale, and 2) conduct ecological investigations comparing primary and secondary marine organisms in terms of abundance, species richness, temporal dynamics, and interactions with biotic and abiotic factors.

Thesis outline

While the studies presented here address the biogeography and ecology of secondary marine organisms, with a focus on arthropods and on southern Africa, the scope extends to global geographical patterns of secondary marine organisms in general. The thesis contains two sections. The first section (chapters II - IV) concerns the biogeography of secondary marine organisms, while the second section (chapters V- IX) concentrates on community and spatial ecology of mangrove pneumatophore arthropods.

Chapter II refers to secondary marine organisms in general, excluding arthropods. However its inclusion in the thesis was considered to be beneficial in 1) supplementing the introduction with information about secondary marine life forms; and 2) offering global distribution patterns from groups of secondary marine organisms that, unlike arthropods, have been extensively studied. Chapter III considers the global distribution patterns of non-halacarid intertidal mites. Taxonomic and geographical patterns are reviewed, in order to assess the evolutionary age in the marine environment for various groups. The diversity and distribution patterns of marine intertidal Acari in southern Africa are described in Chapter IV, and compared to global patterns (as presented in chapter III), and to other animal groups.

Chapter V analyses previously undescribed communities of mesoarthropods from mangrove pneumatophores, in order to assess the comparative representation of primary and secondary marine species. Chapter VI compares the vertical distribution of these two groups, and considers the associations existing within and between them, to decide whether the evolutionary history of species has any effect on resistance to physical stress (e.g. desiccation), or on the strength of biotic interactions. Chapter VII considers small-scale distribution and abundance patterns of pneumatophore arthropods in relation to the algal covering of the pneumatophores and the sediment trapped within it, and monitors temporal changes on defaunated pneumatophores. In Chapter VIII, a nested sampling design is used to assess variation in ecological parameters (assemblage composition, species richness and abundance) of pneumatophore arthropods, across a variety of scales (between 10 cm and 100 km).

All chapters (except for I, VIII and IX) have been structured and prepared independently for journal publication. Some are published, others in press, and others still, are submitted. Given this structure, there is inevitable repetition of information, and this applies especially to the Introduction and Methods sections of the chapters. Furthermore, the study was not undertaken in the same order as that given for the thesis chapters. This means that some chapters occurring later in the thesis may not always refer to earlier stated information. Finally, as the papers for publication were not altered when compiling the thesis, there is no cross-referencing between chapters. For purpose of cross-referencing, and to place the study in the context of the sequence in which it was undertaken, this sequence is given below: 1) Chapter III (Global distribution patterns of non-halacarid marine intertidal mites: implications for their origins in marine habitats), 2) Chapter V (Mangrove pneumatophore arthropod assemblages and seasonality patterns), 3) Chapter II (Back to the sea: secondary marine organisms from a biogeographical perspective.), 4) Chapter VI (Patterns of distribution, abundance and interactions among primary and secondary marine arthropods cohabiting mangrove pneumatophores), 5) Chapter VII (Algal growth and sediment deposition as determinants of distribution and abundance in mangrove pneumatophore arthropods).

Two further papers, written earlier than the rest of the thesis, were included as an appendix, and represent the descriptions of four new species of halacarid mite from the southern African coast. Among these, *Halacaropsis praecognita* (Appendix: Part I) is a rocky shore species, and appears in the biogeographical analyses in Chapter IV, while *Acarothrix umgenica* and *Copidognathus caloglossae* (Appendix: Part II) are mangrove species, and their ecology is investigated in Chapters V-VIII.

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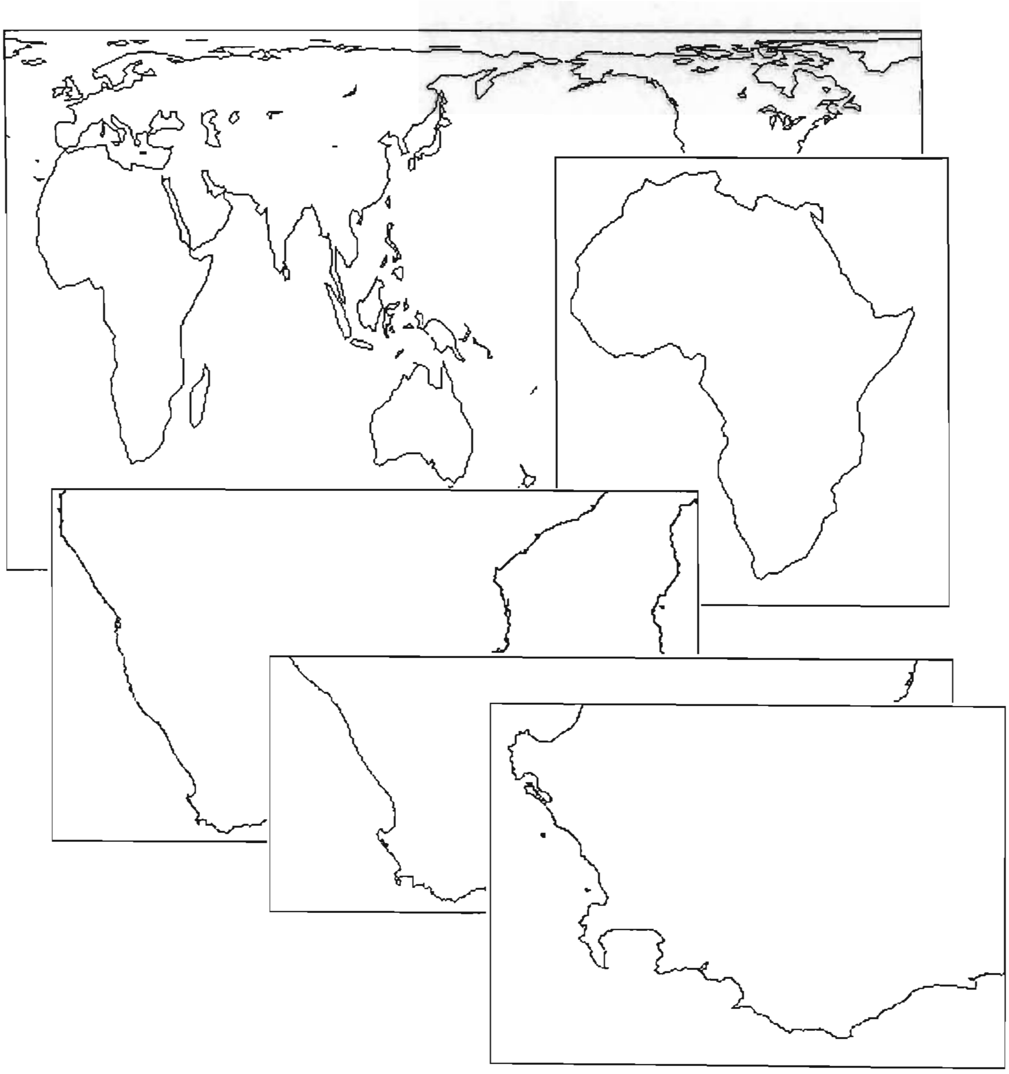
Section I

Biogeography



Chapter II

Back to the sea: secondary marine organisms from a biogeographical perspective

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Abstract

Secondary marine organisms belong to groups of terrestrial ancestry which have recolonized marine habitats. Some of them are, to various degrees, still dependent on the terrestrial habitat where they originated, which imposes certain limits in the expansion of their distribution range. This makes them an ideal subject for historical reconstruction. Here I perform biogeographical analyses on the global distribution of twelve groups of land-dependent secondary marine plants and animals (mangrove trees, sea turtles, sea snakes, seabirds and seals). When all groups are taken together, species diversity shows a unique bimodal pattern for each hemisphere, with high values in cold-temperate and tropical regions, but low values in mid-latitude regions. None of the individual groups considered reaches its highest species concentration in mid-latitude regions. This is shown to be due to the existence of three different species assemblages, inhabiting the three species-rich latitudinal bands (northern cold-temperate, tropical, and southern cold-temperate), and intermixing to a limited degree in the species-poor mid-latitude bands. This is evidence that secondary marine organisms diversified independently in cold-temperate and tropical regions, and strongly suggests that colonization from terrestrial habitats took place independently in the three species-rich latitudinal bands. Different constraints in the terrestrial habitat of origin are put forward as evolutionary incentives for colonizing the sea: glaciation processes in cold regions and competition in tropical regions.

Introduction

The distinction between terrestrial and marine ecosystems is the most prominent dichotomy in the living world. Essentially, each of these types of ecosystems represents a no-go area for the vast majority of the other one's inhabitants (Little, 1983; 1990). There are, however, numerous groups of organisms originating in terrestrial habitats, which have recolonized the marine environment (for a review, see Vermeij & Dudley, 2000). These are known as secondary (or secondarily) marine organisms. The degree to which they became independent of terrestrial habitats varies. Some (such as mangrove trees, and most marine mite and insect species) are restricted to the littoral fringe. Others (sea turtles, seabirds and seals) are mainly marine, but need to come to the shore during the reproductive season. Finally, others (sea grasses, true sea snakes, dolphins and whales) became completely land-independent, and live in either shallow coastal waters or even deep oceanic waters.

In explaining why such transitions took place, it is worth noting that the oceans represent an enormous potential of space, matter and energy. Transfer of matter and energy from marine to terrestrial ecosystems has been documented (e.g. Polis & Hurd, 1996), and entire sea-dependent terrestrial communities are known (see Heatwole, 1971). However marine resources are normally inaccessible to terrestrial organisms, which cannot withstand long submersion periods, and can also be affected by high salinity values. To withstand these, dramatic anatomical and physiological changes are necessary, and the incentive of copious food resources may not provide sufficient selective pressure to this effect. More likely, restrictive conditions in the environment of origin are responsible for these changes.

There is little information on the ecological factors that originally caused marine organisms to invade land. It is known however that present-day marine organisms inhabiting the upper littoral level of rocky shores are forced into this harsh habitat by competition (Connell, 1961) and/ or predators (Seed, 1969). What caused terrestrial life forms to go back to the sea should be easier to understand, given the fact that some major invasions of the sea by terrestrial biota happened relatively recently, and in taxonomic groups we are more familiar with.

Historical factors are essential in explaining distribution patterns in marine environments (Crame, 1993, 2000). One may therefore assume that, in certain groups of secondary marine organisms, present-day biogeographical patterns can be meaningful in indicating the habitat where the land-to-sea transition originally took place. The most obvious candidates were those organisms, which are linked to terrestrial habitats by particular stages in their life history, as they are constrained in expanding their distribution range by both terrestrial (reproduction- and attachment-related), and marine (mainly feeding- and dispersal-related) factors. The present investigation into the biogeography of these organisms will hopefully provide useful insights into the ecological background accounting for recolonization of the marine environment, as well as into subsequent taxonomic diversification within secondary marine groups.

Material and Methods

Twelve groups which are assumed to have independently colonized the marine environment and subsequently diversified within it were considered (see Table 1); biogeographical information for other groups is rather incomplete. The marine representatives in each of these groups are currently thought to have resulted from the diversification of one single land-to-sea transition, with the possible exception of the Combretaceae (Tomlinson, 1983) and Laridae (which apparently are relatively recent colonizers from freshwater habitats – see Warheit, 1992).

To assess the species richness of each group, and for all considered groups taken together, in various parts of the world, the world map was divided into 15 X 15 degrees of latitude/longitude squares (288 squares in all – see Fig. 1). The area north of 30° N was defined as northern; that between 30° N-30° S as tropical, and that south of 30° S, as southern. A special attention was paid to the bands comprised between 30°-45° in each hemisphere, further referred to as mid-latitude regions. The species from each group, currently breeding in each square were counted, following a literature survey (see references in Table 1).

This resulted in a square-group matrix. To define world centres of secondary marine diversity, the squares were arranged in decreasing order of total species number, and the one hundred most speciose squares were mapped. To define any differences among faunas of various world regions, this matrix (untransformed data) was used to calculate Euclidian distances between the squares, and the results were plotted as an MDS (see Legendre, 1990; Clarke, 1993). Only the 100 most speciose squares were used in this analysis, in order to point out the richest species assemblages, and also to avoid overcrowding the plot. For this, I used the SPSS (ver. 9.0) package for Windows.

To see where (in terms of latitude) each group reaches higher/ lower concentrations, the mean number of species per square was calculated for each of the twelve latitudinal belts.

Table 1. Groups of secondary marine organisms. All genera considered in the study include at least one sea-dependent species. Asterisks mark: *genera with a few localized species living in terrestrial or freshwater habitats; ** genera with widespread species living in terrestrial or freshwater habitats. Sources: Tomlinson, 1986; Woodroffe & Grindrod, 1991; Ricklefs & Latham, 1993 (mangrove trees), Cogger, 1975; Halliday & Adler, 1986; Dauner, 1988; Matz & Weber, 1988; Capula 1990; Castroviejo et al., 1994; Keogh, 1998 (marine reptiles), Tuck & Heinzel, 1979; Harrison, 1987; Howard & Moore, 1994 (seabirds), King, 1983; Reeves et al., 1992; Novak, 1994 (seals).

Groups	Marine species	Genera considered in the study
Mangrove trees		
Combretaceae	3	*Laguncularia, Lumnitzera*
Sonneratiaceae	5	*Sonneratia*
Rhizophoraceae	17	*Bruguiera, Ceriops, Kandelia, Rhizophora*
Avicenniaceae	8	*Avicennia*
Marine reptiles		
Chelonia	7	*Caretta, Chelonia, Dermochelys, Eretmochelys, Natator*
Laticaudinae	4	*Laticauda**
Seabirds		
Sphenisciformes	18	*Aptenodytes, Eudyptes, Eudyptula,, Megadyptes, Pygoscelis, Spheniscus*
Procellariiformes	108	*Bulweria, Calonectris, Daption, Diomedea, Fregetta, Fulmarus, Garrodia, Halobaena, Halocyptena, Hydrobates, Loomelania, Macronectes, Nesofregetta, Oceanites, Oceanodroma, Pachyptila, Pagodroma, Pelagodroma, Pelecanoides, Phoebetria, Procellaria, Pseudobulweria, Pterodroma, Puffinus, Thalassoica*
Pelecaniformes	47	*Fregatta, Morus, Nannopterum, Papasula, Pelecanus**, Phaeton Phalacrocorax**, Sula.*

Table 1. (continued).

Laridae	58	*Anous, Catharacta, Creagrus, Gabianus, Gygis, Larosterna, Larus**, Pagophila, Procelsterna, Rhodostethia, Rissa, Sterna**, Stercorarius, Thalasseus, Xema*
Alcidae	22	*Aethia, Alca, Alle, Brachyramphus, Cepphus, Cerorhinca, Cyclorrhynchus, Fratercula, Lunda, Ptychoramphus, Synthliboramphus*
Seals		
Pinnipedia	32	*Arctocephalus, Callorhinus, Cystophora, Erignathus, Eumetopias, Halichoerus, Hydrurga, Leptonychotes, Lobodon, Mirounga, Monachus, Neophoca, Odobenus, Ommatophoca, Otaria, Phoca*, Phocarctos, Zalophus*

Results

Regional and latitudinal patterns of distribution for secondary marine organisms in general

Higher levels of diversity in secondary marine organisms were found to occur in the tropical and southern regions, with a lower diversity in the northern regions (Figure 1). In the tropics, there were two major diversity centers: a very extensive one in the Indo-West Pacific, and a smaller one in tropical America. The southern regions showed no clear pattern of high diversity centers, rather, all sub-Antarctic locations had a relatively high diversity (Figure 1).

Largely glaciated latitudes (75°-90°N and 60°-90°S) had impoverished faunas. The other latitudinal bands, showed a clear tendency towards a bimodal distribution of the high diversity squares for each hemisphere. Species richness was high in northern (45°-75°), tropical (30°-30°) and southern regions (45°-60°), but low the mid-latitude regions (30°-45° in each hemisphere). Only three squares in the northern mid-latitude band were counted among the top one hundred most diverse, despite the fact that neighbouring bands, both to the north and to the south had higher values. In a similar way, eight squares in the southern mid-latitude band had top diversity values, with more squares in both neighbouring bands (Figure 1).

Northern, southern and tropical bands had markedly different faunas, which clustered on the MDS as three different directions. The most distinct regions from the three categories were the Behring Sea (northern), Indo-Malesia (tropical), and New Zealand and the sub-Antarctic islands (southern), corresponding to the largest agglomerations of high diversity squares. The faunas locally intermixed, especially in mid-latitude areas, these having the least differentiated faunas, and were grouped in the central part of the MDS (Figure 2).

Latitudinal patterns of individual secondary marine groups

Out of the twelve groups examined, six (Combretaceae, Rhizophoraceae, Sonneratiaceae, Avicenniaceae, Chelonia and Laticaudidae) were typically tropical, one (Alcidae) typically northern, one (Sphenisciformes) typically southern, and four (Procellariiformes, Pelecaniformes, Laridae and Pinnipedia) cosmopolitan. Among the cosmopolitan groups, two (Pelecaniformes and Laridae) reached top species diversity in tropical regions, one (Procellariiformes) in southern regions and one (Pinnipedia) in both northern and southern regions. No group of secondary marine organisms is best represented in mid-latitude regions of each hemisphere (30°-45°) (Figure 3).

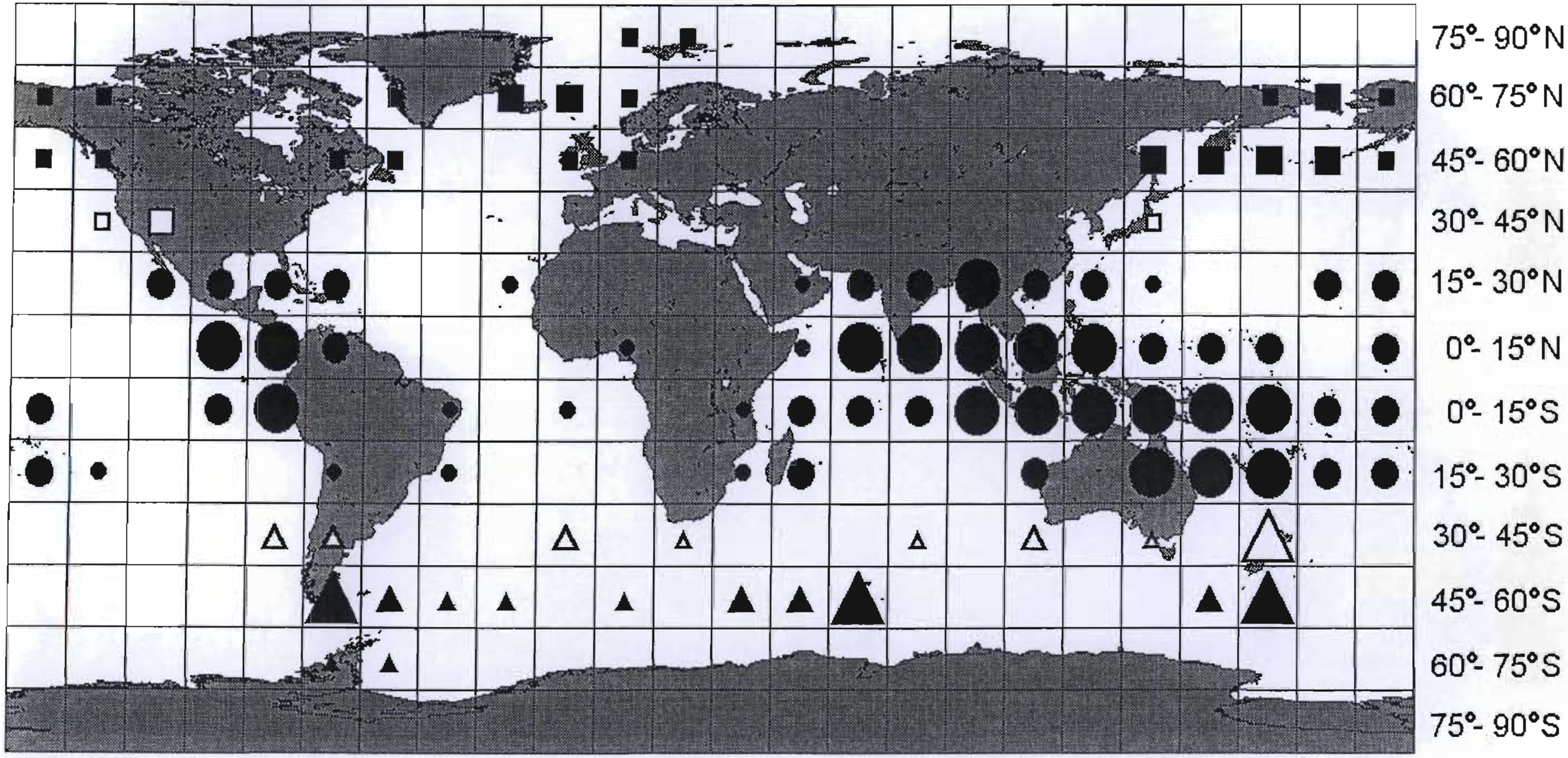

Figure 1. Areas of high diversity for selected groups (see Table 1) of secondary marine organisms. Symbols: squares, northern; circles, tropical; triangles, southern. Open symbols mark mid-latitude regions. The size of the symbols is roughly proportional to the number of species within the squares (large symbols, more than 30; medium symbols, 20-29; small symbols, 12-19 species).

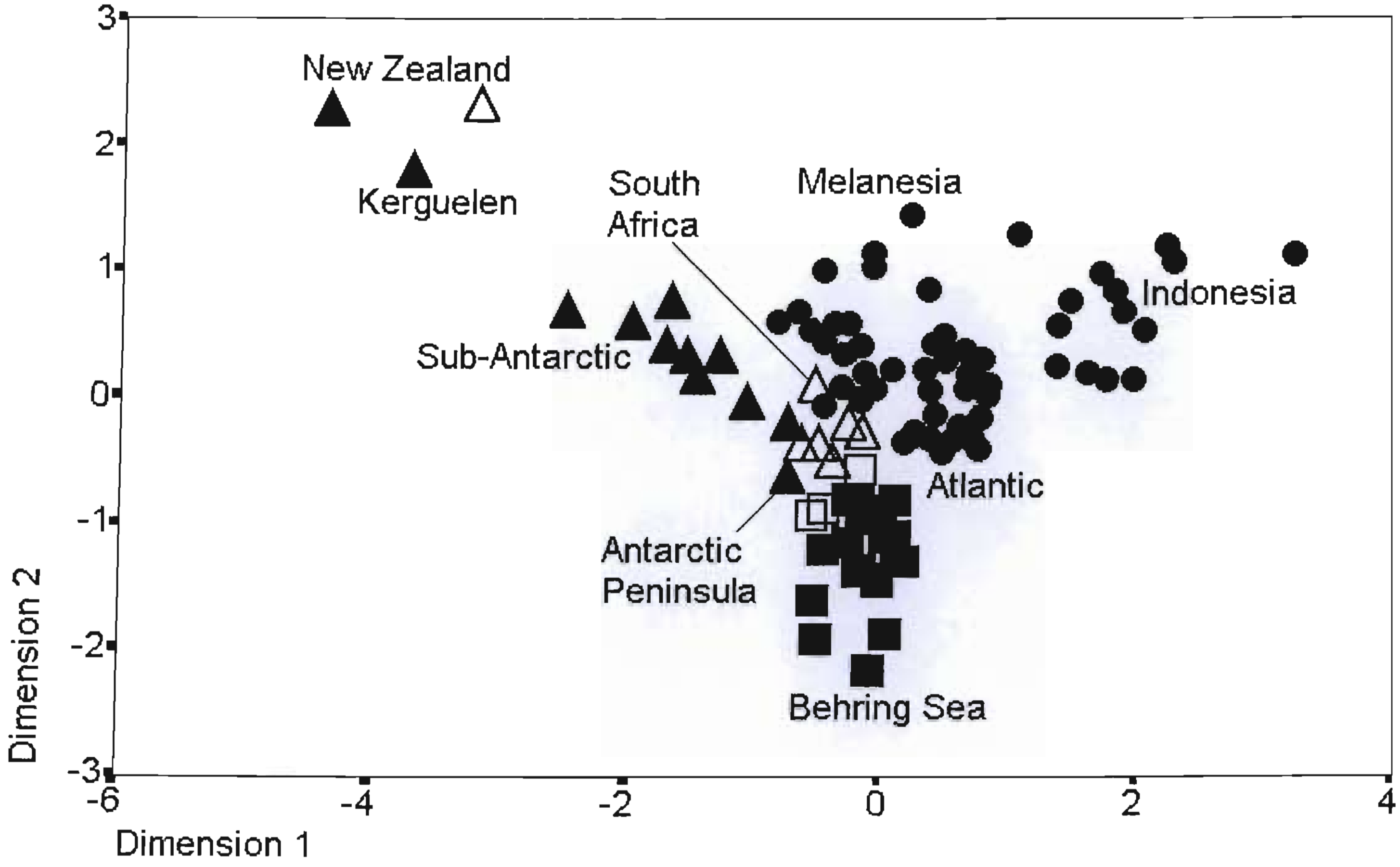

Figure 2. MDS plot for the 100 squares with high species diversity of secondary marine organisms marked in Figure 1. Stress: 0.12

Discussion

Two major patterns emerged from this study: the existence of different assemblages of secondary marine organisms in northern, tropical and southern regions, and bimodal distributions of species richness values in each hemisphere. The existence of distinct northern, tropical and southern species assemblages is by no means unique to secondary marine organisms; in fact this is the most obvious biogeographical pattern in the marine realm (Briggs, 1974, 1995). On the other hand, the existence of three high-diversity latitudinal bands in secondary marine organisms can be considered a major anomaly, and has not been previously reported. Typically, both marine and terrestrial groups show a gradiental decrease in species richness from the equator towards the poles (see Rohde, 1992 and references therein). Although some observations relating to higher marine biodiversity in the southern, as compared to northern, hemisphere have been made (Gray, 1996), and even substantiated for a secondary marine group (Chown et al., 1998; Chown & Gaston, 1999 for Procellariiformes), a decrease in species richness in mid-latitudes has never been reported in any group, whether defined on taxonomic or ecological grounds.

Before trying to explain these patterns in relation to origination in the marine environment, it is important to consider two aspects potentially limiting further interpretation.

Firstly, as these patterns were derived from analyses on a limited number of secondary marine groups, it is questionable to what extent these are representative for the distributions of secondary marine groups in general. The selection of the groups was dictated by both availability and reliability of distribution information, which is only pertinent to organisms with large body sizes, and these may show different patterns to smaller organisms (Gaston & Blackburn, 1996). However, another study (Procheş & Marshall, 2001) shows that the marine ameronothroid mites (Acari: Oribatida) have similarly globally separated faunas and bimodally distributed species numbers in each hemisphere, which indicates that these patterns may be widespread among secondary marine organisms.

Secondly, as the present study included 329 species resulting from twelve land-to-sea transitions, it is worth considering to what extent diversification following a transition leaves room for interpreting present day biogeographical patterns as results of the conditions in which the transition took place. For appreciating this, one needs to have a closer look at the distribution patterns of individual groups (Figure 3). Only four of the twelve groups have a cosmopolitan distribution, indicating range expansions from one latitudinal band to another;

the other groups are clearly centred in one of the bands with high species richness (northern, tropical or southern). While strictly tropical distributions can be interpreted as the result of climatic barriers, the distribution of the auks (Alcidae), limited to the northern hemisphere, and that of the penguins (Sphenisciformes), to the southern hemisphere (although the two groups almost meet on the western American coast), suggest that these are relatively new groups with limited possibilities of expanding their distribution. .In a similar way, among tropical groups, the sea snakes (Laticaudinae) and some groups of mangroves do not span over the entire tropical band, but are limited to parts of it - presumably, those parts where they originated (Figure 3, and references in Table 1).

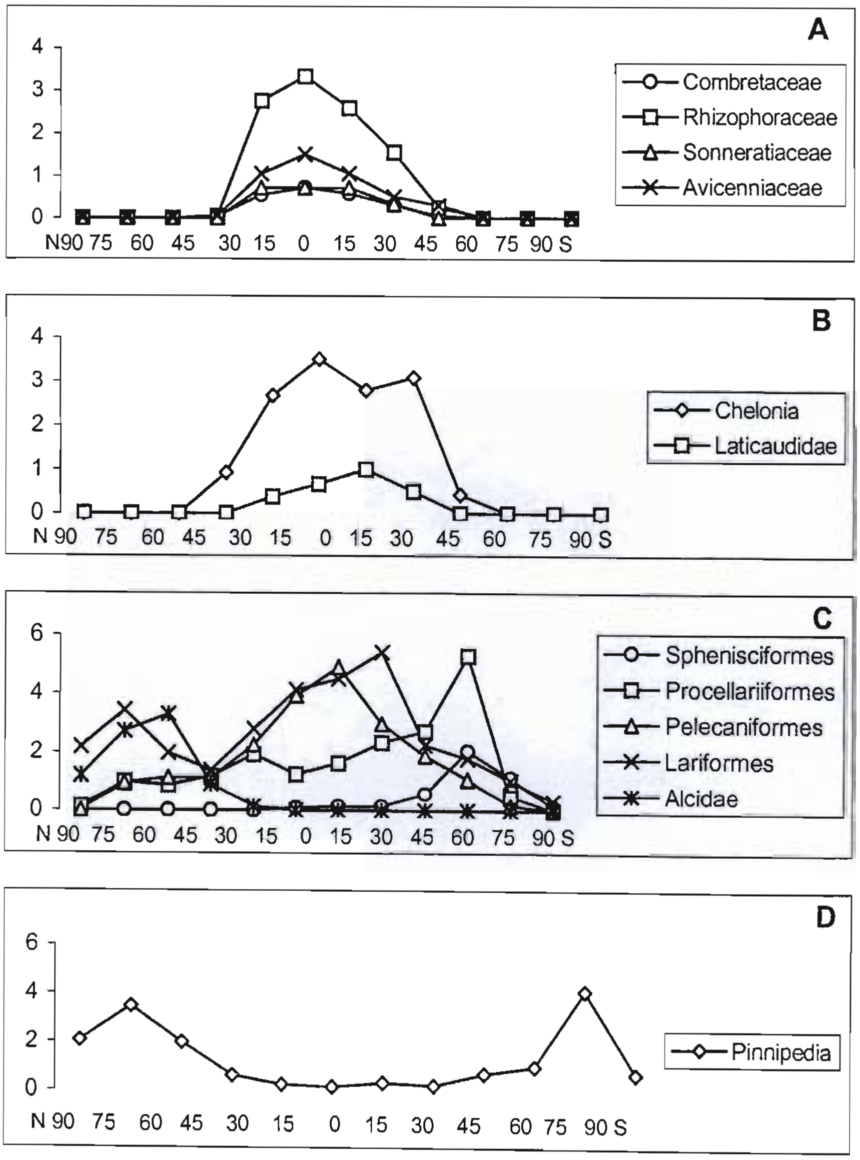

Figure 3. Average species richness for twelve groups of secondary marine organisms in twelve latitudinal bands (see Material and Methods). A, mangrove trees; B, marine reptiles; C, seabirds; D, marine mammals.

Therefore, my original assumption that possibilities of range expansion will be limited in groups of secondary marine organisms with a degree of land dependency is largely supported, and grants further interpretation of the observed patterns.

The high species richness in the tropical band can be explained either according to the theory stipulating higher speciation/ lower extinction rates for tropical regions (see Chown & Gaston, 2000), or by assuming higher rates of origination in the marine environment. The latter would mean that, for some reason, the tropical environment is conducive for land-to-sea transitions. It is generally accepted that biotic factors are essential in structuring complex communities, such as those in the tropics (Grime, 1976, Wilson & Lee, 2000). It would be therefore likely that biotic interactions are responsible for land-to-sea transitions in the tropics. One example supporting this idea is the fact that mangrove trees can occur in freshwater habitats (Woodroffe & Grindrod, 1991), but are generally displaced there by more competitive species.

Explanations for the high diversity bands in the cold-temperate regions of each hemisphere must be based on the assumption that these bands also have high origination rates. According to Grime (1976), communities in extreme environments are mainly structured by physical factors. Glaciation processes have been suggested to represent the most powerful physical factor influencing the natural history of polar regions, both directly, by eliminating species physiologically unable to cope with climatic change, and indirectly, by reducing terrestrial food supply (Crame, 1992, 1993). Climatic changes have been shown to have obvious effects in marine, as compared to terrestrial, environments. For example, it is known that Antarctic terrestrial biota were almost completely eliminated as a result of glaciation processes (but see Marshall & Coetzee, 2000), while marine littoral ecosystems remained fairly species-rich all through the Cenozoic (Clarke & Crame, 1992). Numerous studies suggest that the high species richness of secondary marine invertebrates in intertidal and supralittoral zones of sub-Antarctic islands relates to glaciation processes (Chown, 1990, 1994; Marshall et al., 1999; Mercer et al., 2000).

In summary, I present evidence in support of the independent origination of secondary marine organisms in three latitudinal bands, and suggest that land-to-sea transitions within these bands have been promoted by different factors: biotic interactions, such as competition, in the tropical belt, and physical stress (represented in particular by glaciation processes) in the cold regions.

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Chapter III

Global distribution patterns of non-halacarid marine intertidal mites: implications for their origins in marine habitats

Abstract

Aim We investigated the taxonomic, ecological and global biogeographical trends on non-halacarid marine mites with a view to understanding their origins in the marine environment. While halacarid mites are typicaly marine, numerous other mite taxa occupy littoral habitats, including rocky-shores, boulder beaches, slat marshes and mangrove forest floors, and occur in most geographical regions.

Location This study concerns the extant taxa of non-halacarid marine mite from intertidal zones, worldwide.

Methods A literature survey was undertaken to compile the records for localities and habitats of all the known species of non-halacarid intertidal mite. Simple analyses were used to determine their taxonomic and geographical trends. A multivariate analysis was used to compare how closely the biogeography of selected faunas conformed with the generally accepted marine biogeographical zones.

Results Although the species records are incomplete because of variable sampling intensities among regions, there is clear indication that these faunas are species-poor (only 162 species were recorded in the literature). The records for some groups (ameronothroid and hyadesiid mites), some habitats (rocky-shores) and some world regions (Eastern Atlantic-Boreal, Sub-Antarctic and Southern New Zealand) are apparently representative of the actual faunas, whereas those for the mesostigmatid and non-halacarid prostigmatid mites, and mangrove and salt marsh habitats, are clearly incomplete. The faunas comprise mites from four suborders; mesostigmatid and prostigmatid mites comprise species to genus and species to family ratios, relative to oribatid and astigmatid mites. These mite groups also differ with respect to ecological and geographical attributes; ameronothroid (oribatid) and hyadesiid (astigmatid) mites exibit wider generic geographical distributions and stronger marine trophic links.

Conclusions The emerging trends suggest different geological time-scales for the evolutionary incursions into the marine environment by the mesostigmatid and prostigmatid mite group and the oribatid and hyadesiid mite group. They suggest that members of the latter

have had longer associations with marine intertidal ecosystems. The origins of both groups are also likely to differ of typically marine halacarid mites.

Introduction

Mites have successfully colonized most terrestrial and freshwater habitats on earth, including the deserts and polar regions, but their colonization and radiation in the marine environment has been markedly limited. With the exception of a single family, the Halacaridae (Prostigmata), which shows a high degree of radiation within the marine environment (around 900 known species) and extends subtidally to the ocean depths (Bartsch, 1989; Abe, 1998; for recent biogeographical syntheses), all other mite groups show limited radiation and are restricted to littoral fringes (intertidal and supralittoral zones). This investigation undertakes to characterize these limitations of non-halacarid mites in marine environments by considering taxonomic, biogeographical and ecological patterns.

The restriction of non-halacarid mites to fringe marine habitats suggests that they have not completely transcended the stark ecological barrier between the marine and terrestrial environments. As such they are extremely useful candidates for investigation, offering numerous opportunities into understanding the evolutionary constraints and processes involved in the transition from a terrestrial to a marine existence. However, only a single study considers this subject and its scope is limited to a single mite taxon, the oribatid super-family Ameronothroidea (Weigmann & Schulte, 1977). Numerous investigations have considered other aspects of the ecology of marine mites, specifically concerning community structure, local distribution patterns and feeding behaviour patterns (Luxton, 1964, 1966, 1967a,b; Ganning, 1970; Schulte, Schuster & Schubart, 1975; Schulte 1975, 1976a,b; Schuster, 1979; Sømme & Block, 1984; Pugh & King, 1985a,b, 1988; Bückling, Ernst & Siemer, 1998; Mercer, Chown & Marshall, 2000). Most studies on marine mites, however, deal with their taxonomy.

This study presents a compilation of all known records of non-halacarid marine mite, as accessed from the primary taxonomic literature. In addition to taxonomic data, geographical and ecological data were collated for each record. The emergent taxonomic, geographical and ecological patterns are interpreted within the context of the origination and antiquity of the acarine sub-orders. Our interpretation firstly and most importantly considers the extent to which the records represent actual species numbers and actual faunas.

Materials and Methods

A list of records of non-halacarid mite species was compiled from a literature survey (see Appendix). The habitat (e.g. rocky-shore, mangrove) and geographical region of each record were noted. With respect to vertical position on the shore, we considered only the intertidal species. Species found in the supralittoral zones only were not included in the list as these zones are poorly defined and highly likely to contain numerous "tourists" (see Gaston et al., 1993) from adjacent terrestrial habitats. Species that occur in both the supralittoral and intertidal zones were however included. Where the distinction between these two levels was not made clear in the primary literature, the records were omitted, as were parasitic species (e.g. Halarachnidae). Intermediate taxonomic levels (sub-species, sub-genus) were not taken into account. All reference to marine mites, except where otherwise stated, refers to taxa other than the Halacaridae. Whereas the global biogeographical regions are widely accepted for terrestrial biota, few attempts have been made to derive a similar synthesis for the marine biota. Most marine biogeographical studies focus on regional distributions; the Indo-West Pacific and Antarctic regions in particular have been well studied (for recent examples see Briggs, 1999; Glasby & Alvarez, 1999). Probably the most recognized world biogeography for the littoral and shelf biota is that proposed by Briggs (1974). We used Briggs's scheme in our analyses, but modified this in order to 1) simplify the terminology, 2) remove the sub-regions identified as provinces, and 3) include only the regions from which mites have been recorded. Hong Kong, which falls on the limit between the Indo-West Pacific and Japan regions, was considered part of the Indo-West Pacific. Briggs distinguishes five broad latitudinal, "climatic" zones: northern cold-temperate, northern warm-temperate, tropical, southern warm-temperate and southern cold-temperate. Seventeen regions nested within these zones were found to contain non-halacarid marine mites (see Figure 1).

To assess the degree of conformity of the mite faunas to the global marine biogeographical regions, a multivariate analysis was performed, specifically a multidimensional scaling procedure (MDS). A matrix was established to assess the number of species in each hyadesiid and ameronothroid genus for each biogeographical region. Genera which were recorded from only one region, as well as regions containing a single genus, were excluded from the data set. Euclidean distances among the regions were calculated from untransformed data. The results were plotted in a two-dimension ordination, which included the zero coordinate lines. The data sets closest to the intersection of the coordinates were considered to have the least individualized (common) fauna, while those furthest apart, the most individualized (disparate) fauna. The analysis was performed using SPSS Ver. 9.0 (1999) for Windows.

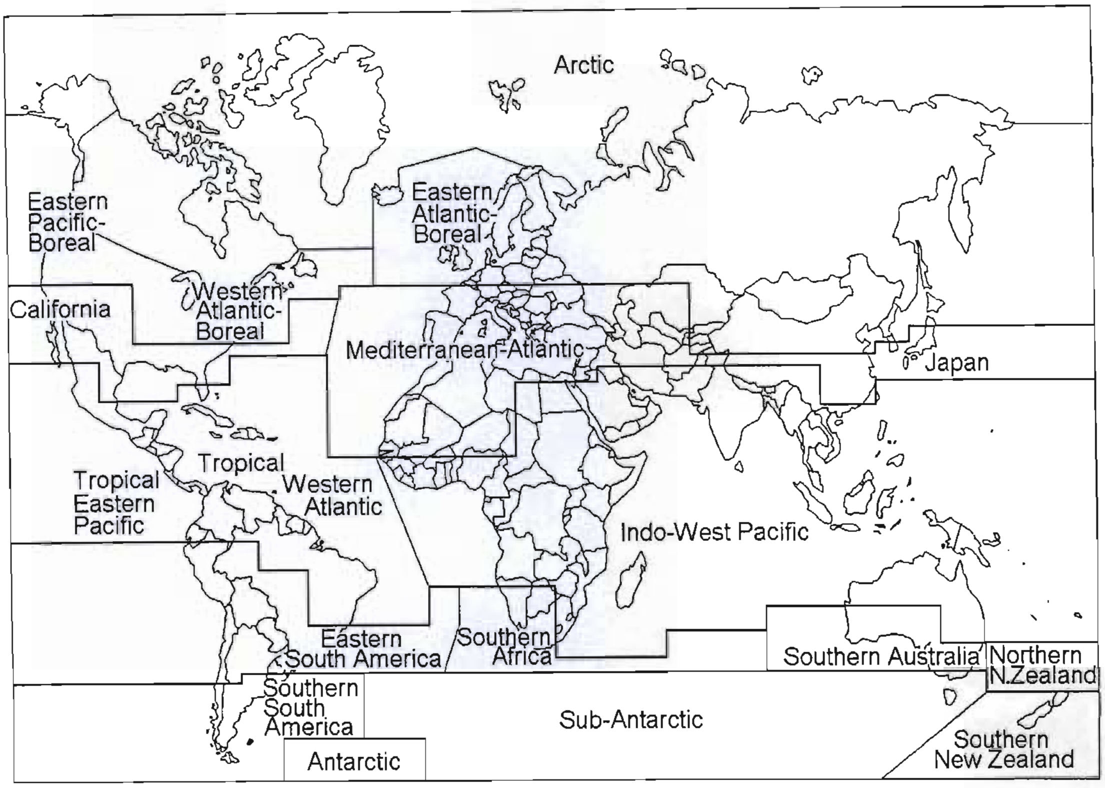

Figure 1. Littoral biogeographical regions of the world (thin line) and climatic zones (thick line) based on those of Briggs (1975). Only the regions in which non-halacarid mites occur are named.

Results

Taxonomic patterns

The species richness of mites living in intertidal habitats worldwide is notably low; only 162 species have been recorded from these habitats. These species are taxonomically partitioned among four mite sub-orders (Mesostigmata, Prostigmata, Oribatida and Astigmata), 21 families and 44 genera. The partitioning of the families and genera within the sub-orders is remarkably skewed. Despite notably more species belonging to the Oribatida and Astigmata than to the Mesostigmata and Prostigmata, the latter two orders comprise more than three times as many families (Table 1, Appendix). More than half of the known marine mite species (57%) belong to two higher taxonomic groups, the Ameronothroidea (Oribatida) (27%) and the Hyadesiidae (Astigmata) (30%). The Ameronothroidea, which contains the families Ameronothridae, Fortuyniidae and Selenoribatidae, comprises 93% of the marine oribatid mite species. The Ameronothridae comprises only two marine genera, with the other thirteen belonging to the latter two families. All of the marine astigmatid mite genera and species belong to the single family, Hyadesiidae (see Appendix).

Ecological patterns

Non-halacarid mites have been collected from intertidal zones of rocky-shores, boulder beaches, salt marshes and mangroves, but not from the intertidal zone of sandy shores. By far the majority of species are found on rocky-shores (and boulder beaches) (91%). In most cases they are specific to rocky-shore habitats, and do not extend distributions to the other intertidal habitats. The Astigmata are only found on rocky-shores and boulder beaches, unlike the other sub-orders, which are represented in all of the above intertidal habitats.

Table 1. Number of species, genera and families for each of the four sub-orders of marine mites and for all marine mites (halacarid mites excluded).

Sub-orders	Lower taxa		
	Species	Genera	Families
Mesostigmata	32	16	9
Prostigmata	37	14	8
Oribatida	45	13	4
Astigmata	48	2	1
All intertidal non-halacarid mites	162	44	21

Geographical patterns

Most non-halacarid intertidal mite species (73%) are contained within only four geographical regions, Indo-West Pacific, East Atlantic-Boreal, Southern New Zealand and Sub-Antarctic. The remaining species (27%) are distributed among fourteen other regions (Table 2). Whereas the cold-temperate and tropical regions are relatively species rich, the warm-temperate regions of both hemispheres are conspicuously species poor (Table 2). Most mesostigmatid and prostigmatid mite genera are restricted to a single geographical region; a few genera, however, are more widely distributed (*Leioseius, Hydrogamasus, Nanorchestes, Microtrombidium*; see Figure 2). In contrast, the major oribatid and astigmatid mite genera are globally widespread (Figures 3 and 4).

The Ameronothroidea is represented in most of the marine littoral geographical regions (Figure 3). The genera of the Ameronothridae are bipolar and to a greater extent are contained within the limits of the cold-temperate zones, whereas the other two families, Fortuyniidae and Selenoribatidae, have mainly tropical to warm-temperate distributions (Figures 1 and 3). The two major marine ameronothrid genera are either strictly Holarctic, as in the case of *Ameronothrus* (assuming that *A. bilineatus* Michael, 1888 recorded from southern Africa, and *A. schneideri* Oudemans, 1903 from Curaçao in the Caribbean are introduced), or largely confined to the Antarctic and Sub-Antarctic regions, as in the case of *Halozetes* (Figure 3).

The astigmatid mite family Hyadesiidae shows a similarly wide distribution to that of the Ameronothroidea (Figure 4). Although there is slight overlap in the latitudinal distribution of the two hyadesiid genera, *Hyadesia* and *Amhyadesia*, there is a tendency for the prevalence of the former in cold-temperate regions, and the latter in the warm-temperate to tropical regions (Figure 4). At the species level, *Amhyadesia heterophallus* Fain & Schuster, 1984 and *Fortuynia elamellata* Luxton, 1967, are particularly widely distributed, extending over most of the Indo-West Pacific region. Extensive specific distributions are also seen in the Northern Hemisphere species, *Ameronothrus nigrofemoratus* Koch, 1879 and *A. lineatus* Thorell, 1871, and in the Antarctic *Halozetes belgicae* (Michael, 1903) and *H. marinus* (Lohmann, 1907) (Table. 3). Levels of generic and specific endemism are difficult to assess given the uncertainty regarding the completeness of the records. However, there is a higher degree of local distribution of species and genera among the Mesostigmata and Prostigmata than among the Oribatida and Astigmata. The ordination of the ameronothroid and hyadesiid mite genera shows three distinct clusters, which approximately coincide with the northern temperate, tropical and southern temperate zones of Briggs (1974; Figure 5). The first cluster comprises the Arctic, Eastern Pacific-Boreal, Western and Eastern Atlantic-Boreal, California and Mediterranean-Atlantic. The second cluster groups the Tropical Eastern Pacific, Tropical Western Atlantic and Indo-West Pacific together with Northern New Zealand, and the third

Table 2. The representation of mite species in the marine biogeographical regions of the world (based on Briggs 1974).

Regions	*Sub-orders*				Total number of species
	Mesostigmata	Prostigmata	Oribatida	Astigmata	
Arctic	-	-	3	-	3
Eastern Pacific-Boreal	-	-	1	2	3
Eastern Atlantic-Boreal	16	13	6	2	37
Western Atlantic-Boreal	-	-	-	2	2
California	-	-	1	2	3
Mediterranean-Atlantic	-	-	6	3	9
Japan	1	-	1	-	2
Tropical Eastern Pacific	-	1	5	1	7
Tropical Western Atlantic	2	1	1	3	7
Indo-West Pacific	6	9	17	9	41
Eastern South America	-	-	2	1	3
Southern Africa	3	1	1	6	11
Northern New Zealand	5	2	2	4	13
Southern South America	-	-	2	1	3
Southern Australia	-	2	-	1	3
Southern New Zealand	9	5	1	5	20
Sub-Antarctic	2	4	6	4	16
Antarctic	4	4	2	3	13

cluster comprises Southern Africa, Southern South America, Southern New Zealand, Sub-Antarctic and Antarctic. The most disparate regions for each of the three climatic zones are East Atlantic-Boreal, Indo-West Pacific and Sub-Antarctic, while the least disparate are Western Atlantic-Boreal, Tropical Western Atlantic and Southern Africa, respectively. The clusters conform with the patterns for the ameronothroid genera, in particular (*Ameronothrus* – northern, Fortuyniidae and Selenoribatidae – tropical, *Halozetes* – southern; Figure 3).

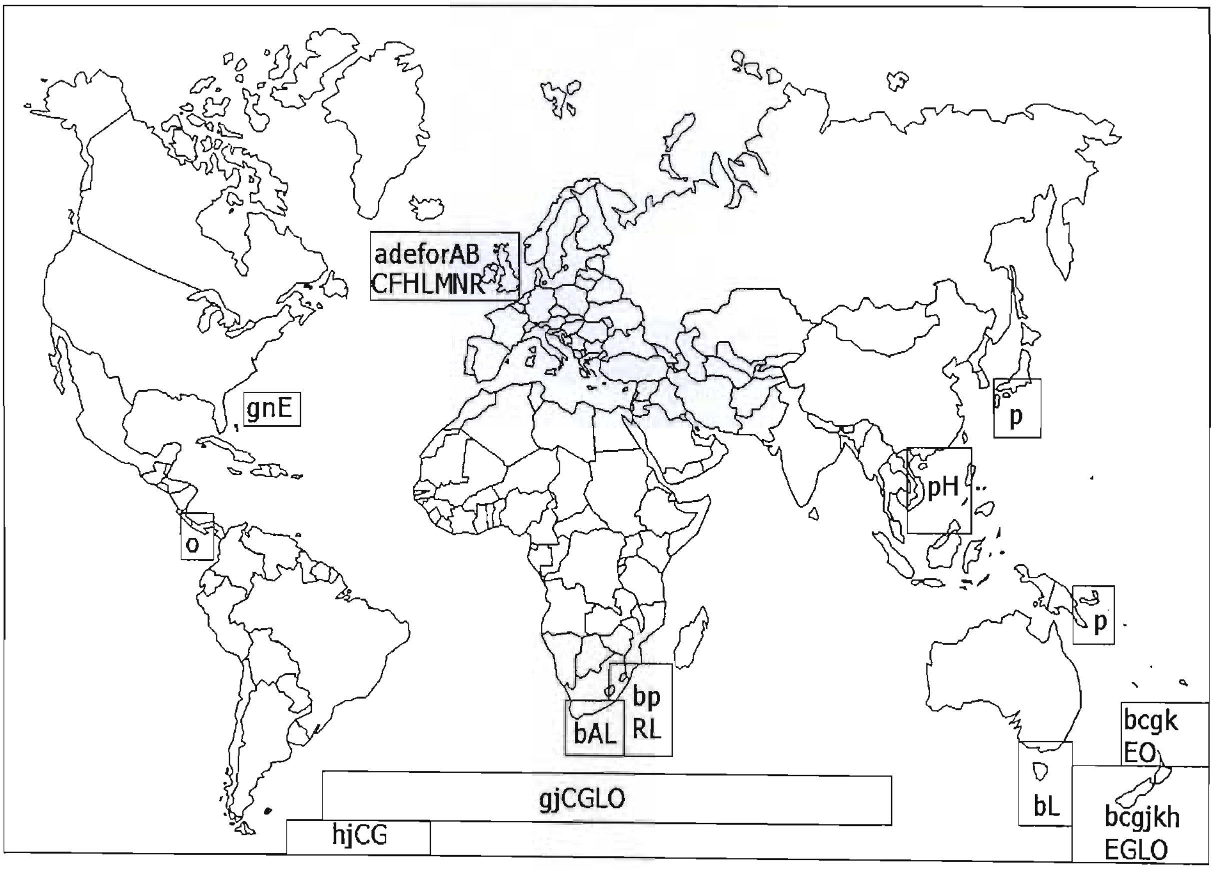

Figure 2. Global distributions of mesostigmatid (lower case) and prostigmatid (upper case) mite genera . Different letters represent different genera, as follows: a, *Arctoseiodes*; b, *Leioseius*; c, *Pontiolaelaps*; d, *Halolaelaps*; e, *Macrocheles*; f, *Parasitus*; g, *Hydrogamasus*; h, *Litogamasus*; j, *Parasitiphis*; k, *Tangaroellus*; l, *Vulgarogamasus*; m, *Thinozercon*; n, *Deraiophorus*; o, *Phaulodinychus*; p, *Uroobovella*; r, *Cyrthydrolaelaps*; A, *Bdella*; B, *Neomolgus*; C, *Ereynetes*; E, *Abrolophus*; F, *Balaustium*; G, *Eupodes*; H, *Halotydeus*; L, *Nanorchestes*; M, *Foveacheles*; N, *Robustocheles*; O, *Microtrombidium*; P, *Platytrombidium* and R, *Lasiotydeus*.

Discussion

Species richness versus species records

Although mites are among the most species-rich taxa, much of their diversification and radiation is restricted to certain habitats, environments, and regions. Whereas soil habitats and tropical rainforests are typically rich in species (see Walter & Behan-Pelletier, 1999), species richness declines considerable in the desert, alpine and polar regions. Speciation and radiation of mites in marine intertidal habitats is markedly constrained, and this is indicated by the relatively few species recorded worldwide (162). Halacarid mites (Prostigmata: Halacaridae) are however the exception. The group comprises relatively many species (around 900) and is ecologically diverse, extending distributions to the ocean depths (for a review of the biogeography of the halacarid mites see Bartsch, 1989).

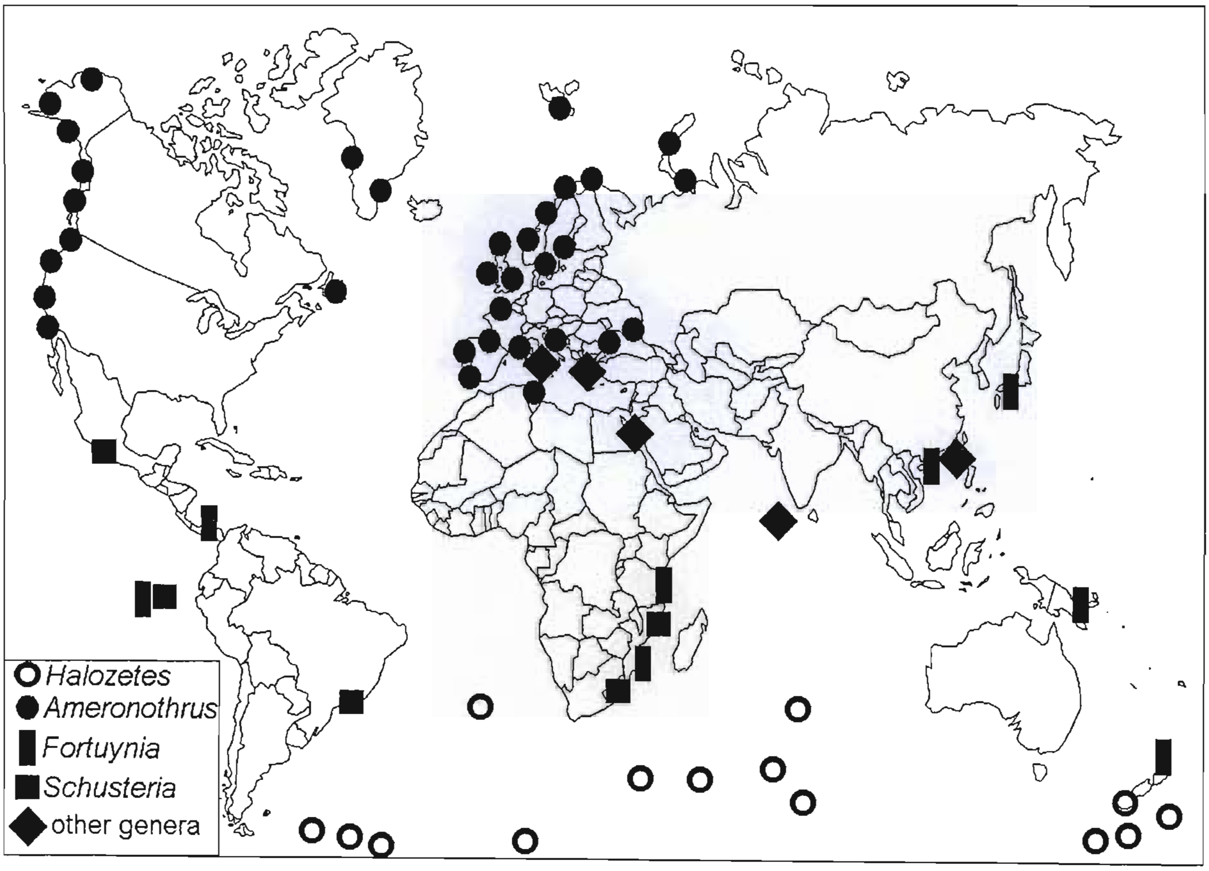

Figure 3. Global distributions of the ameronothroid mite genera.

While the recorded number of species of marine mite is certainly an underestimate of the actual number, the records are seemingly representative of some regions and for some taxonomic groups. For example, the records from the Eastern Atlantic-Boreal, the Sub-Antarctic and Southern New Zealand, which have been extensively studied, probably closely match the actual species number in these regions (Schulte, 1975; Schulte et al., 1975; Pugh & King, 1985; Luxton 1986b, 1992a,b, and also note the number of collection localities in Figs. 2, 3, and 4). Conversely, those records from the northern and southern warm-temperate regions may be an underestimate of the actual species number. These regions may be expected to contain more species than the cold-temperate regions, given the generally accepted inverse relationship between species richness and latitude (Table 2; see Rosenzweig, 1997). However, the observed bimodal relationship of species number against latitude in the southern and

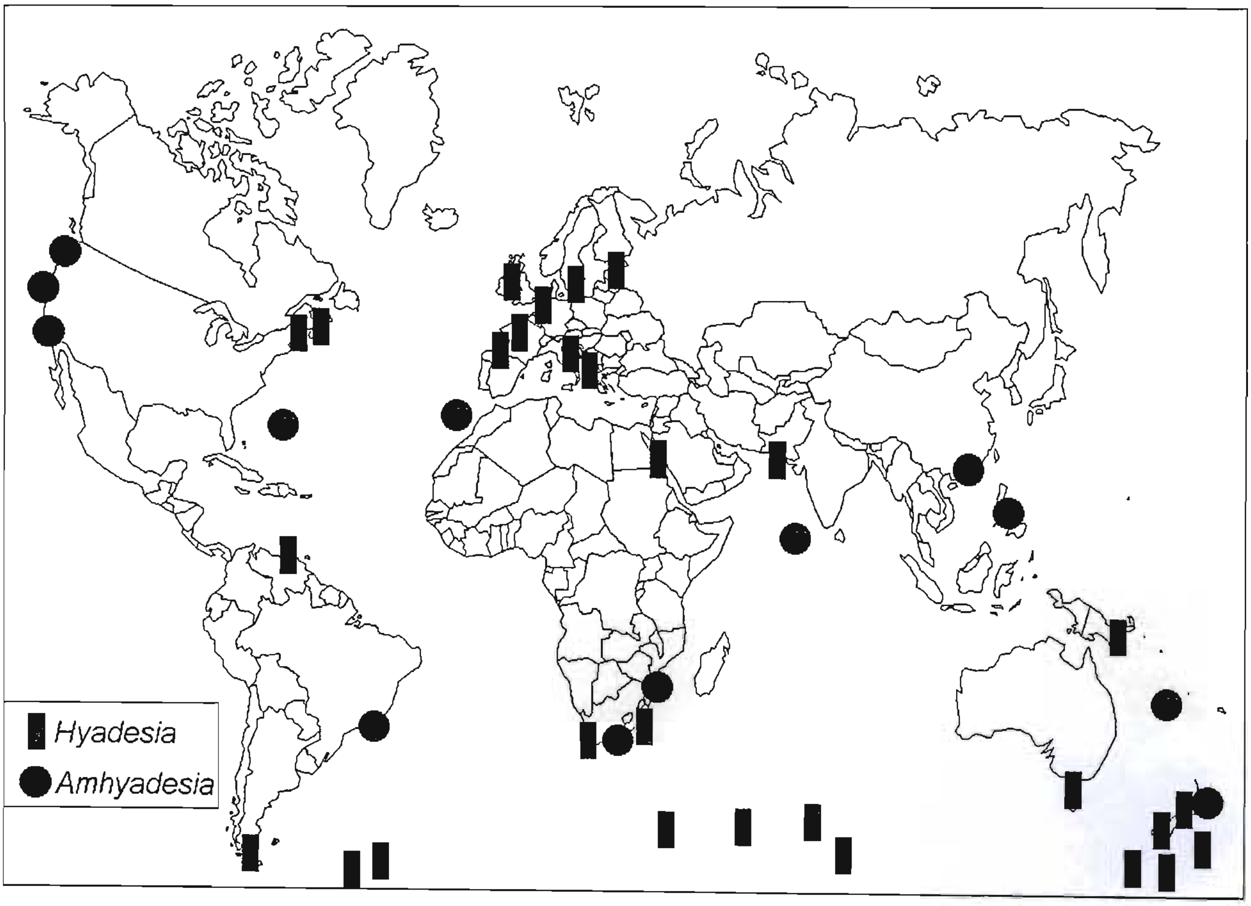

Figure 4. Global distributions of the hyadesiid mite genera.

northern hemispheres may be a natural phenomenon. An increase in species richness in littoral and supralittoral habitats at higher latitudes has been ascribed to an effect relating to the obliteration of adjacent terrestrial habitats by way of ice capping during glaciation events (see Marshall et al., 1999).

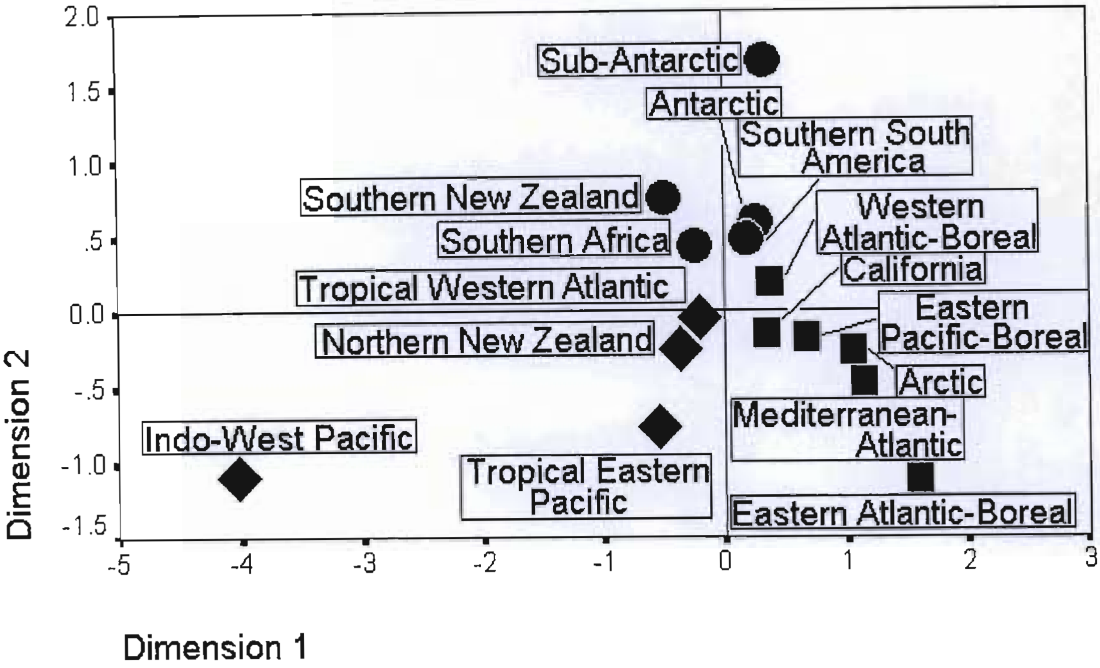

Figure 5. MDS ordination showing the relationships of mite faunas of the world littoral regions. Similar symbols indicate geographical regions belonging to the same latitudinal zones, as follows: northern (squares); tropical (diamonds) and southern (circles). Stress: 0.089.

From a taxonomic perspective, the records more closely reflect species number in the case of the Oribatida and Astigmata, than in the case of the Mesostigmata and Prostigmata. This is suggested by, in particular, few species of the latter two sub-orders in some regions (the warm-temperate and tropical regions) relative to other regions (cold-temperate regions; Fig. 2). The unreliability of the current records regionally and globally is further highlighted by the large number of species known for a single tropical locality (11 species from Hong Kong, Luxton, 1986b, 1992a,b) with no similar records from other localities. With respect to habitat, given that rocky-shores are physically more extreme (greater wave action and potential for desiccation) and further removed from ancestral edaphic habitats than sediment-based mangrove and salt marsh habitats, the latter may be expected to contain more species. The relatively few species known from these habitats (see Appendix) suggests an incompleteness of the records.

Origin and speciation in marine environments

Despite inconsistencies in the reflection of the records of marine mites with the supposed number of species, distinctive patterns emerge from the records, which warrant further interpretation. Taxonomic, ecological and geographical patterns all suggest that the current faunas of the Astigmata and Oribatida have had a long association (in geological time) with the marine environment. In contrast, the faunas of mesostigmatid and prostigmatid mites are relatively recent in marine habitats, in evolutionary terms. The first line of support of this antiquity assumption for the ameronothroid (Oribatida) and hyadesiid (Astigmata) mites arises from the broad generic (Figures 3 and 4) and specific geographical distribution, in the light of dispersal constraining life history characteristics. Unlike most marine invertebrates, which may produce vast numbers of swimming pelagic larvae, these mites produce relatively few crawling larvae, a regression from their ancestral terrestrial lifestyles, which theoretically constrains their capacity to disperse in the marine environment. An increase in species range is, however, not limited to vicariant events, but may also take place by means of incidental dispersal, eventually leading to a greater regional distribution through a stepping-stone effect (Kensler & Crisp, 1965; and see Myers & Giller, 1988).

Additionally, the long association of ameronothroid and hyadesiid mites with marine environments is suggested by the closeness with which the biogeographical trends of the fauna matches those of typically marine faunas, rather than complying with terrestrial trends (see Figure 5; Briggs, 1974). Furthermore, ameronothroid and hyadesiid mites have strong trophic links within marine systems, indicated by their prevalence for feeding on marine plant taxa (Bückling et al., 1998). Characters underpinning their capacity for an evolutionary long existence in marine environments must relate to low rates of speciation and extinction. Both mite groups are characterized by relatively low reproductive rates, which will lower the rate of loss of those genetic attributes most suitable for a marine existence, but potentially also lower rates of speciation (Norton, 1994; OConnor, 1994). Speciation influenced by physiological adaptations will be limited in cases where the physiological capacity is wide, and enables greater survival of extreme environmental conditions. A wide physiological capacity is suggested by the tropical and polar distributions of *Hyadesia*, and has also been proposed as characteristic of some ameronothroids (see Block & Convey, 1995). Indeed, the ability to survive extremely variable environmental conditions may be key to the long-term persistence of these mites in the physically variable intertidal zones.

The geographical distributions, species to genus partitioning, and the predacious lifestyle of many species of mesostigmatid and prostigmatid mite suggest that they have relatively recently colonized intertidal habitats. Even though the available records are limited in this case, the generally restricted geographical distributions of the genera and species indicate a relatively short time frame for dispersal. The relatively high ratios for number of species to number of genera, and species and genera to families (Table 1), suggests a greater rate of speciation (and possibly extinction) of these mites compared to the ameronothroid and hyadesiid mites. In some respects these ratios agree with their relatively more rapid reproductive rates compared to those of ameronothroid and hyadesiid mites. Loose trophic links within the marine environment of mesostigmatid and prostigmatid mites are indicated particularly in the predacious species which are known to feed on secondary marine taxa such as mites, tardigrades and collembolans (Schuster, 1979). Limitations on a high quality food supply coupled with the likelihood of high metabolic requirements are possible factors constraining water-borne dispersal of these mites in marine environments.

In sum, although the records are clearly incomplete for some taxonomic groups, some geographical regions and some habitat types, the patterns that emerge for the taxonomy, geography and ecology of non-halacarid marine mites strongly suggest different underlying processes for the present day taxa of the four sub-orders. During the course of their evolution, predacious mesostigmatid and prostigmatid mites have presumably undergone numerous independent incursions into intertidal habitats from adjacent, local supralittoral and terrestrial habitats, rather than having diversified to any degree within the marine environment. In contrast, the present day oribatid and astigmatid mite taxa have apparently been associated with the marine environment for a long geological time.

Acknowledgements

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Appendix. List of non-halacarid intertidal mites of the world. Numbers in parantheses after species names refer to publications used in compiling this table, as follows: 1, Pugh & King 1985; 2, Luxton 1990; 3, Marshall & Procheş, unpublished data; 4, Pugh, 1993; 5, Pugh & King 1988; 6, Luxton 1986b; 7, van der Hammen 1963; 8, van der Hammen 1960; 9, Schulte et al. 1975; 10, Fain & Ganning 1989; 11, Luxton 1992a, 12, Luxton 1986a; 13, Schatz 1998; 14, Grandjean 1968; 15, Marshall & Pugh 2000; 16, Grandjean 1966; 17, Marshall & Nunkumar 1999; 18, Luxton 1992b; 19, Fain & Schuster 1984b; 20, Fain & Schuster 1984a; 21, Fain & Schuster 1986; 22, Marshall & Ugrasen 2000; 23, Luxton 1989; 24, Fain 1981; 25, Fain & Schuster 1985; 26, Fain & Synnot 1981; 27, Schuster & Bartsch 1986, 28, Marshall & Pugh, 2001. Shore habitats: M, mangroves; R, rocky-shores and boulder beaches; S, saltmarshes. Information on distribution is based on the geographic regions of Briggs (1974) – see methods and Figure 1 for details. Localities are given in parentheses in the case of large and heterogeneous regions.

Taxa	Shore habitat	Geographical distribution
MESOSTIGMATA		
Ascidae Voigts & Oudemans, 1905		
Arctoseiodes ibericus Willmann, 1949 (1)	R	Eastern Atlantic-Boreal
Leioseius australis Luxton, 1984 (2)	R	Northern New Zealand; Southern New Zealand: Nelson
Leioseius vallaensis Luxton, 1989 (23)	R	Southern Australia
Leioseius sp. 1 (3)	R, M	Indo-West Pacific: KwaZulu-Natal; Southern Africa

Appendix. (continued)

Leioseius sp. 2 (3)	M	Indo-West Pacific: KwaZulu-Natal
Digamasellidae Evans, 1957		
Pontiolaelaps salinus Luxton, 1989 (2)	R	Southern New Zealand
Pontiolaelaps crenatus Luxton, 1984 (2)	R	Northern New Zealand
Pontiolaelaps terebratus Luxton, 1984 (2)	R	Northern New Zealand
Halolaelapidae Karg, 1965		
Halolaelaps celticus Halbert, 1915(1)	R	Eastern Atlantic-Boreal
Halolaelaps marinus Brady, 1875 (1)	R	Eastern Atlantic-Boreal
Macrochelidae Vitzthum, 1930		
Macrocheles glaber (Müller, 1860) (1)	R	Eastern Atlantic-Boreal
Macrocheles superbus (Hull, 1918) (1)	R	Eastern Atlantic-Boreal
Parasitidae Oudemans, 1901		
Parasitus kempersi Oudemans, 1902 (1)	R	Eastern Atlantic-Boreal
Rhodacaridae Oudemans, 1902		
Hydrogamasus giardi (Berlese & Trouessart, 1889) (1)	R	Eastern Atlantic – Boreal
Hydrogamasus kensleri Luxton, 1967 (2)	R	Northern New Zealand; Southern New Zealand; Sub-Antarctic
Hydrogamasus salinus (Laboulbène, 1851) (1)	R,S	Eastern Atlantic-Boreal
Hydrogamasus sp. (27)	R	Tropical western Atlantic: Bermuda
Litogamasus falcipes Lee & Hunter, 1974 (2)	R	Southern New Zealand
Litogamasus setosus (Kramer, 1898) (2)	R	Southern New Zealand
Litogamasus sp. (4)	R	Antarctic
Parasitiphis brunneus (Kramer, 1898) (4)	R	Antarctic
Parasitiphis jeannelli (André, 1947) (2)	R	Southern New Zealand; Sub-Antarctic; Antarctic
Parasitiphis aurora Lee, 1970 (2)	R	Southern New Zealand; Sub-Antarctic; Antarctic
Tangaroellus porosus Luxton, 1968 (2)	R	Northern New Zealand; Southern New Zealand
Vulgarogamasus trouessarti (Berlese) (1)	R	Eastern Atlantic-Boreal
Thinozerconidae Halbert, 1915		
Thinozercon michaeli Halbert, 1915 (5)	R	Eastern Atlantic-Boreal

Appendix. (continued)

Uropodidae Berlese, 1900		
Deraiophorus sp. (27)	R	Tropical western Atlantic: Bermuda
Phaulodinychus orchestiidarum Barrois (5)	R,S	Eastern Atlantic-Boreal
Uroobovella magna Hiramatsu & Hirschmann, 1977 (6)	M	Japan; Indo-West Pacific: Hong Kong
Uroobovella sp. (3)	M	Indo-West Pacific: KwaZulu-Natal
Veigaiidae Oudemans, 1939		
Cyrthydrolaelaps hirtus Berlese, 1905 (1)	R	Eastern Atlantic-Boreal
Cyrthydrolaelaps incisus Evans (1)		Eastern Atlantic-Boreal
PROSTIGMATA		
Bdellidae Duges, 1834		
Bdella decipiens Thorell, 1872 (1)	R	Eastern Atlantic-Boreal
Bdella interrupta Evans, 1954 (1)	R	Eastern Atlantic-Boreal
Neomolgus littoralis (Linnaeus, 1758) (1)	R	Eastern Atlantic-Boreal
Bdellidae gen sp. 1 (3)	R	Southern Africa
Bdellidae gen sp. 2 (3)	R	Southern Africa
Ereynetidae Oudemans, 1931		
Ereynetes arcuatus (1)	R	Eastern Atlantic-Boreal
Ereynetes macquariensis Fain, 1962 (2)	R	Sub-Antarctic; Antarctic
Erythreidae Robineau-Desvoidy, 1828		
Abrolophus zelandicus Luxton, 1989 (2)	R	Northern New Zealand; Southern New Zealand
Abrolophus sp. (27)	R	Tropical western Atlantic: Bermuda
Balaustium araneoides Berlese, 1910 (1)	R	Eastern Atlantic-Boreal
Balaustium halberti (Cooremann, 1936) (1)	R	Eastern Atlantic-Boreal
Balaustium harrisoni Hull, 1918 (1)	R	Eastern Atlantic-Boreal
Balaustium rubripes (Trouessart, 1889) (1)	R	Eastern Atlantic-Boreal
Balaustium tardum (Halbert, 1915) (1)	R	Eastern Atlantic-Boreal
Eupodidae C. L. Koch, 1835		
Eupodes minutus (Strandtmann, 1967) (2)	R	Southern New Zealand; Sub-Antarctic
Eupodes sp. (4)	R	Antarctic
Halotydeus hydrodromus Berlese & Trouessart, 1891 (1)	R	Eastern Atlantic-Boreal

Appendix. (continued)

Halotydeus mollis Luxton 1986 (6)	M	Indo-West Pacific: Hong Kong
Halotydeus signiensis Strandtmann & Tilbrook, 1968 (4)	R	Antarctic
Halotydeus sp. (6)		Indo-West Pacific: Philippines
Nanorchestidae Grandjean, 1937		
Nanorchestes amphibius (Topsent & Trouessart, 1890) (1)	R	Eastern Atlantic-Boreal
Nanorchestes dicrosetus Luxton, 1984 (2)	R	Southern New Zealand
Nanorchestes hutchinsoni Luxton 1989 (23)	R	Southern Australia
Nanorchestes macquariensis Strandtmann, 1982 (2)	R	Sub-Antarctic; Antarctic
Nanorchestes sp. 1 (3)	R	Southern Africa
Nanorchestes sp. 2 (3)	M	Indo-West Pacific: KwaZulu-Natal
Rhagidiidae Oudemans, 1902		
Foveacheles canestrinii (Berlese & Trouessart, 1889) (1)	R	Eastern Atlantic-Boreal
Robustocheles mucronata (Willmann, 1936) (1)	R	Eastern Atlantic-Boreal
Trombidiidae Leach, 1814		
Microtrombidium aucklandicum Luxton, 1989 (2)	R	Northern New Zealand
Microtrombidium karriensis Wormesley, 1934 (2)	R	Sub-Antarctic, Southern New Zealand
Microtrombidium littorale Michener, 1946 (7)	M	Tropical eastern Pacific: Panama
Microtrombidium malindiensis Luxton, 1989 (23)	R	Indo-West Pacific: Kenya
Microtrombidium otagoensis Luxton, 1989 (2)	R	Southern New Zealand
Platytrombidium sp. (8)	R	Indo-West Pacific: New Guinea
Tydeidae Kramer, 1877		
Lasiotydeus brevistylus Halbert (5)	R	Eastern Atlantic-Boreal
Tydeidae gen sp. (3)	M	Indo-West Pacific: KwaZulu-Natal
ORIBATIDA		
Ameronothridae Willman, 1931		
Ameronothrus bilineatus Michael 1888 (9)	R,S	Eastern Atlantic-Boreal; Mediterranean-Atlantic; South Africa (introduced ?)
Ameronothrus lineatus Thorell, 1871 (9)	R	Arctic; Eastern Atlantic-Boreal; Eastern Pacific-Boreal

Appendix. (continued)

Ameronothrus maculatus Michael, 1882 (9)	R	Arctic; Eastern Atlantic-Boreal; Mediterranean-Atlantic
Ameronothrus marinus Banks, 1896 (9)	R	Eastern Atlantic-Boreal; Mediterranean-Atlantic
Ameronothrus nigrofemoratus Koch, 1879 (9)	R,S	Arctic; Eastern Atlantic-Boreal; Eastern Pacific-Boreal
Ameronothrus schneideri Oudemans, 1903 (9)	R	Eastern Atlantic-Boreal; Mediterranean-Atlantic; Tropical Western Atlantic: Curaçao (introduced ?)
Ameronothrus schubarti Weigmann & Schulte, 1970 (9)	R	California
Ameronothrus schusteri Schubart, 1970 (9)	R	Mediterranean-Atlantic
Halozetes bathamae Luxton, 1984 (2)	R	Southern New Zealand
Halozetes belgicae (Michael, 1903) (4)	R	Sub-Antarctic; Antarctic
Halozetes intermedius Wallwork, 1963 (4)	R	Sub-Antarctic
Halozetes littoralis Wallwork 1970 (4)	R	Antarctic
Halozetes marinus (Lohmann, 1907) (4)	R	Southern Africa: St Paul & Amsterdam; Southern South America: Falkland; Southern New Zealand; Sub-Antarctic; Antarctic
Halozetes marionensis Engelbrecht, 1974 (4)	R	Southern South America: Gough Island; Sub-Antarctic
Halozetes plumosus Wallwork, 1966 (2)	R	Southern New Zealand
Halozetes sp.1 (4)	R	Sub-Antarctic
Halozetes sp.2 (4)	R	Sub-Antarctic
Fortuyniidae van der Hammen, 1960		
Alismobates reticulatus Luxton, 1992 (11)		Indo-West Pacific: Hong Kong
Alismobates rotundus Luxton, 1992 (11)	R	Indo-West Pacific: Hong Kong
Circellobates venustus Luxton, 1992 (11)	R	Indo-West Pacific: Hong Kong
Fortuynia elamellata Luxton, 1967 (3, 12)	R	Japan; Indo-West Pacific: East coast of Africa; Northern New Zealand
Fortuynia maculata Luxton, 1986 (12)	R	Indo-West Pacific: Kenya
Fortuynia marina van der Hammen, 1960 (12)	R	Indo-West Pacific: New Guinea

Appendix. (continued)

Fortuynia sinensis Luxton, 1992 (11)	R	Indo-West Pacific: Hong Kong
Fortuynia yunkeri van der Hammen, 1963 (12)	R	Tropical eastern Pacific: Panama
Fortuynia inhambanensis Marshall & Pugh, 2001 (28)	R	Indo-West Pacific: Mozambique
Fortuynia rotunda Marshall & Pugh, 2001 (28)	M	Indo-West Pacific: Mozambique
Fortuynia sp. (27)	R	Tropical western Atlantic: Bermuda
Fortuyniidae gen sp. 1 (13)	?	Tropical eastern Pacific: Galápagos Islands
Fortuyniidae gen sp. 2 (13)	?	Tropical eastern Pacific: Galápagos Islands
Oribatulidae Thor, 1929		
Pontiobates denigratus Luxton, 1989 (2)	R	Northern New Zealand
Pontiobates sp (3)	M	Indo-West Pacific: KwaZulu-Natal
Oribatulidae gen sp (3)	M	Indo-West Pacific: KwaZulu-Natal
Selenoribatidae Schuster, 1963		
Arotrobates granulatus Luxton, 1992 (13)	R	Indo-West Pacific: Hong Kong
Arotrobates lanceolatus Luxton, 1992 (13)	M	Indo-West Pacific: Hong Kong
Psednobates uncunguis Luxton, 1992 (13)	S	Indo-West Pacific: Hong Kong
Schusteria littorea Grandjean, 1968 (14)	R	Tropical eastern Pacific: Galápagos Islands (?); Eastern South America
Schusteria sp 1 (14)	R	Eastern South America: São Paolo
Schusteria sp 2 (14)	M	Tropical eastern Pacific: El Salvador
Schusteria sp 3 (15)	R	Indo-West Pacific: KwaZulu-Natal
Schusteria sp 4 (15)	M	Indo-West Pacific: Mozambique
Selenoribates mediterraneus Grandjean, 1966 (16)	R	Mediterranean-Atlantic
Selenoribates foveiventris Strenzke, 1961 (16)	R?	Indo-West Pacific: Red Sea
Thalassozetes riparius Schuster, 1963 (16)	R?	Mediterranean-Atlantic
Selenoribatidae gen sp. (16)	M	Indo-West Pacific: Maldives

Appendix. (continued)

ASTIGMATA

Hyadesiidae Halbert, 1915

Amhyadesia atlantica Fain & Schuster, 1984 (10)	R	Tropical western Atlantic: Bermuda
Amhyadesia austafricana Marshall &Nunkumar, 1999 (17)	R, M	Southern Africa
Amhyadesia bartschae Luxton, 1992 (18)	R	Indo-West Pacific: Hong Kong
Amhyadesia bermudana Fain & Schuster, 1984 (10)	R	Tropical western Atlantic: Bermuda
Amhyadesia brasiliensis Fain & Schuster, 1984 (19)	R	Tropical Atlantic: São Paolo, Brazil
Amhyadesia bursaria Fain & Schuster, 1979 (20)	R	Indo-West Pacific: New Caledonia
Amhyadesia californica Fain & Ganning, 1979 (10)	R	Eastern Pacific-Boreal
Amhyadesia costaricensis Fain & Schuster, 1984 (19)	R	Tropical eastern Pacific: Costa Rica
Amhyadesia elizabethensis Marshall &Nunkumar, 1999 (17)	R	Southern Africa
Amhyadesia glynni (Manson, 1963) (10)	R	Eastern Pacific-Boreal
Amhyadesia heteromorpha Luxton, 1992 (18)	R	Indo-West Pacific: Hong Kong
Amhyadesia heterophallus Fain & Schuster, 1984 (20)	R	Indo-West Pacific: Maldives; Philippines; Mozambique; KwaZulu-Natal
Amhyadesia longipilis Fain & Schuster, 1984 (20)	R	Indo-West Pacific: Philippines
Amhyadesia madeirensis Fain & Schuster, 1986 (21)	R	Mediterranean-Atlantic
Amhyadesia pacifica Fain & Schuster, 1984 (20)	R	Indo-West Pacific: Philippines
Amhyadesia punctulata Luxton, 1989 (2)	R	Northern New Zealand
Hyadesia agulhensis Marshall & Ugrasen, 2000 (22)	R	Indo-West Pacific: South Africa: Eastern Cape
Hyadesia algivorans (Michael, 1893) (24)	R	Eastern Atlantic-Boreal
Hyadesia arabica Fain & Schuster, 1985 (25)	R	Indo-West Pacific: Red Sea (Egypt)
Hyadesia australiana Fain & Synnot, 1981 (26)	R	Southern Australia
Hyadesia benguelensis Marshall & Ugrasen, 2000 (22)	R	Southern Africa
Hyadesia chelopus (Trouessart) André, 1931 (24)	R	Indo-West Pacific: Indian Ocean

Appendix. (continued)

Hyadesia curassaviensis Viets, 1936 (24)	R	Tropical eastern Atlantic: Curaçao
Hyadesia fusca (Lohman, 1896) (10)	R	Western Atlantic-Boreal; Eastern Atlantic-Boreal
Hyadesia glynni Manson, 1963 (10)	R	Eastern Pacific-Boreal
Hyadesia halophila Fain, 1974 (24)	R	Sub-Antarctic; Antarctic
Hyadesia heteromorpha Marshall & Ugrasen, 2000 (22)	R	Southern Africa
Hyadesia kerguelensis (Lohman, 1907) (24)	R	Sub-Antarctic
Hyadesia maxima Fain, Sømme & Block, 1983 (24)	R	Antarctic
Hyadesia microseta Luxton, 1989 (2)	R	Northern New Zealand
Hyadesia mollis Luxton, 1989 (2)	R	Northern New Zealand
Hyadesia nearctica Fain & Ganning, 1978 (10)	R	Western Atlantic-Boreal
Hyadesia pakistanensis Fain & Schuster, 1985 (25)	R	Indo-West Pacific: Karachi
Hyadesia paulensis Fain, 1975 (24)	R	Southern Africa: St. Paul & Amsterdam
Hyadesia plicata Luxton, 1989 (2)	R	Southern New Zealand
Hyadesia reticulata Luxton, 1989 (2)	R	Southern New Zealand
Hyadesia sanjuanensis Fain & Ganning, 1989 (10)	R	Tropical eastern Pacific: Central America
Hyadesia sellai Viets, 1937 (24)	R	Mediterranean-Atlantic
Hyadesia subantarctica Fain, 1974 (24)	R	Sub-Antarctic; Antarctic
Hyadesia tesselata Luxton, 1989 (2)	R	Southern New Zealand
Hyadesia travei Fain, 1975 (2)	R	Southern Africa: St. Paul & Amsterdam
Hyadesia tumida Bénard, 1961 (24)	R	Mediterranean-Atlantic: Brittany
Hyadesia uncifer Mégnin, 1891 (24)	R	Magellan: Tierra del Fuego
Hyadesia verrucosa Fain & Schuster, 1985 (25)	R	Mediterranean-Atlantic
Hyadesia vietsii Wormesley, 1961 (24)	R	Indo-West Pacific: New Guinea
Hyadesia wormesleyi Luxton, 1989 (23)	R	Sub-Antarctic
Hyadesia zelandica Luxton, 1989 (2)	R	Northern New Zealand; Southern New Zealand
Hyadesia sp. (4)	R	Antarctic

Chapter IV

Diversity and biogeography of southern African intertidal Acari

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Abstract

Aim The aims were 1) to describe the diversity and geographical distribution of the intertidal mite fauna of southern Africa, and 2) to show how species richness, endemism and geographical patterns of this fauna (comprising taxa of variable terrestrial ancestry) compare with typically marine faunas.

Location and methods To assess intertidal mite diversity and endemism, records (published and unpublished) were complied for a variety of habitats (mainly rocky shores and mangroves), between Swakopmund (Namibia) and Inhambane (Mozambique). The geographical study was based on a dedicated sampling programme from the rocky shore, at nine localities between Elandsbaai (on the west coast) and St Lucia (on the east coast).

Results Eighty two species of marine mite, from thirty three genera, are currently known from southern Africa. The majority belong to the earlier marine ancestral Halacaridae (forty eight species), with the Ameronothroidea and Hyadesiidae collectively comprising seventeen species. In constituting three faunistic provinces, corresponding with the west (Atlantic), south, and east coast (Indian) regions, the mite fauna conforms with trends for the southern African marine fauna in general. Species richness was greatest in the southern province, which deviates from the general pattern of increase from west to east, but is similar to that of some invertebrate taxonomic groups.

Conclusions Despite their relatively recent marine connections, marine mites show typical geographical distributions, comparable to those of other rocky shore biota in southern Africa. The marine faunistic provinces are "insular" and apparently remain largely intact, across taxonomic groups and with increased taxonomic resolution.

Introduction

High levels of taxonomic diversity and endemism are distinct features of the southern African biota, and this is as much applicable to marine systems as to terrestrial systems. While notable efforts have been (and continue to be) made to document the region's taxonomic richness in as meaningful a way as possible, our knowledge of the marine biota is largely incomplete (Gibbons et al. 2000). Whereas some taxonomic groups, such as the molluscs and fishes, have understandably received considerable attention (Gosliner, 1987; Prochazka,1994; Turpie, 2000), others, comprising rare and cryptic faunas, remain poorly known. It is within this context that studies on the diversity and geography of marine mites (Acari) in southern Africa seem particularly relevant.

The Acari comprises predominantly terrestrial species, with few groups having colonized the marine environment. One family, the Halacaridae (Prostigmata), has been especially successful in this regard; members of this family occur from the ocean depths to the intertidal zones, and radiation is demonstrated by the group comprising over one thousand known species (Barstch, 1989; Otto, 2000). Among the mite groups restricted to intertidal zones, the Ameronothroidea (Oribatida) and Hyadesiidae (Astigmata) have strong ecological and long historical links with marine systems, whereas the Mesostigmata and non-halacarid Prostigmata have tenuous marine associations (Procheş & Marshall, 2001a). Given these different evolutionary backgrounds, marine mites are ideal for investigating evolutionary effects on ecological and biogeographical patterns (see Procheş & Marshall, 2001 a, for biogeography; Procheş & Marshall, 2001b, for ecological relationships). For example it is likely that these patterns will be influenced by the retention, in more recently originated taxa, of traits for a terrestrial existence, such as low fecundity, crawling (as opposed to swimming) larval stages, and the inability for aquatic respiration. As these traits intuitively constrain dispersal in marine environments, geographical studies on marine mites are fertile grounds for investigating vicariance versus dispersal models of distribution.

Geographical variation in southern African marine faunas is thought to be predominantly affected by two processes. In the first instance this arises from variations in seawater temperature along the coast, deriving from prominent adjacent current systems (Branch & Branch, 1981; Field and Griffiths, 1991). Secondly, this arises through the incursion of Indo-Pacific species into the warmer coastal regions (Brown & Jarman, 1978). The extent of this variation is seen by three generally recognised biogeographical provinces falling within the political boundaries of South Africa: a cool temperate province extending along the west coast from Cape Point northwards, a warm temperate province along the south coast, and a sub-tropical province along the east coast (Brown & Jarman, 1978; Branch &

Branch, 1981; Field & Griffiths, 1991). However, less consensus exists as to the actual limits of these provinces (Day, 1967; Stephenson & Stephenson, 1972; Siegfried, 1984; Emanuel et al., 1992; Prochazka, 1994; Briggs 1995; Bolton & Anderson, 1997; Turpie et al., 2000). Furthermore, the limits seemingly vary from one taxonomic group to the next (Day, 1967; Griffiths, 1976; Siegfried, 1981; Gosliner, 1987; Thandar, 1989; Williams, 1992; Whitfield, 1994; Bolton & Anderson, 1997; Turpie et al., 2000; Awad et al., 2001).

The current investigation documents the diversity and geography of the southern African marine mites. As these comprise an evolutionary and taxonomically poorly-associated marine invertebrate fauna, they were also used to test the generality, across taxonomic groups and hierarchies, of commonly observed diversity and geographical patterns for the southern African marine fauna as a whole. This fauna can be described as 1) being highly diverse and endemic (relative to other world faunas), 2) forming three distinct geographical regions and 3) increasing in species richness from west to east. As a key outcome, the investigation highlights the remarkable degree of conformity that exists in southern Africa between the biogeography of marine mites and that of typically marine groups, despite the historical discrepancies between primary and secondary marine organisms.

Material and methods

Records of southern African marine mites were complied from 1) all known publications and unpublished observations as well as 2) collections made towards a dedicated study from nine localities along the coastline (see below). Mite records from coastal habitats below the spring highwater mark were considered, however, collections were concentrated on rocky shore and mangrove communities, with less consideration being given to sandy beaches, saltmarshes and other estuarine communities. The southern African (s-A) region was delimited here on the west coast, at Swakopmund (Namibia), and on the east coast, at Inhambane (Mozambique). For each species, southern African distributions were recorded, as was taxonomic information and distributions outside the region (where applicable). On the basis of known geographical distribution, and with reference to patterns of endemism for other taxonomic groups (Griffiths, 1974; Brown & Jarman, 1978; Turpie et al, 2000), each species was categorized as 1) endemic (only between Orange River and East London), 2) possible endemic (as in 1 and extending north of East London, but never outside the s-A region), 3) possible Indo-Pacific (not south of East London and not outside the s-A region), 4) Indo-Pacific (not south of East London but also outside the s-A, and in the Indo-Pacific region; see Briggs, 1995), 5) Cosmopolitan (outside s-A, but not only in the Indo-Pacific region), 6) Southern (shared with other southern temperate regions).

The biogeographical study concerned nine localities along the coast between Elandsbaai and St Lucia, inclusive (Figure 1). Climatic conditions (sea surface and air temperatures) vary markedly across this geographical range, as indicated in Table 1. Collecting was undertaken between November 2000 and May 2001. At each locality, three sites were selected, and nine samples taken from each site (three in each of the supralittoral fringe, upper mid-littoral, and lower mid-littoral (see Brown & Jarman, 1978; Field & Griffiths, 1991), giving a total of twenty-seven samples per locality. The sites were located tens or hundreds of meters apart, depending on the extent of rocky shore sampled. Each sample comprised the algae, sessile animals and sand covering the rock in a 15 X 15 cm quadrat. The contents of a sample were washed over two sieves in order to retain organisms larger than 0.12 mm but smaller than 5 mm. These were preserved in 70% ethanol (25 ml plastic sample bottles).

In the laboratory, the mites were extracted from each sample (under dissecting microscope at X 100 magnification), cleared in lactic acid, and slide-mounted in Hoyer's medium. Specimens were identified and counted. Only three taxonomic groups, Halacaridae, Ameronothroidea and Hyadesiidae, accounting for 98.9% of all collected mites, were included in further analyses. Brief taxonomic descriptions were undertaken for species previously unknown from the region (see Appendix). While these descriptions were useful in distinguishing the southern African Halacaridae in particular, more detailed investigation referring to the known global taxa is required to confirm new species.

To assess how mite abundance varies across the southern African region, mean abundance was determined for each of the two evolutionary distinct groups (Halacaridae and Ameronothroidea/Hyadesiidae) in relation to position on the shore. Bray-Curtis similarity analysis of presence/ absence data was used to determine the relationship of the faunas of each locality. Additional analyses were performed using species ranges and assuming the occurrence of a species at all localities within the range. Statistical procedures were carried out using PRIMER (Plymouth Routines in Multivariate Ecological Research; Clarke & Warwick, 1994) and SPSS ver. 7.

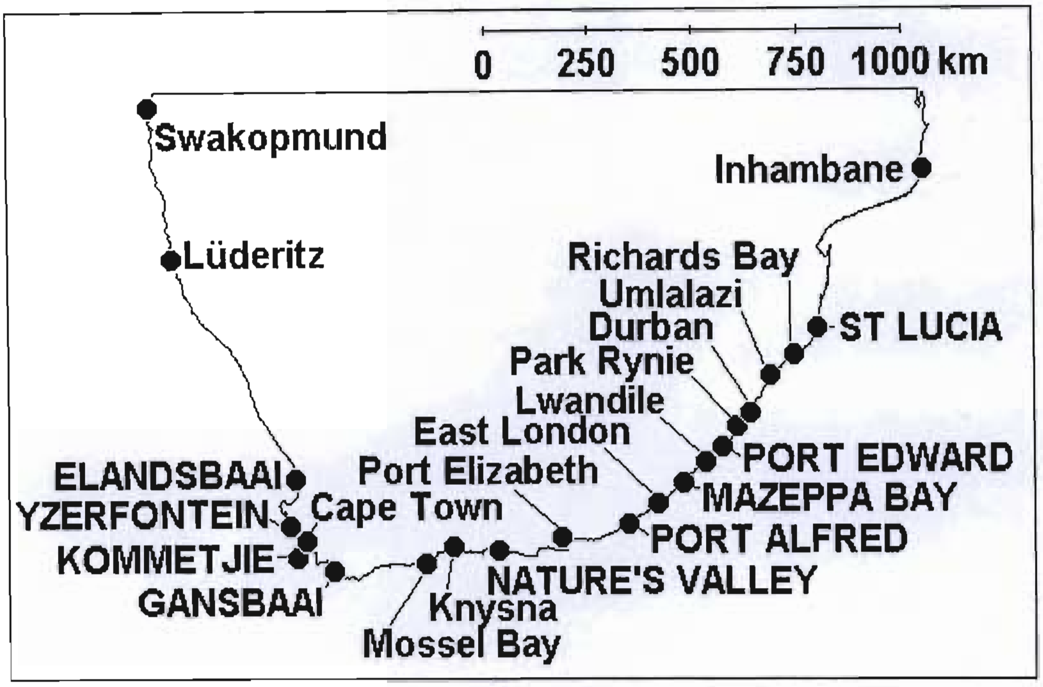

Figure 1. Collection localities for southern African marine mites. Data from localities indicated by capital letters were used in the analyses of the present study. Earlier collections were made from the other localities (see Table 2).

Table 1. Average annual minimum and maximum (±SE; n=10; 1990-1999), for nine localities on the southern African coast (°C; based on monthly minimum and maximum temperature data).

	Air temperature		Seawater temperature	
	Minimum	Maximum	Minimum	Maximum
Doringbaai (55 km N of Elandsbaai)	-	-	11.2±0.3	13.2±0.1
Yzerfontein	-	-	11.3±1.2	12.2±1.3
Kommetjie	7.4±0.9	27.1±1.1	11.5±1.2	12.4±1.2
Gansbaai	-	-	15.5±0.2	16.7±0.2
Tsitsikamma	10.1±1.5	24.5±1.1	15.8±0.2	18.1±0.3
Port Elizabeth (125 km W of Port Alfred)	7.7±1.1	26.0±0.5	16.7±0.1	19.4±0.2
East London (90 km SW of Mazeppa Bay)	10.2±1.1	26.2±0.7	17.4±0.1	18.7±0.1
Port Edward	13.0±0.8	26.7±0.5	20.6±0.2	21.3±0.1
St Lucia	14.3±1.3	28.0±1.1	-	-

Results

Mite diversity and endemism

The currently known southern African marine mite fauna comprises 82 species, representing four major groups (Mesostigmata, Prostigmata, Oribatida and Astigmata), 14 families, and 33 genera (see Tables 2 and 3). The majority of species (68%) are contained within three super/families, the Halacaridae (Prostigmata), Ameronothroidea (Oribatida) and Hyadesiidae (Astigmata). The Mesostigmata and non-halacarid Prostimata are poorly represented; because of their low abundance it is difficult to acquire representative collections. Thirty one new species and seven new genera (*Isobactrus*, *Halacarus*, *Thalassarachna*, *Bradyagaue*, *Actacarus*, *Halozetes*, and an undescribed fortuyniid genus) are reported in the present study. The most speciose genus is the halacarid, *Copidognathus* (20 species), followed by *Rhombognathus* (seven species) and *Agauopsis* (six species). Although no generic endemism was observed for the region, the fauna comprises close to 60% specific endemics (but many of these remain unconfirmed (24%)). Around 34% of the species derive from an IndoPacific component (including unconfirmed records), and the remaining 6% are Cosmopolitan, or from the other southern hemisphere regions. Three halacarid mite species (*Halacarus actenos*, *Copidognathus gibbus* and *Copidognathus bairdii*) have particularly wide distributions and are known from various tropical and temperate locations in the Atlantic and Indian oceans, while *Simognathus glareus* is also known from New Zealand. *Fortuynia elamellata* (Ameronothroidea) and *Amhyadesia heterophallus* (Hyadesiidae) are widely distributed in the Indo-Pacific.

Faunistic patterns

Thirty six mite species were collected during the biogeographical investigation (see Figure 2 for species list and their distributions). There was no indication of greater abundance at any particular level on the shore or for any particular locality for either evolutionary group, when species were grouped into Halacaridae or Ameronothroidea/Hyadesiidae (see Table 4).

However, more detailed ecological investigation taking into account habitat variability within and between localities may yield a different result. Bray-Curtis analyses using 4th root transformed abundances, and presence/absence data for collection records, showed three distinct faunistic groupings, representing west, south, and east coast faunas (Figure 3).

Table 2. Intertidal mite species of southern Africa.

	Genera/Species	Distribution
MESOSTIGMATA		
ASCIDAE	*Leioseius* sp 1.	Endemic (21)
	Leioseius sp 2.	Endemic **(P)** (24)
	Leioseius sp 3.	Indo-Pacific **(P)** (21)
UROPODIDAE	*Uroobovella* sp.	Indo-Pacific **(P)** (21)
PROSTIGMATA		
BDELLIDAE	*Bdella* sp.	Endemic **(P)** (21)
	Spinibdella sp.	Endemic **(P)** (21)
NANORCHESTIDAE	*Nanorchestes* sp 1	Endemic **(P)** (21)
	Nanorchestes sp 2	Indo-Pacific **(P)** (21)
HALACARIDAE	*Isobactrus* sp 1.	Endemic (25)
	Isobactrus sp 2.	Indo-Pacific **(P)** (25)
	Rhombognathus sp 1.	Endemic (23,24,25)
	Rhombognathus litoralis Bartsch.	Endemic (3,24,25)
	Rhombognathus sp 3.	Endemic (25)
	Rhombognathus sp 4.	Indo-Pacific **(P)** (25)
	Rhombognathus sp 5.	Indo-Pacific **(P)** (25)
	Rhombognathus sp 6.	Indo-Pacific **(P)** (25)
	Rhombognathus sp 7.	Endemic (23)
	Halacarus actenos Trouessart.	Cosmopolitan. (12,25).
	Thalassarachna sp.	Endemic (24,25)
	Actacarus sp.	Endemic **(P)** (24)
	Bradyagaue sp.	Endemic **(P)** (24)
	Agaue sp.	Endemic (1)
	Agaue debilis Lohmann.	Endemic (1)
	Agaue hypertrophica Lohmann.	Endemic (1)
	Agaue papillifera Gimbel.	Endemic (2)
	Agauopsis crassipes Gimbel.	Endemic **(P)** (2,23,25)
	Agauopsis sp 2.	Endemic **(P)** (25)
	Agauopsis sp 3.	Endemic **(P)** (24,24,25)
	Agauopsis papillata Bartsch.	Endemic **(P)** (3,24,25)
	Agauopsis sp 5.	Endemic (23,25)
	Agauopsis chelipes, Bartsch.	Endemic (3)

Table 2. (continued)

	Halacaropsis praecognita Procheş.	Indo-Pacific **(P)** (18,24,25)
	Arhodeoporus kunzi Bartsch.	Endemic **(P)** (11)
	Acarothrix umgenica Procheş.	Indo-Pacific **(P)** (19)
	Copidognathus sp. 1.	Endemic (3,25)
	Copidognathus sp. 2.	Endemic (25)
	Copidognathus gibbus Trouessart.	Cosmopolitan. (1,12,25).
	Copidognathus sp. 4.	Endemic (25)
	Copidognathus sp. 5.	Endemic (25)
	Copidognathus bairdi Newell.	Cosmopolitan (3,8,24,25).
	Copidognathus sp. 7.	Endemic (25)
	Copidognathus sp. 8. (17)	Endemic **(P)** (25)
	Copidognathus sp. 9.	Indo-Pacific **(P)** (25)
	Copidognathus sp. 10.	Endemic **(P)** (24)
	Copidognathus sp. 11.	Indo-Pacific **(P)** (24)
	Copidognathus sp. 12.	Endemic **(P)** (24)
	Copidognathus sp. 13.	Endemic **(P)** (24)
	Copidognathus sp. 14.	Endemic **(P)** (24)
	Copidognathus pulcher Lohmann.	Endemic (1)
	Copidognathus simonis Lohmann.	Endemic (1)
	Copidognathus hartmanni Bartsch.	Endemic (3)
	Copidognathus isopunctatus Bartsch.	Endemic (3)
	Copidognathus caloglossae Procheş.	Indo-Pacific **(P)** (19)
	Copidognathus xaixaiensis Procheş.	Indo-Pacific **(P)** (19)
	Simognathus glareus Bartsch.	Southern (10,25).
	Simognathus latitarsus Procheş.	Indo-Pacific **(P)** (25)
	Lohmannella africana Bartsch.	Endemic **(P)** (13)
PONTARACHNIDAE	*Pontarachna capensis* Lohmann.	Indo-Pacific (1,8,24)
	Pontarachna sp.	Endemic (24)
	Litarachna sp 1.	Endemic (24)
	Litarachna sp 2.	Endemic (24)
TROMBIDIIDAE	*Microtrombidium* sp.	Indo-Pacific **(P)** (21)
TYDEIDAE	*Tydeus* sp.	Indo-Pacific **(P)** (21)
ORIBATIDA		
AMERONOTHRIDAE	*Ameronothrus bilineatus* Michael.	Introduced? Northern Atlantic (6,7).
	Halozetes sp.	Endemic (25)
FORTUYNIIDAE	*Fortuynia elamellata* Luxton.	Indo-Pacific. (4,5,17)
	Fortuynia inhambanensis Marshall & Pugh.	Indo-Pacific **(P)** (17)
	Fortuynia rotunda Marshall & Pugh.	Indo-Pacific **(P)** (17)

Table 2. (continued)

		Indo-Pacific **(P)** (24)
	N. g., n. sp.	
SELENORIBATIDAE	*Schusteria ugraseni* Marshall & Pugh.	Endemic **(P)** (16,25)
	Schusteria sp 2.	Indo-Pacific **(P)** (25)
	Schusteria sp 3.	Indo-Pacific **(P)** (24)
	Schusteria melanomerus Marshall & Pugh.	Indo-Pacific **(P)** (16)
ORIBATULIDAE	*Pontiobates* sp.	Indo-Pacific **(P)** (21)
	N. g., n. sp.	Indo-Pacific **(P)** (21)
ASTIGMATA		
HYADESIIDAE	*Amhyadesia austafricana* Marshall & Nunkumar	Endemic (14,25)
	Amhyadesia elizabethensis Marshall & Nunkumar.	Endemic (14,25)
	Amhyadesia sp 3.	Endemic (25)
	Amhyadesia heterophallus Fain & Schuster.	Indo-Pacific. (9,14,25)
	Hyadesia benguelensis Marshall & Ugrasen.	Endemic **(P)** (15,25)
	Hyadesia agulhensis Marshall & Ugrasen.	Indo-Pacific **(P)** (15)
	Hyadesia heteromorpha Marshall & Ugrasen.	Endemic **(P)** (15)
ACARIDAE	*Tyrophagus putrescentiae* Schrank	Cosmopolitan (22)

Distribution information from: Lohmann 1898; 1907a; 1907b (1); Gimbel 1919; 1920 (2); Bartsch, 1972 (3); Luxton, 1967 (4); Aoki, 1974 (5); Schulte et al., 1975 (6); Weigmann, 1975 (7); Konnerth-Ionescu, 1977 (8); Fain & Schuster, 1984 (9); Bartsch, 1985 (10); Bartsch, 1987 (11); Green & Macquitty, 1987 (12); Bartsch, 1992 (13); Marshall & Nunkumar, 1999 (14); Marshall & Ugrasen, 2000 (15); Marshall & Pugh, 2001a (16); Marshall & Pugh, 2001b (17); Procheş, 2001b (18); Procheş, 2001c (19); Procheş & Marshall, 2001 (21); Marshall et al., 2001 (22); Bartsch & Marshall, unpublished data (23); Procheş & Marshall, unpublished data (24), present study (25). Endemic **(P)** and Indo-Pacific **(P)** refer to possible endemics and possible (unconfirmed) Indo-Pacific distributions, respectively (see Material and Methods).

Separation of the three faunas is seen at c. 30 % similarity in the 4th root analysis and 37 % similarity in the presence/absence analysis (Figure 3). However, local faunas were differently grouped in each analysis. In the 4th root analysis, Kommetjie grouped with the west and not the south coast, and Mazeppa Bay with the south and not the east coast. Given that numerous ecological factors known to influence local abundance were not taken into account, the presence/absence pattern is probably of greater biogeographical relevance (Figure 3B). Although the pattern of three sub-provincial faunas is obscured by Gansbaai being associated with the west coast, and Kommetjie with the south coast in the presence/absence analysis, distinctness is indicated by the high similarity between adjacent localities within each province in the case of Elandsbaai and Yzerfontein (c. 58% similarity), Nature's Valley and Port Alfred (c. 87% similarity), and Port Edward and St Lucia (c. 56% similarity; Figure 3). The distinctness of the east coast fauna (Mazeppa Bay, Port Edward and St Lucia) from the rest of the southern African fauna (at 23% similarity) is accountable to the introduction of an Indo-Pacific element into this fauna (see Figure 2 and Table 2).

Because our sampling procedure may have overlooked some species which occur at particular localities, another similarity analysis was derived using distribution ranges and assuming presence at all localities within the known geographical range of a species. This had a minor effect on the faunistic scheme, other than improving similarity among localities and grouping both Gansbaai and Kommetjie into the south coast province (Figure 3C).

Geographical pattern of species richness

Species richness of both the Halacaridae and Ameronothroidea/Hyadesiidae was depressed almost twofold for the west coast localities, as compared to the south and east coast localities (which were similar) when actual collections were analysed (Figure 4A). However the pattern changed somewhat when species ranges were taken into account (recording presence at all localities with the range). This shows a distinct peak for the south coast with richness declining towards the cool temperate west coast and the subtropical east coast (Figure 4B).

Discussion

Diversity and endemism

Biodiversity and endemism studies are becoming an increasingly important basis for the management and preservation of faunas, which is receiving increased attention in the light of the threat of global warming and man's ongoing destruction of the environment. Both the

Table 3 Intertidal mite species richness for southern Africa, according to taxonomic group and biogeographical affinity. Endemic **(P)** and Indo-Pacific **(P)** refer to possible endemics and possible (unconfirmed) Indo-Pacific distributions, respectively (see Material and Methods).

	Total	Mesostigmata	Prostigmata	Oribatida	Astigmata	Halacaridae	Ameronothroidea+ Hyadesiidae	Other
Families	14	2	6	4	2	1	4	9
Genera	33	2	2	7	3	14	7	12
Species	82	4	58	12	8	48	17	17
Cosmopolitan	4	0	3	0	1	3	0	1
Indo-Pacific	3	0	1	1	1	0	2	1
Indo-Pacific **(P)**	25	2	14	8	1	11	7	7
Endemic	29	1	24	1	3	21	4	4
Endemic **(P)**	20	1	16	1	2	13	3	4
Southern	1	0	1	0	0	1	0	0

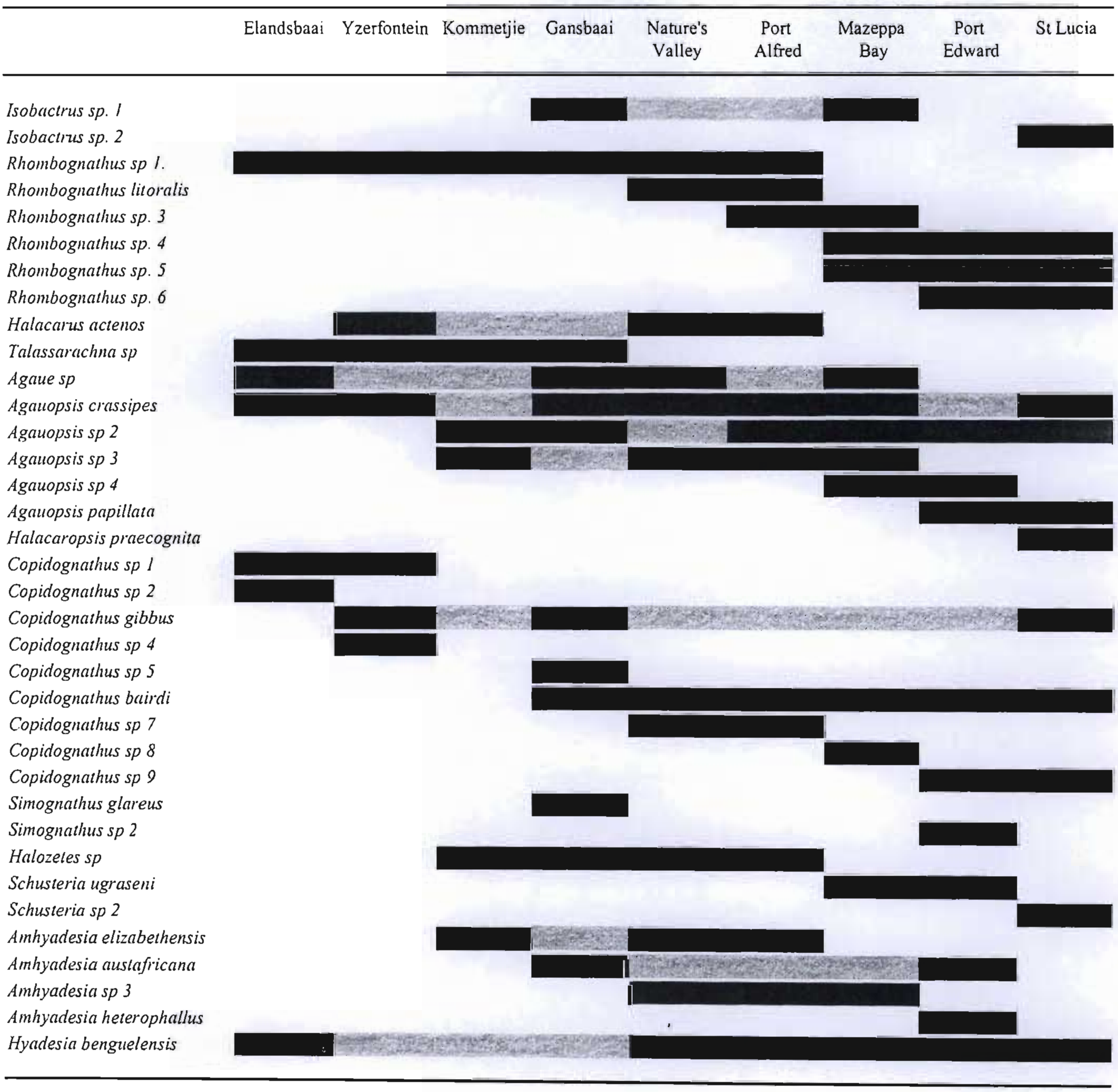

Figure 2. Distributions of southern African intertidal mite species. Actual records are given in black, while gray indicates localities within the distribution range where the species was not collected.

terrestrial and marine environment of southern Africa are centres of high biodiversity, and are thus relevant and important for investigation. Gibbons et al. (1999) review the current status of our knowledge of marine biodiversity in the region. Comprehensive diversity studies on marine mites are known from only few regions, including the British Isles, New Zealand, and some sub-Antarctic islands (Pugh & King, 1985; 1988; Green & McQuitty, 1987; Luxton, 1990; Pugh & Bartsch, 1993; Pugh, 1995). However, attempts have been made to describe their global distribution patterns (Procheş & Marshall, 2001a).

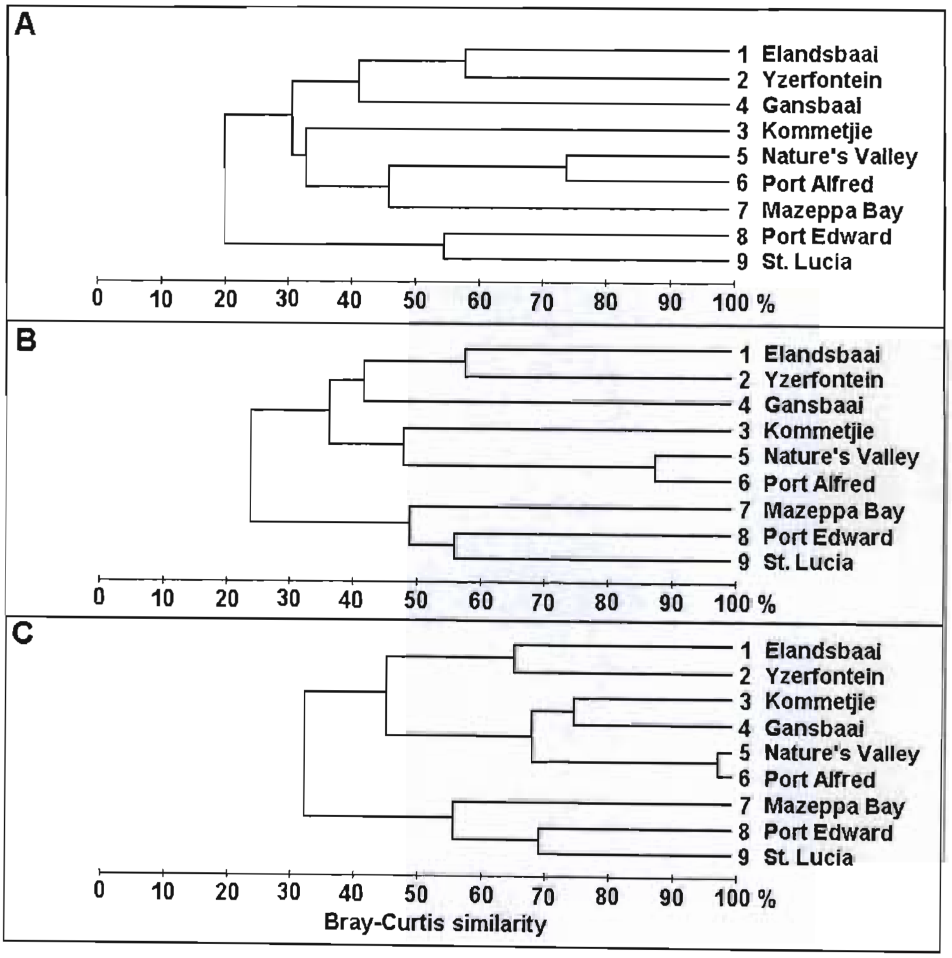

Figure 3. Dendrograms based on Bray-Curtis similarity for southern African marine mite faunas of nine localities. Figures next to each locality indicate the order of the localities on the coast, from west to east. A, 4th root-transformed abundance data; B, presence/absence for actual records; C, presence/absence for species ranges (see Figure 2).

Table 4. Mite abundance (mean ±SE; N=9 for S, U, L; N=27 for T; for 15 x 15 cm quadrats) in three tidal levels (S, supralittoral fringe; U, upper mid-littoral; L, lower mid-littora; T, total), at nine localities along the southern African shore. Data are given separately for the two evolutionary distinct marine mite groups.

Halacaridae	S	U	L	T
Elandsbaai	1.22±0.55	3.67±1.46	2.89±0.87	2.59±0.60
Yzerfontein	1.78±1.09	5.56±2.60	0.67±0.29	2.67±1.00
Kommetjie	0.11±0.11	3.11±1.07	0.44±0.24	1.22±0.44
Gansbaai	1.56±0.77	23.00±9.48	9.56±2.80	11.37±3.62
Nature's Valley	0.56±0.44	2.56±0.69	5.89±1.76	3.00±0.76
Port Alfred	8.33±3.12	3.33±0.82	2.44±0.93	4.70±1.19
Mazeppa Bay	10.11±6.21	3.56±1.76	3.67±1.39	5.78±2.20
Port Edward	0.67±0.37	6.67±2.44	2.89±1.16	3.41±1.00
St Lucia	0.56±0.36	1.11±0.31	15.44±3.47	5.70±1.76

Ameronothroidea and Hyadesiidae	S	U	L	T
Elandsbaai	1.44±1.44	14.11±14.11	-	5.19±4.71
Yzerfontein	-	-	-	-
Kommetjie	0.22±0.22	76.00±9.45	0.33±0.33	25.52±7.63
Gansbaai	-	0.22±0.15	-	0.07±0.05
Nature's Valley	8.78±3.81	2.44±1.28	0.56±0.38	3.93±1.47
Port Alfred	1.44±0.44	5.56±3.49	-	2.33±1.22
Mazeppa Bay	3.33±1.07	58.00±30.60	0.22±0.15	20.52±11.10
Port Edward	1.22±0.70	5.11±1.44	1.33±0.83	2.56±0.68
St Lucia	1.11±0.48	0.44±0.34	0.11±0.11	0.56±0.21

The present study reports eighty two species of intertidal mite from the southern African region. While this number is likely to be accurate in the case of some taxa (for example the ameronothroid and hyadesiid group), it apparently underestimates the actual number of species in the case of others. The high rate at which new halacarid mites were collected in the present study, and their known high global diversity (Bartsch, 1989; Abé, 1998; Otto, 2000), suggest that the number of southern African species may be more than double the forty eight recorded here. Likewise, the records probably underestimate the mesostigmatid and prostigmatid mite diversity, given the rarity of these mites. Nevertheless, the recorded species richness for the non-halacarid mites compares favourably with that for New Zealand (which is 11 ameronothroid/hyadesiid mite species and 15 mesostigmatid/prostigmatid mite species). Additionally, the species richness of the ameronothroid/hyadessid group, represents 10% of the world's species known in this group, though this figure may be an artefact of elevated collecting effort in southern Africa (see Procheş & Marshall, 2001).

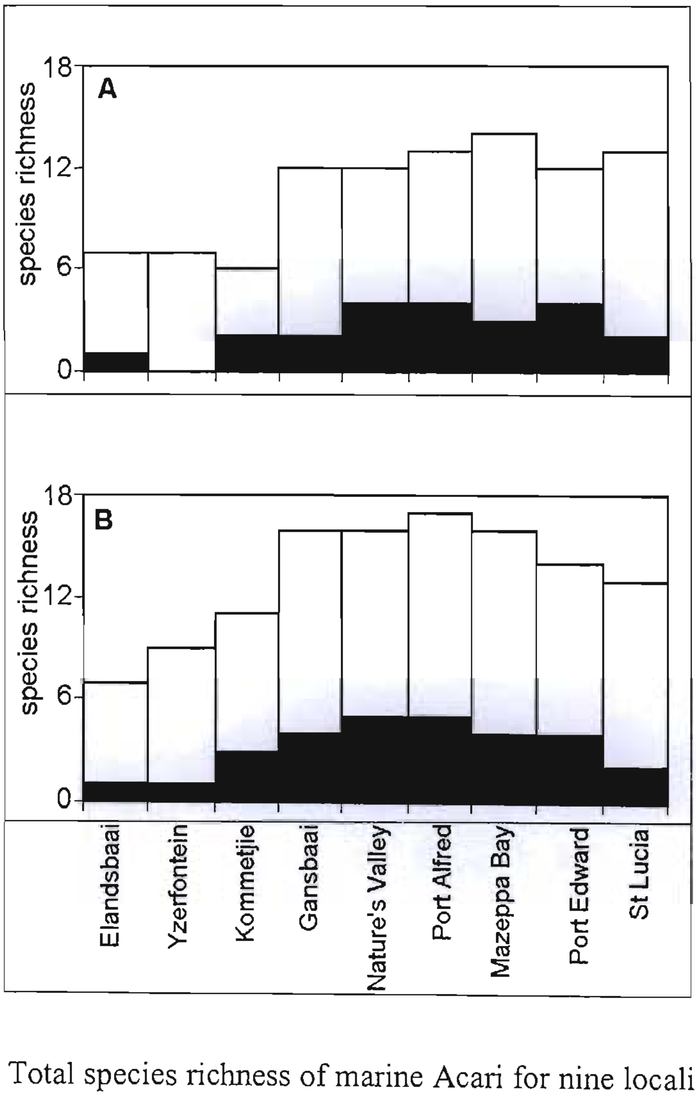

Figure 4. Total species richness of marine Acari for nine localities along the southern African coast. A, actual records; B, species ranges (see Figure 2). White, Halacaridae; black, Ameronothroidea and Hyadesiidae.

The southern African marine mites show a high level of endemism, characteristic of many other marine taxonomic groups in the region. The inferred endemism of 50% is comparable to that for amphipods (40%), bivalves (45%) and opisthobranch molluscs (48%), (Awad et al., 2001), though lower and higher values are known for other groups (e.g. 9% for fishes, Turpie et al, 2000; 21% for polychaetes, 84% for isopods, Awad et al., 2001). This generally high level of endemism can be largely attributed to the geographical isolation of southern Africa, as well as to effects of current systems precluding dispersal from the south and west. The low temperatures and current directions of the Benguela and Southern Ocean systems are of particular importance in this respect. An obvious route of dispersal to the region exists via the Indo-Pacific (Agulhas current system), however, southern distributions are limited by cooler temperatures. Some endemic fish taxa have close relatives in South America and Australia (Smith 1965), but the extent to which such connections are historically based (i.e., Gondwanan associations) has not been well explored for southern African marine taxa, in general.

Faunistic provinces

Three biogeographical provinces are now well recognised for southern African marine animals (delimited here by the political borders of South Africa, extending from Namibia to Mozambique; see Brown & Jarman, 1978, and Field & Griffiths, 1991). A cool temperate West Coast province, a warm temperate South Coast province and a subtropical East Coast province have been established for a variety of taxonomic groups (phyla or groups of phyla) of intertidal invertebrates and fishes (Stephenson & Stephenson, 1972; Brown & Jarman, 1978; Emanuel et al., 1992; Field & Griffiths, 1991; Bustamante & Branch, 1996; Turpie, 2000; Awad, 2001). The present study shows that this pattern remains intact for the marine mite fauna, even though this comprises a poorly taxonomically associated group of families (Halacaridae, Ameronothroidea and Hyadesiidae). The only deviation from the typical regional pattern was seen in the case of Kommetjie, which consistently clustered with the south coast fauna. However, with respect to the general faunistic pattern, less consensus exists as to the limits of the provinces, and some authors suggest transitional zones between Kommetjie and Cape Columbine and between East London and Port Edward (see Brown &

Jarman, 1978; Turpie et al., 2000). The former transition zone would account for the Kommetjie anomaly in our observations.

The basis for the origin of the three provinces is not always clear at the super/family level, but is distinctive in the case of ameronothroid mites. In the southern hemisphere, this mite group comprises a typically tropical element of low latitudinal genera, such as *Fortuynia* and *Schusteria* (largely limited to between 30°N and 30°S), and a typically high latitudinal sub-polar element, the genus *Halozetes* (between 30° and 70°S) (Luxton, 1967; Procheş and Marshall 2001a; also Procheş 2001a). In the southern African region, the southerly limit of the tropical genera is at 33°S, whereas *Halozetes* is only found south of this latitude. Furthermore, this first recording of *Halozetes* in southern African represents a new northerly limit for this widespread and speciose peri-Antarctic genus.

Geographical pattern of species richness

When marine animals are considered as a group, species richness along the southern African coastline shows a distinctive trend of increase from west to east (West Coast province to East Coast province). As previously implied, this is largely accountable to the incursion of a species rich Indo-Pacific element into the southern African fauna on the east coast (see Turpie et al., 2000). When taxonomic resolution increases, however, this pattern either persists as in the case of the fishes and echinoderms, or it breaks down, as in the case of isopods, polychaetes and ascidians (see Figure 5). In common with some of these latter invertebrate groups, the marine mites are best represented on the south, and not the east coast. One explanation for these differences may derive from the inclusion both subtidal reef and intertidal habitats in surveys of the fish and echinoderms including both sub-tidal reef and intertidal habitats, whereas other studies including the present one, consider only the intertidal habitats. Eastwards along the coastline towards the equator, intertidal rocky habitat availability and diversity decline, whereas the converse applies in the case of sub-tidal reef systems which become more diverse with the introduction of coral reefs. The species richness of marine mites would, however, be expected to increase markedly along the subtropical east coast if other habitats in addition to rocky shores were also considered. For example, mangroves in particular are known to support an array of habitat specific mites (Marshall & Pugh, 2001a; 2001b; Procheş, 2001c; Procheş et al., 2001).

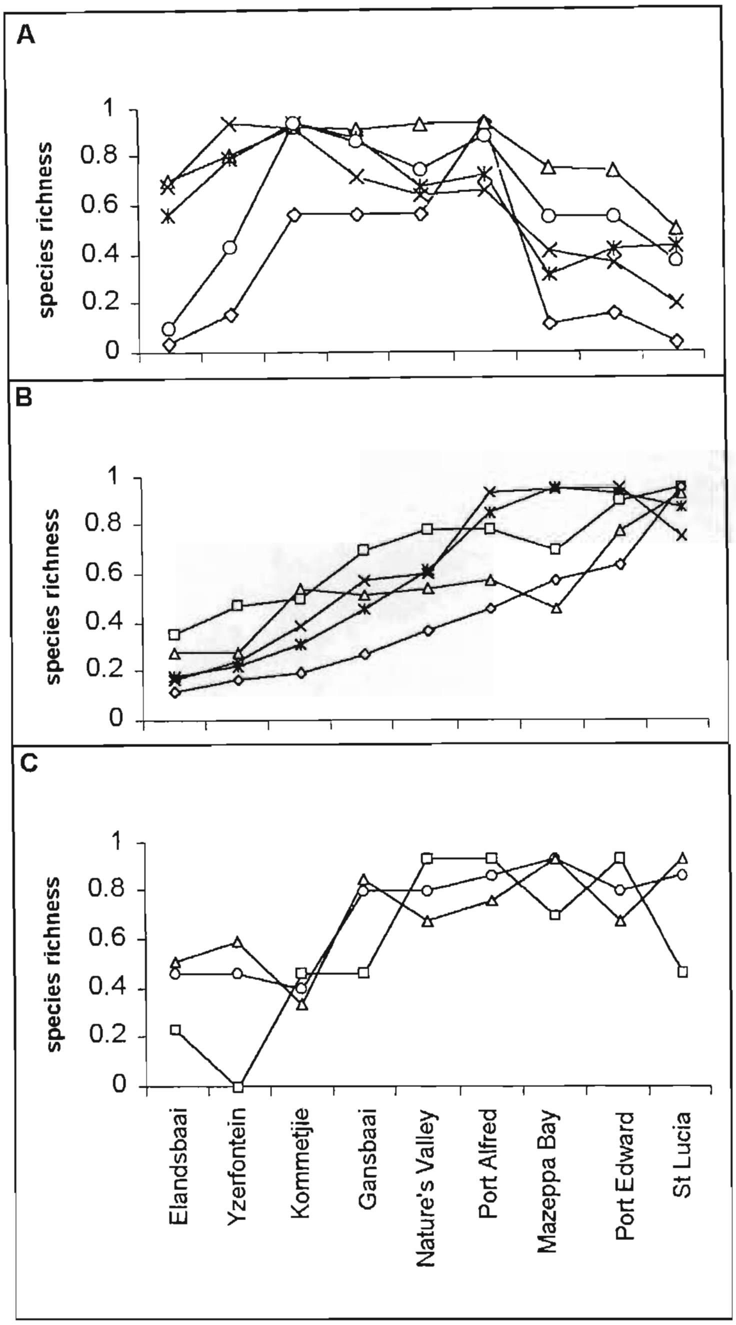

Figure 5. Trends in relative species richness along the southern African coast for various marine animal groups. A, groups with highest richness on the south coast (data from Awad et al., 2001): diamonds = octocorallians, triangles = polychaetes, stars = isopods, x-signs = amphipods, circles = ascidians; B, groups with highest richness on east coast (data from Turpie et al., 2000; Awad et al., 2001): squares = echinoderms, triangles = brachyurans, stars = bivalves, x-signs = gastropods, diamonds = fish; C, Acari: triangles = halacarids, circles = ameronothrids + hyadesiids, squares = total. The data were scaled from zero to one (no species present, to greatest number present of at any locality).

Concluding remarks

This study confirms well-established geographical patterns for southern Africa marine biota. It suggests that these patterns persist for most animal taxonomic groups, including evolutionary divergent marine mite groups (which may maintain physiological, life-history and ecological features similar to terrestrial arthropods). It also shows that the patterns are generally applicable over a broad range of taxonomic hierarchies (considering that the mites were examined down to family). Although geographical trends are clearly discernible, the factors governing these have received limited consideration. In this respect, studies have been conducted to assess geographical variation of some community attributes (e.g. biomass, see Bustamante & Branch, 1996) and some physical effects (such as habitat diversity, geology, and wave action; Emanuel et al., 1992; Bustamante & Branch, 1996). However there scope for investigation into habitat variability within and among the geographical provinces, as well as into patterns of genetic variation across geographical scale. Even though present day temperature seems to be the overriding determinant of geographical patterns of the southern African marine biota, studies adding a historical perspective would be of interest.

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Appendix. Diagnoses for halacarid mites. Abbreviations: AD, anterior dorsal plate; AE, anterior epimeral plate; AG, ano-genital plate; OC, ocular plate; PD, posterior dorsal plate; PE, posterior epimeral plate; pgs, perigenital setae. Legs numbered I to IV.

RHOMBOGNATHINAE Palpi short, in contact with the rostrum all along their length, none of the segments more than twice longer than wide. Flexible portion between end of tarsus and claws with a small sclerite.

Isobactrus Newell. OC without setae. Opening in AD for insertion of gnathosoma ventral. Sclerite between tarsus and claw moniliform.

Isobactrus sp 1. Dorsal plates (AD, PD, OC) separate, with strong reticulation. Male with more than 70 pgs. Gnathosoma completely covered by AD. Tibiae I and II with one strong, slightly barbed seta. Claws smooth.

Isobactrus sp 2. Dorsal plates (AD, PD, OC) separate, smooth. Male with 50-60 pgs. Gnathosoma half covered by AD. Tibiae I and II with one feather seta. Claws smooth.

Rhombognathus Trouessart. OC with two setae. Opening in AD for insertion of gnathosoma antero-ventral. Sclerite between tarsus and claw elongated.

Rhombognathus sp 1. Dorsal plates (AD, PD, OC) separate, with slight reticulation, generally only visible at the posterior end of PD. Male with 14-16 pgs, all branched towards the end. Feather setae on tibiae 2-1-1-2, rarely 3-1-1-2. Claw comb present, with 8-12 teeth.

R. litoralis Bartsch. Dorsal plates (AD, PD, OC) separate, with slight reticulation. Male with 20 pgs, all branched towards the end, one pair on a separate, inner circle. Feather setae on tibiae 2-1-1-0 or 2-1-0-0. Claw comb present, with 18-21 teeth.

Rhombognathus sp 3. Dorsal plates (AD, PD, OC) separate, smooth, OC, twice longer than wide. Male with 26-30 branched pgs, branches few and scattered all along the length of the setae. Feather setae on tibiae 2-2-2-2, barbs on the two posterior pairs of legs less prominent than on the anterior pairs. Claw comb absent.

Rhombognathus sp 4. Dorsal plates (AD, PD, OC) separate, smooth, OC round. Male with 24 branched pgs, branches dense, scattered all along the length of the setae. Feather setae on tibiae 2-2-2-2. Claw comb absent.

Rhombognathus sp 5. Dorsal plates (AD, PD, OC) separate. Male with 16-18 pgs, some bi- or tri-furcated from the base. Feather setae on tibiae 2-1-2-2, 2-1-1-2 or 2-2-1-2. Claws comb present, with 6 teeth at all legs.

Rhombognathus sp 6. Dorsal plates fused, or at least margins adjacent, with clear reticulation, more obvious along three longitudinal bands. Male with 14-18 short, not branched pgs. Feather setae on tibiae 2-1-1-2. Claws comb present, with 15-18 teeth.

HALACARINAE. Palpi long, laterally inserted on the rostrum, of 3-4 segments, at least the 2nd more than twice longer than wide, 3rd with a seta.

Halacarus Gosse. Patella I comparable in length with telofemur I and tibia I. Tibia I with more than 10 setae.

H. actenos Trouessart. PD and OC absent, AD with pointed tip, five pairs of large dorsal pores. Telofemur and patella I with a pair of strong spiniform setae each, tibia I with two pairs.

Appendix. (continued)

Talassarachna Packard. Patella I much shorter than telofemur I and tibia I. Tibia I with more than 10 setae.

Talassarachna sp. AD with two reticulated areas, one large, posterior, one small, anterior, and a series of 12-15 pores along the posterior margin. OC kidney shaped, with a reticulated area along the convex, internal side. PD small, covering the posterior third of the body, with three longitudinal reticulated bands, the median one broad. Legs slender. This species is similar to *T. lubrica* (Bartsch), known from Australia and New Zealand, and noted for its variability (see Bartsch, 1985, Otto, 1994). However, the African populations probably deserve specific status.

Agaue Lohmann. Body and legs generally adorned with lamellae. Mouthparts long, the distance between basirostral and tritorostral setae similar or greater than between left and right basirostrals. Patella I much shorter than telofemur I and tibia I. Tibia I with 10 or more setae.

Agaue sp. Dorsal plates with thickened areas where punctuation and pigmentation are easily visible: one V-shaped on AD, one round, anterior on OC, two band-shaped on PD. Legs flattened, lamellae most obvious on telofemur I. This species is similar, but probably not identical, with *A. chevreuxi* Trouessart.

Agauopsis Viets. Legs, especially the first pair, with numerous peg-like setae. Patella I much shorter than telofemur I and tibia I. Tibia I with less than 10 setae.

A. crassipes Gimbel. Dorsal plates tightly juxtaposed, punctuation vague, more obvious on two longitudinal bands on AD and PD. Mouthparts shorter than gnathosomal base. Peg-like setae on the segments of leg I: 0-0-3-2-3-1, thick and flattened. Claw I with accessory tooth, but no obvious comb, claws II-IV with fine-toothed combs.

Agauopsis sp 2. Dorsal plates loosely juxtaposed, punctuation clear, especially on an H-shaped area of AD and four costae on PD, clear reticualtion in the intervals. Mouthparts longer than gnathosomal base. Peg-like setae on the segments of leg I short, 0-0-4-2-3-1. Claw I with accessory tooth, but no obvious comb, claws II-IV with very fine-toothed combs.

Agauopsis sp 3. Dorsal plates loosely juxtaposed, with uniform reticulation. Mouthparts shorter than gnathosomal base. Peg-like setae on the segments of leg I short, 0-0-2-2-3-1. Claw I with accessory tooth, but no obvious comb, claws II-IV with barely visible teeth.

Agauopsis sp 4. Dorsal plates with clear punctuation, especially on two longitudinal bands on AD and PD. AE very large, spanning over two thirds the length of the idiosoma. Gnathosomal base once and a half longer than wide, mouthparts very short. Peg-like setae on the segments of leg I short, 0-0-3-2-4-1. The two internal peg-like setae on tibia I starting from the same base. Claws smooth.

A. papillata Bartsch. Dorsal plates tightly juxtaposed, punctuation clear, especially on two longitudinal bands on AD and PD, with clear reticulation in between. Mouthparts as long as the base of gnathosoma. Peg-like setae on the segments of leg I relatively small, 0-0-1-1-3-1. Claw I with accessory tooth, but no obvious comb, claws II-IV with fine-toothed combs.

Halacaropsis Bartsch. Patella I much shorter than telofemur I and tibia I. Tibia I with more than 10 setae.

H. praecognita Procheş. Anterior tip of AD with lateral lobes. Rostrum slightly longer than gnathosomal base. Seta on third article of palpus with terminal spines. Postero-ventral seta on tibia I denticulate, lateral claws smooth, no accessory tooth on middle claws.

COPIDOGNATHINAE. AE with a pair of gland pores. Palpi laterally inserted on rostrum, of 4 segments, at least the second clearly longer than wide, third without a seta.

Copidognathus Trouessart. Diagnosis as for the subfamily.

Copidognathus sp. 1 (similar to the unnamed species in Bartsch, 1972). Dorsal plates with small pores, more obvious on two longitudinal bands on the AD and PD. Mouthparts more than three times longer than gnathosomal base. Tibia I with one anterior pectinate seta, one short posterior branched seta, and seven normal setae.

Copidognathus sp. 2. AD with punctuation more visible on a H-shaped area. OC sickle-shaped, five times longer than wide. All leg segment flattened, with strongly punctuated lamellae, most obvious on telofemur I. Two anterior spiniform setae and one posterior pectinate seta on tibia I. Trochanter III with long thorn-like expansion.

C. gibbus Trouessart. Dorsal plates strongly convex, margins of AD and PD adjacent to each other. OC narrow, lateral. AD with a strong prominence covering the gnathosoma, and two lateral expansions towards the base of legs I on either side. Legs flattened, with wing-like expansions with strong punctuation.

Appendix. (continued)

Copidognathus sp. 4. Body flattened, egg-shaped in dorsal view. AD divided in one anterior and one posterior half. Posterior AD and PD with strongly punctuated costae, and reticulated intervals. OC as long as wide. Tarsus I minute, less than half the length of tibia I. Tibia I with one strong thorn and seven setae. Claws I more than twice smaller, as compared to claws II.

Copidognathus sp. 5. AD and PD with vague, uniform reticulation. OC sickle-shaped, twice longer than wide. Tibia I with one posterior pectinate seta, two anterior spiniform setae, and four normal setae. Claws with strong accessory process, as long as the main tip, and strong comb teeth.

C. bairdi ssp. *africanus* Bartsch. AD with four elevated areas, one anterior, elongated, two medial, round, and one posterior, transversal, all with clear punctuation; and one anterior prominence. OC with clear punctuation in the anterior half, and pointed posterior tip. PD with four costae, the medial ones strongly elevated. Ventral plates fused, sometimes PE separate.

Copidognathus sp. 7. AD with punctuation more visible on a H-shaped area. OC sickle-shaped, four times longer than wide. All leg segments flattened, but without wing-like expansions. Two short anterior spiniform setae and one posterior pectinate seta on tibia I. Trochanter III without thorn-like expansion. Anterior middle claws with rounded tooth.

Copidognathus sp. 8. Palpi twice longer than gnathosomal base. Tibia I with two slightly thicker setae, but no pectinate setae. Tarsi with square claw fossae, claws with around 12 long, fine teeth.

Copidognathus sp. 9. AD with three round elevated areas, one anterior and two posterior. PD with four costae, the medial ones strongly elevated. Ventral plates (AE, PE, AG) separate.

SIMOGNATHINAE. OC small or absent. Palpi short, of 2-3 segments, dorsally inserted on the triangular rostrum. Tarsus I forms a chela together with a spine on tibia I.

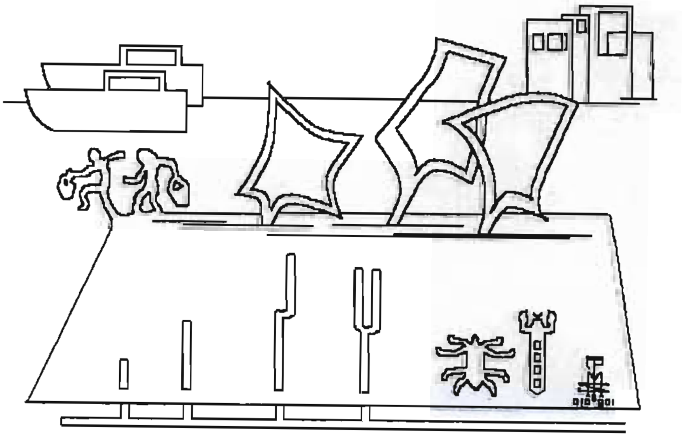
Simognathus Trouessart. Leg I with one strong median claw and two setiform lateral claws. Palpi of three segments.

S. glareus Bartsch. OC reduced, AE large, with uniformly distributed pores, posterior half strongly pigmented. PD small. Chela robust, with setal digit blunt.

Simognathus sp. 2. OC reduced, AE large, without pigmented areas, central area lacking pores. PD small. Chela weak, with setal digit pointed.

Section II

Ecology



Chapter V

Mangrove pneumatophore arthropod assemblages and temporal patterns

Abstract

Arthropod assemblages comprising mites, crustaceans and hexapods are characterized here for mangrove pneumatophores in southeastern Africa. Initial sampling showed that pneumatophore assemblages differed markedly from benthic sediment assemblages, not only in being more species rich, but also in having lower abundances. Differences among pneumatophore arthropod assemblages were observed in comparisons of two mangrove stands (in the Durban region) and habitats within each stand. Strikingly higher arthropod abundances were found in assemblages associated with pneumatophores on the seaward fringes of the mangrove stands, as compared to those situated inside the mangrove stands or along minor waterways. These differences in abundance are ascribed to differences in physical conditions among habitat types, relating to wetting frequency and sunlight exposure. The assemblages associated with minor waterways varied among themselves according to variations in salinity. Temporal variation in abundance showed that some species peaked in summer and others in winter, indicating effects more closely related to terrestrial seasonal patterns, than to seawater temperature. This study highlights the uniqueness of the mangrove pneumatophore arthropod assemblages, and the need for further investigation into these in order to better understand mangrove meiofaunal ecology.

Introduction

Mangroves are thought to play a major role in supporting tropical estuarine and coastal marine systems by providing an important source of organic material and acting as nursery grounds and habitats for fishes. The benthic meiofauna, in particular, is postulated to function in litter degradation in high detritus areas, and to provide prey for fishes (Alongi, 1987; Gee, 1989). Numerous investigations have documented the composition and abundance of meiofaunal species for a variety of mangrove systems around the world (see Alongi & Sasekumar 1992 for a review). These highlight the taxonomic complexity and variability of meiofaunas from one region to the next. The current investigation focuses on the meiofauna of the southeastern African mangroves, the subject of a few previous investigations (Dye, 1983a; 1983b; Ólafsson, 1995; Ndaro & Ólafson, 1999; Ólafson et al., 2000).

Most mangrove meiofaunal studies consider the assemblages associated with benthic sediments, with considerably less attention being given to other habitats, such as decaying mangrove litter layers (Gee & Somerfield, 1997) or stems and pneumatophores of mangrove trees. Pneumatophores of the mangrove tree, *Avicennia marina* (Forssk.) Vierh., in particular, not only provide large surfaces for the attachment of epiphytic plants and animals, but accumulate sediment that supports a suite of unattached biota. Additionally, pneumatophores experience considerably more variable physical conditions than benthic sediments. These arise from variable exposure to tidal and sunlight conditions along pneumatophore lengths and between pneumatophores, in relation to their position in a mangrove stand, and are likely to increase microhabitat diversity and hence species richness.

While some investigations on pneumatophores have considered algal communities (Wilkinson et al., 1981; Aikanathan & Sasekumar, 1994; Phillips et al., 1994; 1996), cyanobacteria (Potts, 1980), fungi (Hyde, 1990), barnacles and other sessile animals (Farnsworth & Ellison, 1996; Saturmanatpan et al., 1999) associated with pneumatophores, virtually nothing is known about the meiofaunas inhabiting these structures. Estuarine meiofaunal studies classically consider nematodes and harpacticoid copepods, with relatively less attention given to groups such as mites and hexapods (collembolans and dipterans), even though these are common components of marine intertidal systems (Cheng, 1976; Pugh & King, 1985; Thibaud & Christian, 1997). The only known ecological studies considering estuarine mites concern temperate saltmarsh systems (Luxton, 1966; 1967a; 1967b).

The objectives of the current study were therefore as follows: 1) to characterize the marine arthropod assemblages associated with mangrove pneumatophores; 2) to determine whether these differ from benthic sediment assemblages; and 3) to examine spatial and temporal variability in assemblage structure within and between mangrove stands.

Materials and Methods

Study area

Sampling was undertaken at two localities (Beachwood and Bayhead Lagoon) near Durban, KwaZulu-Natal, South Africa, between June 1999 and June 2000. The mangrove stand at

Beachwood (~44 ha) is located at the mouth of the Umgeni River, while the one at Bayhead (~15 ha) is located in the Durban harbour, approximately 10 km south of Beachwood (Figure 1; Ward & Steinke, 1982). Nine sites were established at each locality (see Figure 1). Site selection took account of three apparently different sets of environmental conditions that the pneumatophores are likely to experience: the pneumatophores growing at the seaward edge of a mangrove stand (fringe, sensu Woodroffe, 1992) experience typical tidal conditions and fairly normal salinities (25 – 35); those associated with minor waterways such as creeks (riverine) are exposed to reduced salinities (below 15) arising from freshwater inflow (Phillips et al., 1994, 1996), and those located deep inside mangrove stands (basin), experience limited sunlight exposure, infrequent wetting and variable salinities. No fringe sites were available at Beachwood, dictating the selection of six riverine and three basin sites there, whereas at Bayhead, three of each habitat type was selected (see Fig. 1 for site locations and numbering details).

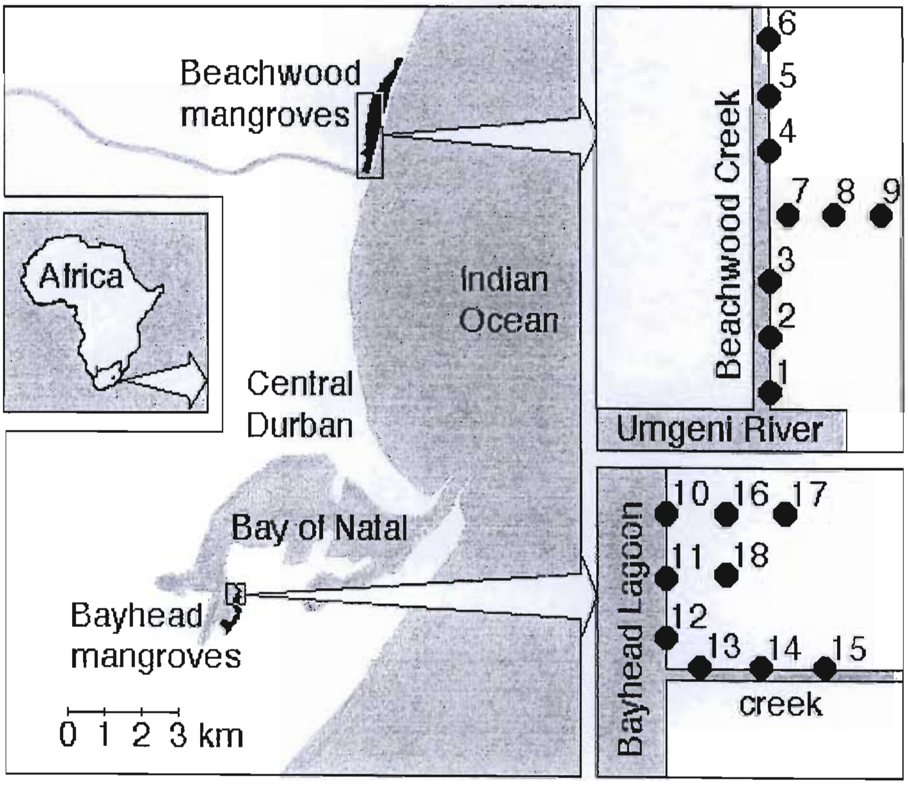


Figure 1. Map of Durban with the position of the collecting sites. The distance between adjacent sites is roughly 50 m.

Sample collection and abundance determination

In the initial study to assess how pneumatophore and benthic sediment meiofaunas compare, samples were collected from the Bayhead fringe and riverine sites (sites 10 – 15), as they contained the most abundant faunas. The spatial studies included sampling from all eighteen sites of the two localities, on three separate occasions (August, October and December 1999). For the assessment of temporal abundance patterns, additional sampling was undertaken at Bayhead (sites 10 – 15), in February, April and June 2000. On each sampling occasion, five randomly selected replicate samples were collected, comprising the *Avicennia* pneumatophores within a 15 x 15 cm area, or in the case of benthic sediments, the upper 1 cm of sediment within a disc area of 22.5 cm^2. Pneumatophores were cut at ground level and placed in plastic bags. In the laboratory they were washed over two sieves (5 mm and 0.1 mm), to retain all the mites, copepods, collembolans, tanaidaceans, isopods, amphipods and dipteran larvae. These arthropods were preserved in 70% ethanol for later identification, sorting and counting.

The extraction procedure followed two steps. Firstly, the mites, tanaidaceans and some insect larvae were extracted from each ethanol sample by hypersaline flotation (Fain & Hart, 1986). The remainder of the sample, which contained mainly copepods and insect larvae, was then brought to a homogeneous aqueous solution of standard volume (50 ml). This was then sub-sampled to give three 5 ml volumes. The number of arthropods in each sub-sample was determined, averaged, and multiplied by ten to obtain an estimate for the entire 50 ml sample. The total number of individuals of the various taxa for the sample was obtained by addition of the numbers in each fraction (hypersaline and aqueous). Benthic samples were treated as above; at the end of the procedure both pneumatophore and sediment values were normalized to 0.1 m^2. Attempts were made to resolve taxa down to species, but in the **cases** of taxonomically complex groups, more than one species was counted together. Samples were counted under X100 magnification using a dissecting microscope.

Statistical procedures and data presentation

Using the data for August, October and December 1999, mean abundances (individuals in 0.1m^2; N = 45) were determined for each group of three sites (1 – 3, 4 – 6, 7 – 9, 10 – 12, 13 – 15, 16 – 18; see Figure 1). Because numbers and lengths of the pneumatophores varied among quadrats, total pneumatophore length was also determined. Paired t-tests were used to assess significant differences in abundance of taxa in pneumatophore and benthic sediments. To see how closely the sites were associated with one another in terms of species composition and abundance, a non–metric multidimensional scaling ordination (MDS) was performed from a Bray-Curtis dissimilarity model, using 4th root transformed abundance values to account for rare taxa (Clarke & Warwick, 1994). Plots are given for temporal variations in abundance, as well as for abundances of some Beachwood riverine taxa along a salinity gradient. All statistical procedures were undertaken using SPSS ver. 9.0 for Windows (1999).

Results

Species composition and abundance

The mesoarthropod fauna of southern African mangroves comprises three similarly species diverse, taxonomic groups: mites (Acari – mesotigmatids, prostigmatids, and oribatids), crustaceans (copepods, tanaidaceans, isopods and amphipods) and hexapods (collembolans and dipterans) (Table 1). Thirty taxa in total were identified, however, this excludes some copepod taxa that were not readily discernible. Of the twenty-two easily identifiable taxa, twelve were found at both Bayhead and Beachwood, while four and six were exclusive to Beachwood and Bayhead, respectively (Table 1).

Arthropod faunas of the benthic sediment below pneumatophores differed markedly from those associated with the pneumatophores themselves. Of ten taxa, four were more abundant on the pneumatophores, two were more abundant in the sediment, and four showed no significant differences between the two habitat types (Figure 2). The most abundant taxon in the sediment (Harpacticoidea, 1900 individuals for 0.1 m^2) differed by one order of magnitude from the most abundant taxon on the pneumatophores (*Tanais*, 190 individuals for 0.1 m^2). The mites (Acari) were restricted to pneumatophore habitats. Different groups of crustaceans dominated on the pneumatophores (tanaids), and in the sediment (harpacticoids). Generally, dipteran larvae showed similar abundances, both in the sediment and on the pneumatophores, but the Empidoidea were more abundant in the sediment (Figure 2).

The crustaceans were the most abundant pneumatophore mesoarthropods (~100 individuals for 0.1 m^2), followed by the mites (~60 individuals) and then the hexapods (~30 individuals). Crustacean abundance was dominated by the abundance of tanaidaceans, though this varied among sites (0 to ~430 individuals for 0.1 m^2). Occupancy was higher than 10% in most species from the three taxonomic groups, but highest in *Leioseius*, a mite present in relativey low abundances. The greatest arthropod abundance was found at the Bayhead fringe sites (~900 individuals for 0.1 m^2) (Table 2). Overall abundances were overwhelmingly influenced by the fringe arthropods and particularly the dominant species of each major taxonomic group, *Copidognathus* (Acari), *Tanais* (Crustacea) and *Culicoides* (Hexapoda) (Table 2). Although total pneumatophore lengths were variable among groups of sites, there was apparently no relationship between total mesoarthropod abundance and total pneumatophore length (Table 2).

Table 1. Mesoarthropod taxa occuring in mangrove pneumatophores and benthic sediment. (Asterisks indicate putative complexes of species.)

		TAXA		Further referred to as:
Acari	Mesostigmata	Ascidae:	*Leioseius* sp. nov.	*Leioseius*
		Uropodidae:	*Uroobovella* sp.	*Uroobovella*
	Prostigmata	Nanorchestidae	*Nanorchestes* sp.	*Nanorchestes*
		Halacaridae:	*Copidognathus caloglossae*	*Copidognathus*
			Acarothrix umgenica	*Acarothrix*
			Agauopsis sp. nov.	*Agauopsis*
		Tydaeidae indet.		Tydaeidae
		Tarsonemidae indet.		Tarsonemidae
	Oribatida	Oribatulidae indet.		Oribatulidae*
Crustacea	Copepoda	Harpacticoidea:		
		Canthocamptidae: *Amphibiperita* sp.,		
		Diosaccidae:	*Robertsonia robusta*, etc.	Non–metid Harpacticoidea*
		Metidae:	*Metis* sp. nov.	*Metis*
	Tanaidacea	Tanaididae	*Tanais philetaerus*	*Tanais*
	Isopoda	Sphaeromatidae indet.		Sphaeromatidae
	Amphipoda	Hyalidae	*Hyale grandicornis*	*Hyale*
		Melitidae	*Melita zeylanica*	*Melita*
		Podoceridae indet.		Podoceridae
		Corophiidae:	*Corophium triaenonyx*	*Corophium*
Hexapoda	Poduromorpha	Neanuridae:	*Anurida maritima*	*Anurida*
	Diptera	Tipulidae indet.		Tipulidae
		Cecidomyiidae:	Lestremyiinae indet.	Cecidomyiidae
		Empidoidea indet.		Empidoidea*
		Ceratopogonidae:	*Culicoides* sp. nov.	*Culicoides*

Table 2. Abundance of mangrove pneumatophore arthropods (mean ±SE for 0.1 m^2; N=45 for groups of three sites, n=270 for the grand mean). Total pneumatophore length (cm) is also given.

	Beachwood			Bayhead				
Taxa	Riverine sites 1–3	Riverine Sites 4–6	Basin Sites 7–9	Fringe Sites 10–12	Riverine Sites 13–15	Basin Sites 16–18	Grand mean sites 1–18	Occupancy (%)
Leioseius	8.12 ±1.84	4.58 ±0.82	4.56 ±1.06	10.00 ±1.53	6.88 ±1.37	3.51 ±0.85	6.31 ±0.54	50.00
Uroobovella	–	0.29 ±0.29	0.30 ±0.22	43.03 ±5.89	3.10 ±1.11	0.61 ±0.34	7.77 ±1.37	21.85
Nanorchestes	0.77 ±0.32	2.33 ±0.59	2.14 ±0.60	2.32 ±1.16	–	0.03 ±0.03	1.26 ±0.25	14.44
Copidognathus	–	–	–	223.61 ±37.96	16.26 ±6.03	3.92 ±1.33	40.06 ±8.06	29.63
Acarothrix	0.77 ±0.40	13.92 ±2.29	3.62 ±1.24	–	–	–	3.10 ±0.54	18.89
Tydaeidae	0.77 ±0.32	0.88 ±0.43	5.52 ±1.68	–	–	0.10 ±0.10	1.23 ±0.32	10.74
Tarsonemidae	1.06 ±0.35	0.97 ±0.48	0.11 ±0.10	–	–	–	0.36 ±0.10	5.56
Oribatulidae	1.16 ±0.57	0.98 ±0.28	1.46 ±0.68	0.61 ±0.23	1.07 ±0.35	0.68 ±0.24	1.00 ±0.18	16.67
Total Acari	11.94 ±2.21	24.39 ±2.99	17.97 ±3.46	276.81 ±42.65	27.84 ±7.74	8.00 ±1.70	61.10 ±9.30	
Non-metid Harpacticoidea	3.28 ±1.02	0.12 ±0.10	–	26.77 ±5.26	10.35 ±3.07	1.27 ±0.48	7.05 ±1.19	29.26
Metis	–	–	–	21.80 ±9.09	15.01 ±6.14	3.39 ±1.64	6.63 ±1.92	12.96
Tanais	38.55 ±8.02	1.72 ±0.94	0.12 ±0.10	432.48 ±50.80	15.52 ±4.05	14.82 ±3.07	85.50 ±12.93	49.26
Sphaeromatidae	–	–	–	1.41 ±0.56	0.77 ±0.35	0.01 ±0.01	0.36 ±0.11	5.56
Hyale	1.45 ±1.00	1.37 ±0.48	2.43 ±1.25	–	–	–	0.89 ±0.28	7.78
Melita	6.57 ±2.12	1.21 ±0.72	1.08 ±0.47	0.40 ±0.31	0.50 ±0.21	1.07 ±0.70	1.82 ±0.42	15.19

Table 2. (continued).

	Beachwood			Bayhead				
Taxa	Riverine sites 1–3	Riverine Sites 4–6	Basin Sites 7–9	Fringe sites 10–12	Riverine Sites 13–15	Basin Sites 16–18	Grand mean sites 1–18	Occupancy (%)
Podoceridae	0.10 ±0.10	–	0.10 ±0.10	–	–	–	0.03 ±0.02	0.74
Corophium	0.39 ±0.39	0.01 ±0.01	0.10 ±0.10	–	–	–	0.08 ±0.07	0.74
Total Crustacea	51.35 ±10.15	4.25 ±1.72	3.85 ±1.55	494.36 ±53.41	43.00 ±9.16	19.56 ±4.21	102.37 ±14.08	
Anurida	–	–	–	23.84 ±6.01	11.23 ±2.76	1.77 ±1.28	6.33 ±1.25	22.22
Cecidomyiidae	0.10 ±0.10	1.64 ±1.32	0.03 ±0.03	7.98 ±3.47	0.39 ±0.19	0.17 ±0.12	1.71 ±0.64	5.93
Empidoidea	0.29 ±0.17	0.68 ±0.28	2.13 ±2.05	5.05 ±1.49	0.89 ±0.27	1.87 ±1.06	1.82 ±0.47	15.16
Culicoides	0.10 ±0.10	0.58 ±0.30	0.30 ±0.17	120.39 ±23.19	2.68 ±1.21	15.86 ±3.41	23.14 ±4.71	28.89
Total Hexapoda	0.49 ±0.21	2.96 ±1.35	2.47 ±2.08	158.01 ±28.67	15.41 ±3.03	19.35 ±4.07	32.99 ±5.91	
Total mesoarthropods	63.80 ±10.40	31.60 ±4.19	24.29 ±5.57	929.18 ±112.67	86.26 ±11.83	46.91 ±7.97	196.46 ±27.45	
Total pneumatophore length	222.11 ±33.11	285.39 ±42.54	241.35 ±35.98	285.93 ±42.62	224.42 ±33.45	114.03 ±17.00	272.60 ±16.59	

Comparisons of assemblages within and between localities

The multidimensional scaling ordination showed a clear distinction between the Beachwood and Bayhead assemblages (Figure 3). This was largely due to differences in species composition at each locality (see Table 2; only twelve of the twenty taxa were common to the two localities). The riverine and basin assemblages were separated at both localities, and showed similar patterns of association for each locality (Figure 3).

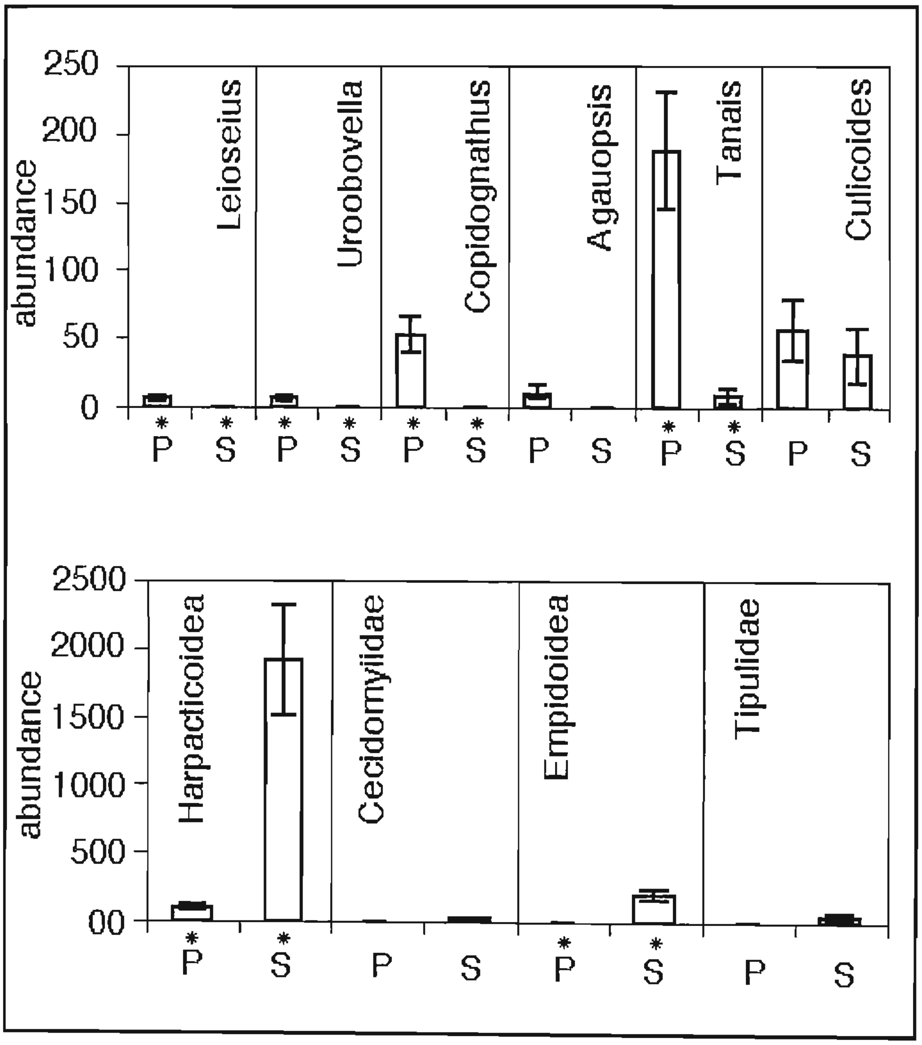


Figure 2. Abundances (mean ±SE for 0.1 m^2; N=30) for arthropod taxa on the pneumatophores (P) and in the benthic sediment (S). Pairs of asterisks indicate significant differences between the pneumatophores and the sediment (paired t-test, P<0.05).

At Bayhead, the fringe assemblages were, however, closely associated, and broadly separated from both the basin and riverine assemblages, an effect attributable to the greater species abundances in the fringe assemblages. Separation of the assemblages at riverine sites in Beachwood, seemed to be influenced by a salinity gradient along the Beachwood Creek. The ordination showed that the assemblages were separated almost linearly from site 1 to site 6 (Figure 3), which respectively represented the highest and lowest salinities of the gradient. Assemblage differences were apparently linked to changing abundances of the dominant taxa along this gradient; abundances of the two dominant crustacean taxa decreased (Figure 4), while those of the halacarid mite *Acarothrix*, increased along the gradient of decreasing salinity. Abundances of the predatory mesostigmatid mite, *Leioseius*, were seemingly independent of salinity (Figure 4).

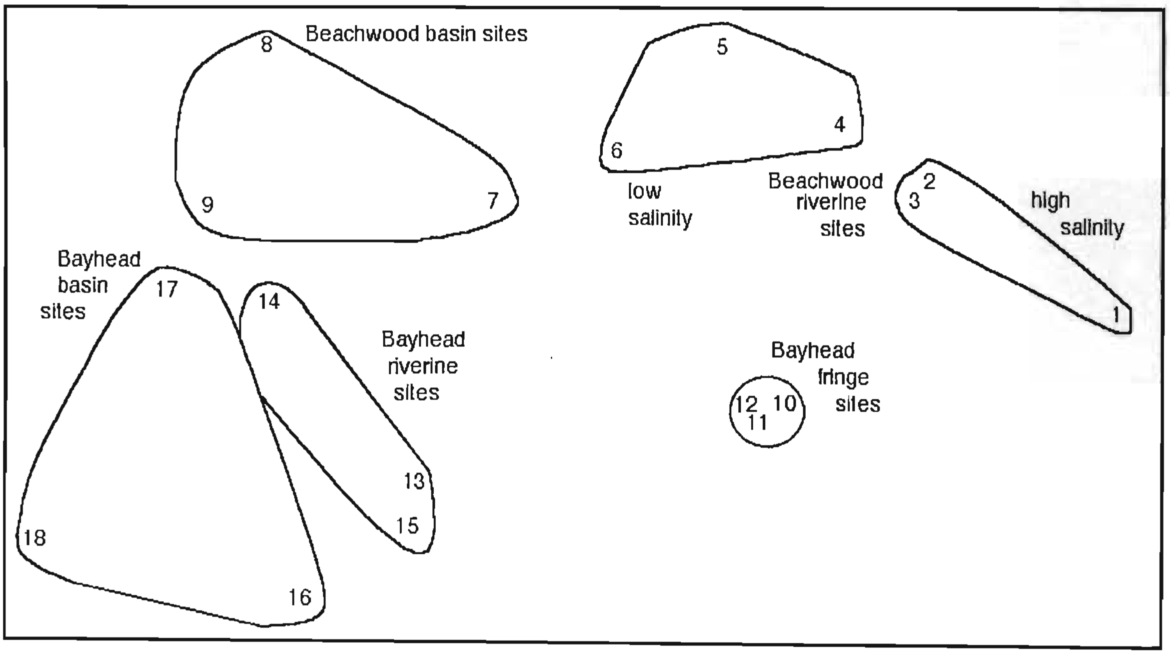


Figure 3. MDS plot for the arthropod assemblages in the 18 sample sites (stress = 0.13).

Temporal variation

The abundance values for all the mesoarthropods combined showed a prominent summer and a less prominent winter peak (Figure 5). These patterns were to a large extent influenced by the three most dominant species (*Copidognathus* (Acari), *Tanais* (Crustacea) and *Culicoides* (Hexapoda) (Table 1)). Some of the less abundant species showed slightly different trends (e.g. Empidoidea and Harpacticoidea; Figure 5).

Discussion

Comparisons between pneumatophores and the benthic sediment

We show here that the mesoarthropod assemblages associated with mangrove pneumatophores differ considerably from those of benthic sediments. A new suite of arthropods, containing tanaidaceans and mites, was found exclusively on the pneumatophores investigated, and abundances of other species varied greatly between pneumatophores and benthic sediments. The single known study concerning pneumatophore meiofaunas, shows abundances to be lower on pneumatophores relative to benthic sediments (see Alongi & Sasekumar, 1992), but this excludes mites and tanaidaceans. Even though mites are known to colonize mangrove benthic sediments (Bartsch, 1990; Gee & Warwick, 1996; Chapman, 1998), they were absent from these in the present investigation. Tanaidaceans have been reported in relatively few mangrove meiofaunal studies (Branch & Grindley, 1979; Gee & Warwick, 1996; Chapman, 1998), and the extent to which they colonize benthic sediments remains unclear.

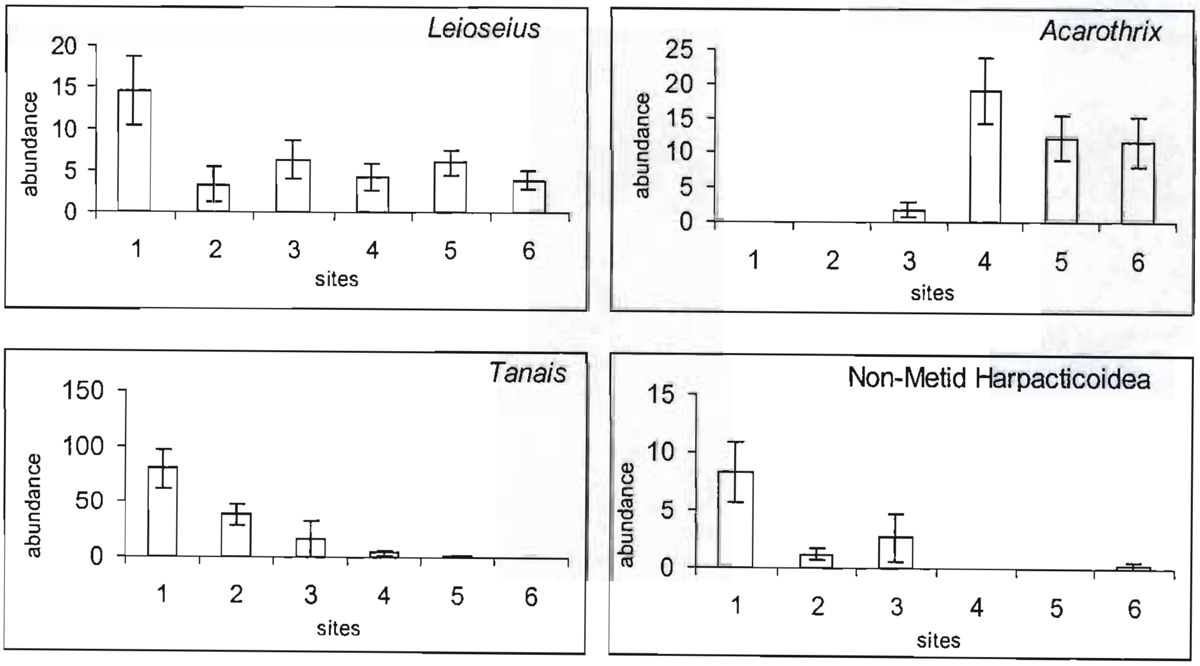


Figure 4. Abundance values (mean ±SE for 0.1 m^2; N=15) for four arthropod taxa at sites 1–6. Salinity decreases from site 1 to site 6.

Spatial and temporal variability in marine meiofaunal assemblages has been attributed to a variety of biotic factors (including food availability) and habitat conditions. For example, in lotic systems, biotic interactions include large scale effects resulting from fish predation and small scale effects resulting from meiofaunal predation (Swan & Palmer, 2000). Another example for deep–sea sediments, ascribes variability to worm–related disturbance (Gage, 1997). Habitat conditions of relevance include sediment particle size, habitat salinity and the

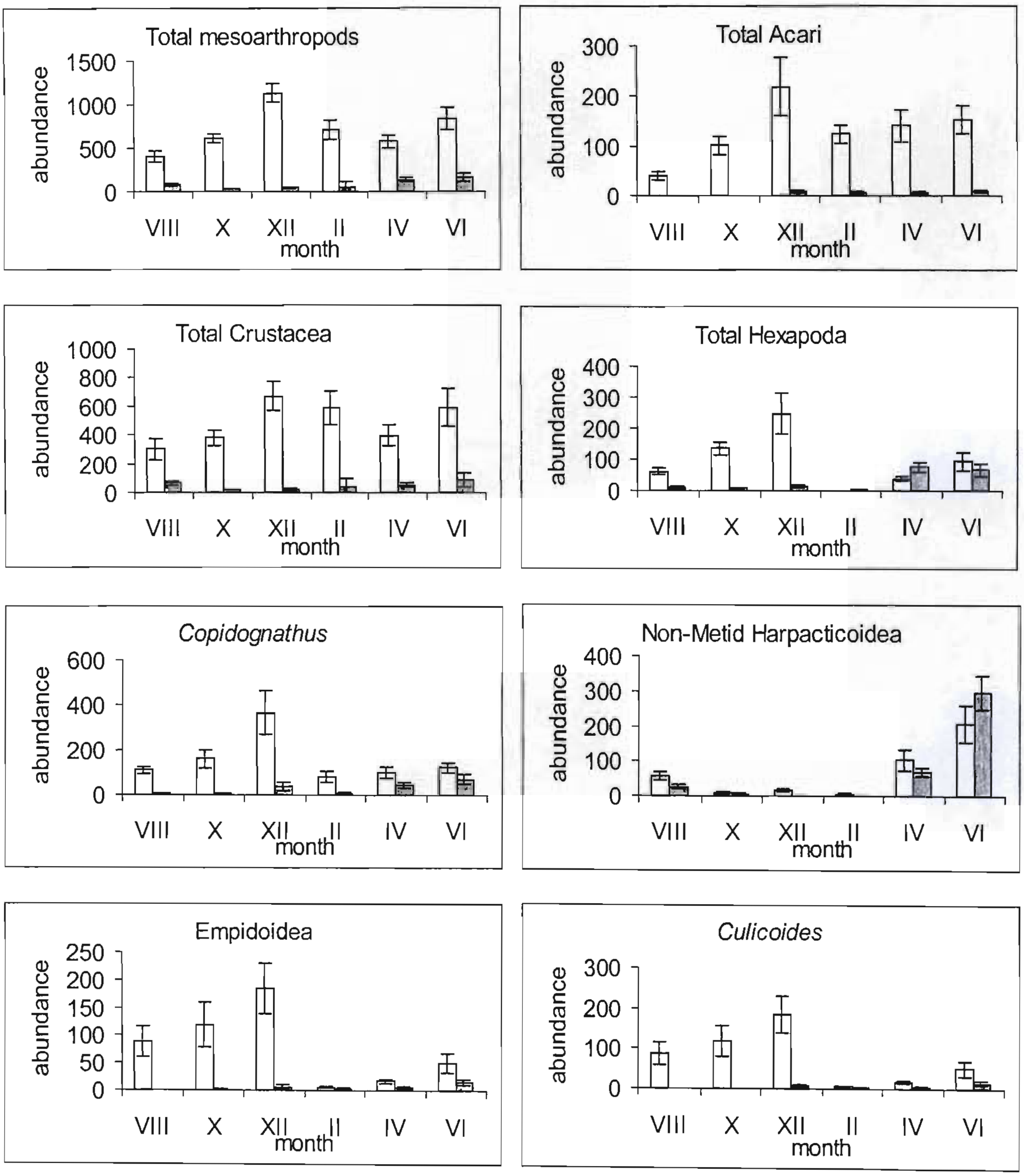


Figure 5. Mean abundance values (for 0.1 m^2; N=5) for arthropods in sites 10–16 at six moments (August, October, December 1999, February, April, June 2000). White bars, fringe sites (10-12); grey bars, creek sites (13-15).

potential for dehydration (Alongi & Sasekumar, 1992; Ólafsson et al., 2000). Salinity is known to vary considerably in relation to position on the shore, and depressions in the sediment (Phillips et al., 1996; Chapman, 1998; Ólafsson et al., 2000). Probably the greatest cause of the observed increase in species richness on pneumatophores relative to benthic sediments, derives from the physical and structural attributes of the pneumatophores. Pneumatophores introduce a unique structural feature to the physical environment of mudflats, which significantly increases habitat complexity (Beck, 2000). Additionally, they provide surfaces for the attachment of sessile biota (for example, algae, barnacles), which form a habitat for other smaller biota (for example, mites). Furthermore, pneumatophores experience differential dehydration along their lengths during air exposure (following tidal recession). The exclusive occurrence of some taxa on pneumatophores may well relate to their enhanced capacities to withstand dehydration.

Comparisons of assemblages between and within mangrove stands

A second definitive result is that the meiofaunal arthropod assemblages of pneumatophores vary remarkably among mangrove stands, and within stands depending on the position relative to the edge, and to minor waterways. The way in which assemblages change in tandem with changes in salinity between Bayhead and Beachwood, and between sites at the latter, suggests the predominant role of salinity in structuring these assemblages. Numerous other studies have suggested how salinity influences mangrove meiofaunal assemblages (Ólafsson, 1995; Somerfield et al., 1998; Ndaro & Ólafsson, 1999, Ólafsson et. al., 2000). Differences between the fringe and basin pneumatophore assemblages apparently also relate to differences in habitat conditions; fringe pneumatophores experience a higher frequency of wetting and are often exposed to direct sunlight. At least the latter condition is likely to yield greater algal productivity, and thus support larger meiofaunal colonies. This would explain the considerably greater arthropod abundances associated with fringe pneumatophores relative to basin pneumatophores. The lower species richness of fringe assemblages is probably explained by the loss from these assemblages of dehydration intolerant species, as exposure to direct sunlight causes rapid dehydration of these pneumatophores, compared to basin pneumatophores which are shaded by the tree canopy.

Temporal patterns

The temporal patterns of the mangrove pneumatophore arthopods are open to interpretation in terms of terrestrial or marine variations in climatic conditions. Because there is very little variation in the seawater temperature conditions during the year (the warm Agulhas current in the region keeps this parameter between 20 and 25°C year round; Bolton & Anderson, 1997), it is unlikely that the arthropods are at any moment limited by either low, or high seawater temperatures, as compared to the rest of the year. More likely, the observed patterns relate to terrestrial conditions. Summers in Durban are considerably hotter and wetter than winters (when temperatures often fall below 15°C; Cockcroft & Forbes, 1981). The observed differences among taxa in seasonal abundances may relate to their different preferences of air temperatures prevailing at different times of the year. Besides temperature, the decrease in salinity caused by summer rainfall can be taken into consideration. However, the occurrence of summer peaks in taxa which apparently prefer relatively low salinity conditions as well as those which prefer relatively high salinity conditions, suggest that salinity variation caused by summer rains can be discounted as a factor influencing abundance variation among taxa.

Concluding remarks

In summary, we show that mangrove pneumatophores provide an additional dimension of habitat to the mud surface below them, and that the physical characteristics of this habitat explain differences between pneumatophore and sediment assemblages. While we show that pneumatophore arthropod assemblages differ at two different spatial scales: between and within mangrove stands, it is obvious that complex gradients of habitat conditions must exist over a variety of spatial scales. There is certainly scope to investigate much finer scales than those considered here. For instance, it would be interesting to know whether vertical gradients of assemblages exist along the pneumatophore length, considering the potential for differential dehydration along pneumatophores. Even more challenging would be to consider the scale of the sediment particle, which presumably represents the actual habitat space of some of the smaller meiofauna, like nematodes and copepods.

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Chapter VI

Assemblage structure of two phylogenetically distinct arthropod groups inhabiting mangrove pneumatophores

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Abstract

Intertidal marine habitats support two groups of evolutionary widely-separated arthropods; one having had a long marine evolutionary history (e.g. crustaceans) and the other, comprising relatively recent colonizers (e.g. insects). Secondary marine ('terrestrial') taxa generally differ from their typically 'marine' counterparts with respect to physiological and life history traits, and biological interactions. For example, many taxa have enhanced capacities to tolerate desiccation, and exhibit weak interspecific interactions. These propositions are examined here by considering the ecological patterns of coexisting 'terrestrial' and 'marine' arthropods on mangrove pneumatophores. Species abundances of nine taxa (five 'terrestrial' including acarine and dipteran species, and four 'marine' including halacarid mite and copepod species) were compared along an ecological stress gradient, by considering three pneumatophore elevations for pneumatophores exposed to direct sunlight or in the shade. No clear distribution pattern emerged to suggest that the 'terrestrial' arthropods were more tolerant of desiccation stress than the 'marine' arthropods. The 'terrestrial' arthropods, which occurred in lower abundance, showed greatest abundance at the lowest pneumatophore elevation, whereas the 'marine' arthropods were more abundant on the middle and upper pneumatophore segments. These patterns however closely mirrored those of the most dominant species for each group. Marked reductions in abundance of both groups of arthropod in the sun, as compared to the shade, are interpreted as relating to limited food resources on sunned pneumatophores. Abundance covariations for both groups of species and all species combined indicated highly significant positive interactions for pneumatophores in the sun, but not those in the shade. This is interpreted as an increase in competition among species (regardless of evolutionary background) arising from synchronized fluctuations in populations tracking a limited resource, under conditions of environmental stress. The similarity of this response in both evolutionary groups suggests that they may not be as ecologically disparate as previously thought. There are marked differences in ecological patterns among primary and secondary marine arthropods

for some taxa and some intertidal habitats, but this investigation highlights the limitations of generalizing among taxa and habitats for either group.

Introduction

The need to include historical perspectives into community ecological investigations has been realized for some time (Brooks, 1985; Waring, 1989; Wanntorp et al., 1990), but there are numerous and seemingly insurmountable difficulties in achieving this (Holt, 1995). A simple approach would require examining an ecological situation comprising evolutionary distinctive taxonomic groups. While most ecological systems support taxa having diverse historical backgrounds, in only a few are the differences in evolutionary history as clear as those found in some marine intertidal systems. These usually support invertebrate taxa of marine origin, e.g. cnidarians, annelids, molluscs, crustaceans, echinoderms (hereafter primary marine or 'marine') as well as taxa of recent terrestrial descent, e.g. insects and mites (hereafter secondary marine or 'terrestrial') (Glynne-Williams & Hobart, 1952; Morton, 1954; Chapman, 1998).

Differences in the evolutionary origin of the two groups appear to have different consequences in respect of their ecological and biogeographical distributions (Procheş & Marshall, 2001a). For example, the restricted distribution of most 'terrestrial' arthropods to intertidal habitats (as opposed to sub-tidal habitats), relates to phylogenetically constrained physiological, life history and dispersal traits associated with their earlier terrestrial backgrounds (Little, 1990; Vermeij & Dudley, 2000). More specifically, their life history traits include, low fecundity (egg production), long generation times, and complex life-cycles (cf. dipteran larval stages), and no 'terrestrial' arthropods produce pelagic larvae nor have the capacity for aquatic respiration. Even though the evolutionary constraints of many 'terrestrial' arthropods present fertile ground for investigation, their ecology remains poorly known. The few ecological studies concerning rocky-shore, salt marsh and estuarine mites, are mostly not quantitative (Luxton, 1967a; 1967b; Pugh & King, 1985a; 1985b; 1988; but see Kronberg, 1988; Mercer et al., 2000; Procheş et al., 2001), and none concern both primary and secondary marine taxa, nor integrate evolutionary aspects into ecological interpretations.

Identifying the patterns and understanding the underlying processes which influence variations in assemblage structure across vertical gradients, is an integral facet of intertidal ecology (Underwood & Denley, 1984; Menge et al., 1994; Roughgarden et al., 1994;

Underwood & Chapman, 1996; Connolly & Roughgarden, 1999). In general, intrinsic physiological capacities of species for tolerance of physical stress determine upper shore distribution limits, whereas low shore limits are largely influenced by biological interactions (Menge, 2000). While this applies to most typically marine intertidal invertebrates and especially to rocky shore situations, there is evidence to suggest that the opposite is applicable in the case of secondary marine arthropods. They are intolerant of both submersion and wave action, but are relatively more tolerant than 'marine' arthropods of air exposure and desiccation (Neumann, 1976; Schulte, 1976a; 1976b; Witteveen & Joosse 1987; 1988; King et al., 1990; Pugh et al., 1990; Chown & van Drimmelen, 1992; Mercer et al., 2001). While biological interactions probably largely influence the structuring of their upper-shore assemblages, some evidence suggests that interactions between 'terrestrial' and 'marine' taxa are weak or non-existent (for example, some predatory mites feed only on other 'terrestrial' species) (see Procheş & Marshall, 2001a).

This investigation, undertaken to compare the ecological patterns of arthropods from different evolutionary backgrounds, considered intertidal mangrove pneumatophore taxa. Pneumatophores are particularly suitable for a study of this nature, in that 1) they support a variety of arthropods from the two evolutionary-distinct backgrounds, 2) the arthropods can be readily collected and quantified, without loss of specimens, by cutting and bagging pneumatophore segments, 3) vertical intertidal zonation patterns can be assessed by considering different pneumatophore lengths (Phillips et al. 1994, 1996), and 4) their habitat structure is easily definable (Beck, 1998; 2000). Although numerous studies have considered mangrove meiofauna (usually excluding 'terrestrial' taxa), these concern mainly benthic sediments rather than the pneumatophores themselves (see Procheş et al., 2001). The present investigation intended to determine whether the evolutionary-distinct groups respond in different ways to physical environmental conditions and with respect to their biological interactions. More specifically, it considered whether 1) intertidal vertical distributions and abundances of species differed between the two evolutionary groups, 2) species interactions were stronger within than between the groups of different origin, and 3) interactions between and within these groups vary with varying degrees of physical stress.

Material and methods

Sampling locality

Mangroves are found in isolated stands in estuaries and bays along the eastern seaboard of southern Africa, and typically comprise three widespread tree species, *Avicennia marina* Forsk. (Vierh.), *Bruguiera gymnorrhiza* (L.) and *Rhizophora mucronata* Lam. (Macnae, 1963). We sampled *Avicennia marina* pneumatophores from the Bayhead mangrove forest in the Durban Harbour, South Africa, (approximately 15 ha; 29° 53' S, 30° 61' E, Ward & Steinke, 1982). An earlier study describing pneumatophore arthropod assemblages identified the seaward fringe pneumatophores at Bayhead as being the most abundant and diverse (Procheş et al., 2001). These became the focus of the present study, which was undertaken in March 2000.

Mangrove pneumatophore arthropod taxa

Only the most abundant arthropod species (taxa) were considered here, including mites (Acari), dipterans, copepods and tanaids, giving four primary marine and five secondary marine taxa (see Table 1 for taxonomic details). The secondary marine ('terrestrial') taxa included insects and mites, but excluded the typically marine mite family, Halacaridae (see Bartsch, 1989; 1996; Abé, 1996). The taxa are usually referred throughout by family (or superfamily) name, as indicated in the table. In all but two cases, the taxa represent single species; the Empidoidea contains three species from two families, while the Harpacticoidea comprise two species from two families (see Table 1). Species of these taxa could not be distinguished under the dissecting microscope.

Sample collection and processing

Twenty by one meter long line transects were established; ten in a shaded area (approximately 3m X 3m) and ten in an area exposed to direct sunlight for most of the day (approximately 3m X 3m, and 5 m from the shaded area). The areas were otherwise similar with respect to tidal position (110 - 120 cm above low spring tide level), and density and length of pneumatophores (400 – 500 pneumatophores/ m^2, 10 - 25 cm long). Considering that habitat usage in most of the meiofaunal arthropods is not much greater than the size of a thumbnail, and that colonization and recruitment is limited (Procheş & Marshall, 2001b), it was assumed that each transect represented an independent site.

Table 1. Taxonomic information for the 'terrestrial' and 'marine' arthropods investigated.

	Class, Order, Suborder	Family (sub/super)	Genus/ species
'Terrestrial'	Acari: Mesostigmata	Ascidae	*Leioseius* sp.
	Acari: Mesostigmata	Uropodidae	*Uroobovella* sp.
	Insecta: Diptera	Cecidomyiidae: Lestremyiinae	*Lestremyinae* sp.
	Insecta: Diptera	Empidoidea	*Empidoidea* sp. [1]
	Insecta: Diptera	Ceratopogonidae	*Culicoides* sp.
'Marine'	Acari: Prostigmata	Halacaridae: Copidognathinae	*Copidognathus* sp.
	Crustacea: Copepoda	Harpacticoidea	*Harpacticoidea* sp. [2]
	Crustacea: Copepoda	Harpacticoidea: Metidae	*Metis* sp. nov.
	Crustacea: Tanaidaea	Tanaididae	*Tanais philetaerus* Stebbing

[1] A complex of three species from two families. [2] Harpacticoidea other than Metidae; complex of two species: *Amphibiperita* sp. (Canthocamptidae) and *Robertsonia robusta* Wells & Rao (Diosaccidae).

Ten pneumatophores longer than 15 cm were randomly selected from each transect and cut at ground level. They were then cut into 5 cm long segments, to give three segments representing vertical heights from the substratum of 0-5 cm, 5-10 cm and 10 - 15 cm. The ten segments for each vertical height were bagged together, to give three height-based sampling units for each transect. The pneumatophore tips above 15 cm were discarded, and recumbent or branched pneumatophores were avoided. The pneumatophore samples were returned to the laboratory and washed over a sieve to retain organisms larger than 0.12 mm. These were preserved in 70% ethanol (25 ml plastic sample bottles) for later extraction, identification, and counting.

By considering both vertical height, and sun and shade conditions, the sampling procedure included a range of desiccation effects. Evaporative water loss from pneumatophore surfaces occurs more rapidly in the sun than the shade and increases with increasing vertical height. Furthermore, the lower parts of pneumatophores are wetted more frequently and for longer periods with changing tidal conditions (see Phillips et al., 1994; 1996).

In order to extract the mites, tanaids, and some insect larvae, the contents of the bottles were first treated with hypersaline solution (see Fain and Hart, 1986). All floating specimens were removed from the sample bottles, identified and counted under a dissecting microscope (X 100 magnification). The remaining fraction was then brought to a 50 ml volume homogeneous aqueous solution. Three by 5 ml sub-samples were taken from this solution and the arthropods contained (mainly copepods and insect larvae) were determined and counted. The average number of individuals per 50 ml volume was derived by multiplication. The total number of individuals for each sample was determined by addition of each fraction. From the ten replicate transects, mean abundances of each arthropod species, and that of total 'terrestrial' or 'marine' arthropods (number of individuals per 10 pneumatophores) were determined for each vertical level, for pneumatophores in the shade and sun.

Statistical analysis

Two-way ANOVA's (applied on log-transformed data) were used to assess significant levels of the effects of sunlight and elevation on abundance, for the species (species against sunlight and species against elevation), and evolutionary groups (groups against sunlight and groups against elevation). As a first measure of species interactions, Pearson's correlation coefficients were determined for abundances of species pairs, without considering elevation or sunlight condition. Both within ('terrestrial' or 'marine' species) and between ('marine' versus 'terrestrial' species) evolutionary group relationships were determined.

A second analysis considered species abundance covariation (according to Schluter, 1984). This analysis determined the ratio of the variance (V) for total abundance of the group to the sum of the variances for abundance of each component of a group. Ratios of greater than one ($V>1$) indicate positive interactions while those of less than one ($V<1$), negative interactions (see Schluter, 1984; Gabriel et al., 2001). Levels of significance were determined using an associated statistic (W), which equals nV and has a chi-squared distribution (Schluter, 1984). We undertook analyses to assess the abundance covariation for three groups of arthropods for the six combination of sunlight and elevation conditions, and overall. The groups comprised 'terrestrial' species only, 'marine' species only, and all species irrespective of evolutionary background.

Results

Abundances in relation to sunlight and elevation

All nine arthropod species were distributed along the entire length of pneumatophores, for both pneumatophores in the direct sun and those in the shade. However, abundances differed significantly among species and between the two evolutionary groups; the 'marine' arthropods were more abundant than the 'terrestrial' arthropods by nearly an order of magnitude (Figures 1 and 2; Tables 1 and 2). At both the level of species and evolutionary group, abundances varied significantly with elevation and between pneumatophores in the sun and shade (Figures 1 and 2; Tables 1 and 2). Total abundance of each evolutionary group, however, reflected that of the dominant species. In the 'marine' group, the Tanaididae was dominant, occurring at an average of 408.1 individuals/ 10 pneumatophores. In the 'terrestrial' group, the Ceratopogonidae was dominant, occurring at 52.1 individuals/ 10 pneumatophores. The least abundant 'marine' and 'terrestrial' species were, respectively, the Metidae and Ascidae, occurring at 34.1 and 5.75 individuals/ 10 pneumatophores (Figure 1). Pneumatophore density in the area sampled was approximately 450 per m^2.

Direct sunlight significantly reduced abundances of both 'marine' and 'terrestrial' arthropods (Figure 2; Table 3). However, the effect of sun exposure on abundance varied among species. For example, abundances on sun-exposed pneumatophores compared to shaded pneumatophores were significantly lower for the Halacaridae, Tanaididae, and Ceratopogonidae and significantly greater for the Harpacticoidea (Figure 1). Although elevation had a significant effect on arthropod abundance in general (Tables 2 and 3), this differed among the evolutionary groups. Abundance decreased almost linearly with increasing elevation for the 'terrestrial' arthropods, but was maximal at the intermediate level of elevation (though not significantly different from the uppermost level) for 'marine' arthropods (Figure 2). These trends for abundance in relation to elevation were mirrored for conditions of sunlight and shade (Figure 2). As a whole, the patterns largely mirrored those of the most abundant species of each group (see above; Figures 1 and 2).

Table 2. Two-way analysis of variance showing the effects of exposure to sunlight and elevation on the abundance of pneumatophore arthropod species.

Source of Variation	SS	*df*	*MS*	*F*	*P-value*	*F crit*
Sunlight	6.63	1	6.63	26.41	0.000	3.86
Species	107.43	8	13.43	53.45	0.000	1.96
Interaction	18.13	8	2.27	9.03	0.000	1.96
Elevation	0.27	2	0.134	0.51	0.599	3.01
Species	107.43	8	13.43	50.80	0.000	1.96
Interaction	19.91	16	1.24	4.71	0.000	1.66

Table 3. Two-way analysis of variance showing the effects of exposure to sunlight and elevation on the abundance of pneumatophore arthropods from two different backgrounds (terrestrial and marine).

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Sunlight	0.33	1	0.33	29.34	0.000	3.92
'Terrestrial'/ 'marine'	0.72	1	0.72	63.53	0.000	3.92
Interaction	0.04	1	0.04	3.17	0.078	3.92
Elevation	0.36	2	0.18	0.98	0.379	3.08
'Terrestrial'/ 'marine'	19.25	1	19.25	105.28	0.000	3.92
Interaction	2.46	2	1.23	6.73	0.002	3.08

Figure 1. Abundance values (mean and SE for n=10 sets of ten pneumatophore segments each) for individual arthropod taxon in the shade and in the sun, at three levels of elevation. Grey bars indicate pneumatophores in the shade, and white bars, pneumatophores in the sun. The elevation levels indicated represent: 1: 0-5 cm; 2: 5-10 cm; 3: 10-15 cm above ground. A, 'terrestrial' arthropods; B, 'marine' arthropods. One-way ANOVA's were used to check for differences between the different environmental conditions (*P*<0.05): * significant differences between shade and sun; ** significant differences between elevation levels.

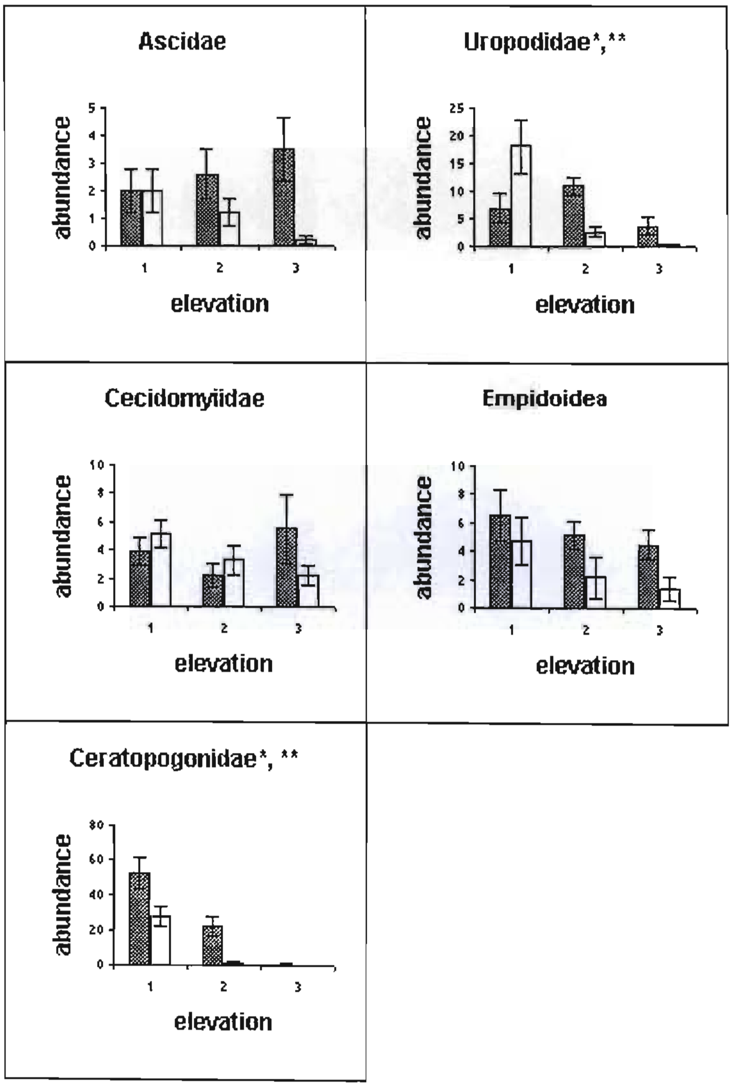

Figure 1A.

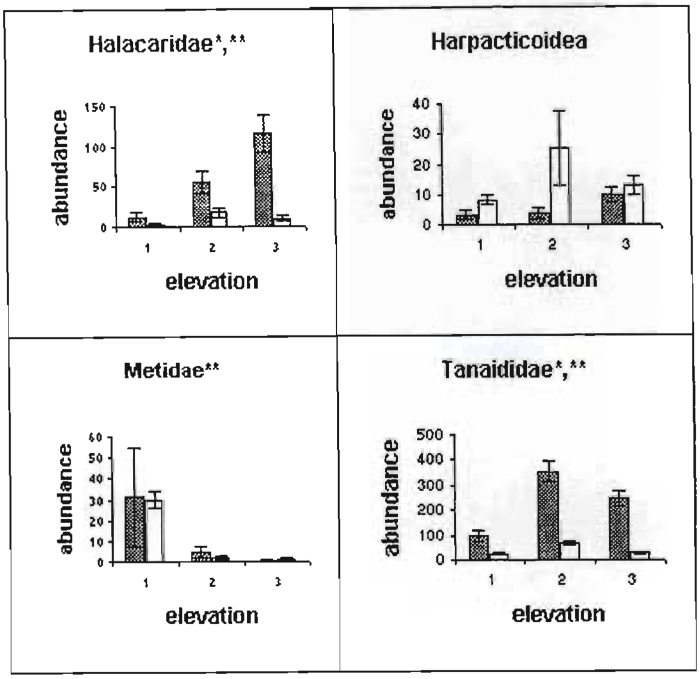

Figure 1B.

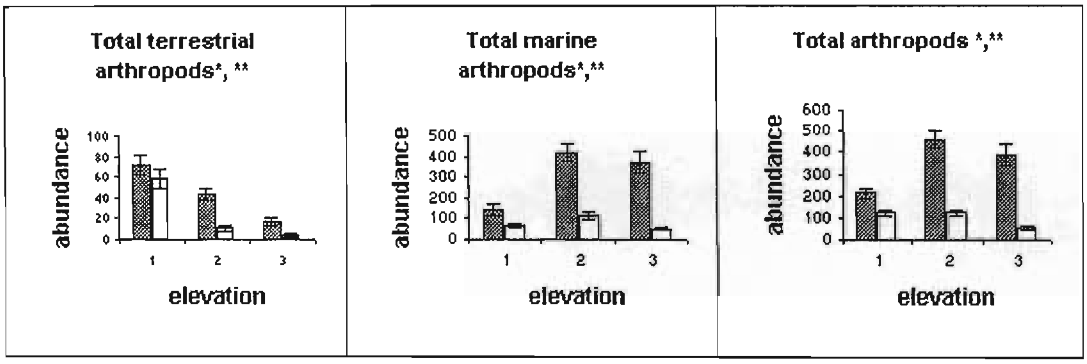

Figure 2. Total abundance values for 'terrestrial', 'marine', and 'all' arthropods. Shading of bars and asterisks have the same meaning as in Figure 1.

Abundance relationships among species

Pearson's correlation coefficients for abundance relationships are shown in Table 4. These were all positive within the 'terrestrial' group with the exception of one relationship, but only half of the relationships were significant. Within the 'marine' group, half the relationships were negative with a single relationship being significant. Abundance relationships between the 'terrestrial' and the 'marine' species gave three significantly negative and three significantly positive correlations. The strongest positive relationship was noted between two 'marine' species (the Halacaridae and Tanaididae), while the strongest negative relationship occurred between a 'terrestrial' and a 'marine' species (the Ceratopogonidae and Halacaridae) (Table 4).

Table 4. Pearson's correlation coefficient for abundance relationships among nine arthropod taxa (ASCI, Ascidae; UROP, Uropodidae; EMPI, Empidoidea; CECI, Cecidomyiidae; CERA, Ceratopogonidae; HALA, Halacaridae; HARP, Harpacticoidea; METI, Metidae; TANA, Tanaididae). Bold indicates significant relationships (*P* < 0.05).

'Terrestrial'-'terrestrial'	ASCI-UROP	**+0.291**	'Terrestrial'-'marine'	ASCI-HALA	**+0.306**
	ASCI-EMPI	+0.094		ASCI-HARP	-0.044
	ASCI-CECI	**+0.254**		ASCI-METI	-0.068
	ASCI-CERA	-0.067		ASCI-TANA	**+0.299**
	UROP-EMPI	**+0.323**		UROP-HALA	-0.082
	UROP-CECI	+0.105		UROP-HARP	-0.145
	UROP-CERA	**+0.264**		UROP-METI	+0.140
	CECI-CERA	+0.020		UROP-TANA	+0.110
	CECI-EMPI	+0.122		CECI-HALA	+0.032
	EMPI-CERA	**+0.377**		CECI-HARP	-0.061
				CECI-METI	**+0.266**
				CECI-TANA	-0.097
				EMPI-HALA	+0.072
				EMPI-HARP	**-0.262**
'Marine'-'marine'	HALA-HARP	+0.062		EMPI-METI	+0.028
	HALA-METI	-0.187		EMPI-TANA	+0.126
	HALA-TANA	**+0.543**		CERA-HALA	**-0.275**
	HARP-METI	+0.014		CERA-HARP	**-0.273**
	HARP-TANA	-0.113		CERA-METI	+0.232
	METI-TANA	-0.219		CERA-TANA	-0.010

Effects of sunlight and elevation on abundance covariation

The variance ratios (*V*) indicating abundance covariation were low, and significant, for 'marine'arthropods at low elevations on the pneumatophores (both in the shade and in the sun) (Table 5), indicating strong negative interactions. On the contrary, 'terrestrial species' did not yield significant results for any of the specific habitat types, but only when all samples were considered together, in this case suggesting mildly positive interactions. However, when all arthropod species were considered together, the values were remarkably high, especially in the sun and at higher elevations (Table 5), indicating strong positive interactions.

Table 5. Variance ratios (*V*) of abundance covariation for three groups of arthropod species on shaded and sunlit mangrove pneumatophores, at three elevation levels (1: 0-5 cm; 2: 5-10 cm; 3: 10-15 cm); n=10 for each combination of elevation/sunlight, n=60 for the total. Asterisks mark significant values, as indicated by the associated test statistic *W*, with a chi-squared distribution (Schluter, 1984): * *P*<0.05; ** *P*<0.005.

	'Terrestrial' species	'Marine' species	All species
Shade, low elevation	0.99	0.03**	0.46
Shade, middle elevation	0.70	0.11**	1.04
Shade, upper elevation	1.19	0.48	2.27*
Sun, low elevation	1.54	0.03**	1.93*
Sun, middle elevation	1.26	0.23*	1.24
Sun, upper elevation	1.59	0.51	3.09**
Total	1.36*	1.21	1.21

Discussion

Mangrove meiofaunas have been examined mainly with respect to understanding their diversity and assemblage structure (Dye, 1983a; Gee, 1989; Ólafsson, 1995; Gee & Somerfield, 1999; Ndaro & Ólafsson, 1999; Ólafsson et al., 2000). The majority of studies concentrate on the benthic sediment meiofauna with considerably less known about the pneumatophore meiofaunal assemblages. These have been shown to differ from benthic sediment assemblages in their species composition and abundance (Procheş et al., 2001), and such differences are thought to relate to greater habitat variability along the vertical lengths of pneumatophores (Procheş & Marshall, 2001b). Even though mangrove pneumatophores can be readily sampled and their meiofaunal assemblages accurately determined, and thus they offer unique possibilities for exploring ecological theory (regarding distribution, abundance, recruitment, and colonization) over very small spatial scales, surprisingly few studies have taken advantage of this (Alongi, 1987; Bingham & Young, 1992; Farnsworth & Ellison, 1996). The disparate evolutionary backgrounds of the taxa comprising pneumatophore meiofaunal assemblages (typically marine, or of recent terrestrial decent), make these assemblages particularly suitable for investigating the effects of evolutionary history on ecological patterns, as was the objective of the present investigation.

We show here that distributions and abundances of arthropods on pneumatophores are distinctly variable 1) among the evolutionary disparate groups, and 2) in relation to elevation and conditions of sun exposure. The total abundance of 'marine' arthropods was almost an order of magnitude greater than that of the 'terrestrial' arthropods. With respect to relative abundance of each group in relation to elevation, the 'marine' arthropods predominated at the middle and upper levels and the 'terrestrial' species at the lower level, patterns corresponding with those of the dominant species of each group (see Ceratopogonidae and Tanaididae; Figs. 1 and 2). Although increased activity/inactivity and vertical migrations in relation to tidal cycles characterize the behaviour of many intertidal invertebrates, this is unknown for meiofaunal arthropods. Therefore, other than the potentially active predatory mite, Ascidae (see Krantz, 1978), the abundance distributions observed here are likely to persist temporally during the tidal cycle.

While the foregoing account highlights discrepancies in abundance in relation to pneumatophore elevation, a more striking effect was observed in comparisons between pneumatophores in the sun and those in the shade. The low abundance of arthropods on sun-exposed pneumatophores throughout, may relate to their intolerance of dehydration. But, given that no taxonomic patterns were apparent to suggest species differences in stress tolerance, these abundances more likely relate to changes in habitat and food availability deriving from reduced algal or detrital development on dehydrated pneumatophores. Irrespective of taxonomic resolution, be it species, evolutionary group, or the arthropods as a whole, lowest abundances consistently occurred on the uppermost pneumatophore level, for pneumatophores in the sun (the most extreme physical condition). Species distributional limits are probably realized on these pneumatophore segments, and this is particularly apparent in the case of two taxa (Ceratopogonidae - 'terrestrial' and Metidae - 'marine'; Figure 1).

Studies on intertidal benthic communities are at the forefront of testing ecological theory concerning biological interactions (e.g. Underwood & Denley, 1984; Menge et al., 1994; Underwood & Chapman, 1996; Berlow, 1997; 1999; Berlow et al., 1999; Leonard, 2000; Menge, 2000). These have considered the implications, for community structuring, of directions and strengths of interactions in relation to environmental stress. Although it is frequently argued that definitive conclusions concerning species interactions require field experimental manipulations, and often the removal of one or more components of the community (see Menge et al., 1994; Menge 2000), in many circumstances this is practically impossible. The only alternative to achieving insights into species interactions of meioarthropods is through derivations of correlation or covariation in species abundance (see Gabriel et al., 2001). Species abundance correlations of the pneumatophore arthropods where largely not statistically significant, and therefore limited in interpretation, but they could suggest weak interactions. There were no clear patterns within or between evolutionary groups to distinguish one group from the other. The strongest association was seen between the Halacaridae and the Tanaididae, which were the most abundant taxa on the middle and upper pneumatophore segments in the shade. This may represent a real interaction, even when habitat circumstances (elevation and sunlight) are not taken into account.

Distinct abundance covariation patterns were observed with respect to both elevation and the sunlight conditions, although these affected differently the different groups of arthropods, and were not observed in 'terrestrial' species. The covariations for the uppermost elevation (suggesting weak non-significant positive or negative interactions for 'terrestrial' and 'marine' arthropods respectively, but significant positive interactions when all species were considered together), is probably accountable to the low abundances and differential species limits at this elevation (Table 5). As previously mentioned, reduced abundances on pneumatophores is best explained as relating to a limitation on food resources. In competing for this limited resource, species populations will fluctuate in unison, and be observable as positive associations (see Schluter, 1984). The amelioration of potential food resources as occurs on the lower levels of the pneumatophores, is likely to increase interspecific competition and be observed as stronger negative interactions. However, the findings here presented suggest that these interactions differ between 'terrestrial' and 'marine' arthropods in relation to physical conditions.

Our ecological distribution findings suggest that mangrove pneumatophores contain arthropod species having an array of possible physiological tolerances, which are not necessarily group-specific for any particular evolutionary group. Furthermore, there is little evidence to suggest that interactions among the 'marine' arthropods are stronger and better developed than those among the 'terrestrial' arthropods. However, physical aspects on mangrove pneumatophores play an important role in increasing the degree of interaction among the arthropods. A more in-depth understanding of what influences distributions and abundances of these arthropods, requires investigations into the availability of primary food resources and habitat. The similarity of responses for both evolutionary groups suggests that they may not be as ecologically disparate as previously thought. There are marked differences in ecological patterns among primary and secondary marine arthropods for some taxa and some intertidal habitats (see Schulte, 1976a; 1976b; Kronberg, 1988; Cheng & Frank, 1993), but this investigation highlights the limitations on generalizing among taxa and habitats for either group.

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Chapter VII

Epiphytic algal cover and sediment deposition as determinants of arthropod distribution and abundance on mangrove pneumatophores

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Abstract

Intertidal mangrove pneumatophores often support a variety of epiphytes (of both animal and plant taxa). These may facilitate sediment deposition on pneumatophores, especially in the cases of finely structured algae, and in estuarine systems where fine sediments are characteristic. The sediment covering on pneumatophores shelters complex arthropod communities, comprising mites, crustaceans and insects. We report here an investigation on mangrove pneumatophores examining the relationships between arthropod abundance (for nine meiofaunal taxa), algal growth and sediment cover. There was a strong correlation between mass of the sediment and mass of the macroalgae, supporting the assumption that pneumatophore sediment cover depends on algal growth. These two components of pneumatophore cover were negatively related to elevation, an effect probably relating to desiccation-limited algal growth towards the pneumatophore tips. Total arthropod abundance and that of some taxa (particularly, Uropodidae (Acari), Metidae (Crustacea), Ceratopogonidae (Insecta) and Empidoidea (Insecta)), was negatively correlated with elevation and positively correlated with sediment and algal cover, suggesting a good relationship between abundance and habitat availability. Other arthropod taxa (particularly, Halacaridae (Acari)), however, showed the opposite pattern of relationships. Their distributions and abundances on pneumatophores must therefore depend to a greater extent on other factors (habitat conditions and biotic interactions for example) than on available habitat. When pneumatophore cover was physically removed, in an experiment to assess assemblage recovery rates, some arthropod taxa (Halacaridae (Acari), Harpacticoidea (Crustacea) and Ceratopogonidae (Insecta)) had completely recovered by twenty five weeks. Their recovery is therefore only partially dependent on the recovery of the pneumatophore cover. Those taxa which showed incomplete recovery (Tanaididae (Crustacea) and Empidoidea (Insecta)) are likely to be constrained by life history characteristics and/or habitat availability. In conclusion, epiphytic

growth (and its associated sediment) has a key role in determining the assemblage composition and structure of pneumatophore meiofaunal arthropods. Given the considerable taxonomic variability of pneumatophore epiphytes among systems and geographically, there is much scope for comparison, through similar investigations from other regions.

Introduction

The habitat structure of mangrove systems is extremely complex and variable between and within systems. Mangrove habitats comprise hard substrata (pneumatophores and tree trunks) interspersed in a soft substratum matrix (benthic sediment). These elements of habitat support vastly differing suits of biota: sediments typically can support burrowing organisms, whereas sedentary organisms can attach to pneumatophores. Habitat variety appears even more remarkable when considering spatial scale. For example, pneumatophore structure is variable over small scales (Beck, 2000) and depressions in the otherwise near homogeneous benthic sediment may vary considerably in physicochemical conditions (Ólafsson et al., 2000). Superimposed on entire mangrove systems are effects deriving from tidal cycles in the intertidal zone (variable wetting, see Dye, 1983b), and those deriving from exposure to direct sunlight (as opposed to shading under tree canopies, see Procheş & Marshall, 2001).

Although a bulk of information is available for mangrove communities, this appears to be skewed towards studies examining the benthic component of these communities (Alongi & Sasekumar, 1992; Kathiresan & Bingham, 2001). Much less known about the pneumatophore component, which can contribute an extensive surface area to mangrove systems. Most studies on pneumatophores concern epiphytic ecology, particularly that of algae (de Oliveira, 1984; Davey & Woelkerling, 1985; Tanaka & Chihara, 1987; Mann & Steinke, 1988; Coppejans & Gallin, 1989; Phillips et al., 1994; 1996), though a few do consider the sessile fauna (Bingham, 1992; Bingham & Young, 1994; Satumanatpan et al., 1999; Satumanatpan & Keough, 2000). With respect to meiofaunal assemblages of mangrove systems (especially nematode and copepod assemblages), those of the benthic sediments have received significant attention (Ólafsson, 1995; Schrijvers et al., 1995; Somerfield et al, 1998; Gee & Somerfield, 1999; Ndaro & Ólafsson, 1999; Ólafsson et al., 2000), with relatively little known about the assemblages associated with pneumatophores.

A recent study has however shown that pneumatophore arthropod assemblages differ markedly from those of benthic sediments (Procheş et al., 2001). Differences are suggested to arise from the steep gradient of drying along the vertical length of pneumatophores (Procheş & Marshall 2001; Procheş et al., 2001), but there is much scope for further investigation here.

Mangrove pneumatophore arthropod faunas are of special interest in that they comprise proportionally more secondary marine taxa than faunas of most other intertidal systems, and thus offer unique opportunities for examining evolutionary constraints on ecological patterns (Procheş & Marshall 2001). In addition, they provide opportunities for testing ecological theory over small scales and across extremely narrow physical gradients. However, this task is not easily attained, given that arthropod abundance and species richness could be directly affected by the environmental conditions (microclimate) on the pneumatophore, indirectly, as these conditions affect algal biomass and sediment deposition, or in both ways. Separating these effects is only possible by combining mass/abundance measurements with experimental work. Therefore, this study examined the relationships of arthropod abundances (including mites, insects, copepods and tanaids) with pneumatophore algal growth and sediment cover (the primary elements of microhabitat of these arthropods), and related these with the rates of arthropod recolonization after the algal and sediment cover is removed from pneumatophores.

Material and methods

Locality and arthropod taxa

Sampling was undertaken in the Bayhead mangrove forest, Durban, South Africa (29° 53' S, 30° 61' E), between March and December 2000. This forest covers an area of approximately 15 ha (Ward and Steinke, 1982) and experiences a regular tidal cycle with salinity fluctuating between 27 and 35 (Begg, 1976). Previous studies identified the seaward fringe pneumatophores at Bayhead as comprising the most complex and abundant arthropod assemblages (Procheş & Marshall, 2001; Procheş et al., 2001). These pneumatophores therefore became the focus of the present study. The ten most abundant arthropod taxa were considered, which included three mite (Acari), two copepod, and three dipteran species, and a single species each of tanaid and barnacle (see Table 1). All other species present in the samples were only represented by one or two individuals, and were considered to be terrestrial contaminants.

Table 1. Arthropod taxa considered in the present study.

Acari	Ascidae	*Leioseius* sp. nov.
	Uropodidae	*Uroobovella* sp.
	Halacaridae	*Copidognathus caloglossae* Procheş
Crustacea	Harpacticoidea	At least 2 spp. (Canthocamptidae; Diosaccidae)
	Metidae	*Metis* sp. Nov.
	Tanaididae	*Tanais philetaerus* Stebbing
Insecta	Cecidomyiidae	Lestremyiinae sp.
	Empidoidea	At least 3 spp. (2 families); not identified
	Ceratopogonidae	*Culicoides* sp.

Field collections and abundance determinations

Four (X 5 m) transects were established and 50 pneumatophores longer than 10 cm were randomly selected from each transect. The pneumatophores were cut at ground level, and then cut into 5 cm long segments towards the tip, complying with a measurement commonly used in pneumatophore studies (see Davey & Woelkerling, 1985; Tanaka & Chihara, 1987; Coppejans & Gallin, 1989). This gave four elevation levels as follows, 0-5, 5-10, 10-15 and 15-20 cm, with segments above 20 cm being discarded. The mean length of considered pneumatophores was 24.7 cm (±SE 2.1cm).

The pneumatophore segments were bagged, returned to the laboratory and washed over a 0.12 mm mesh to retrieve arthropods, macroalgae and coarse sediment. The wash-water was collected and evaporated to retain the fine sediment (particles smaller that 0.12 mm). Samples retrieved in the mesh were transferred to small plastic bottles and treated with 25 ml hypersaline solution (Fain and Hart 1986). Floating specimens (mainly mites, tanaids and insect larvae) were removed from each bottle, identified and counted under a dissecting microscope (X 160 magnification). The remaining contents of each bottle were brought to a 50 ml aqueous solution, and the arthropods (mainly copepods and insect larvae) in three 5 ml sub-samples of this, were determined and counted. Based on these sub-samples, the number of individuals was determined for the 50 ml volume, and the total number of arthropods for each sample determined by addition of the fractions deriving from the two extraction procedures.

The sediment in both collections (greater than, and less than 0.12 mm particle size) and the algae retrieved with the coarse sediment, were oven-dried at 60° C for 24 h, and weighed. These samples were then burnt for 5 h at 500° C to eliminate the organic component, and re-weighed. Macroalgal dry mass (which dominated the organic biomass) was taken to be the difference between total mass and the inorganic mass of the coarse fraction. The pneumatophore cover components were related to elevation, and Spearman's rank correlation coefficients were determined for relationships between the abundance of each taxon and elevation, sediment dry mass, and algal dry mass (using data from the sixteen samples - 4 transects x 4 elevation levels). To determine the proportion of variability in assemblage structure explained by elevation, sediment and macroalgae, multiple regressions were performed for the abundance of each species, total abundance, and species richness. The most important factor in each regression was determined by multiplying the average value of each factor with its coefficient, as determined from the multiple regression. The total mass of the pneumatophore segments was included in the correlation analysis, but as correlation values were very low ($r_s<0.250$ for all taxa but the Ascidae), and never significant, it was not presented, nor further considered in the regressions.

Assemblage recovery experiment

This experiment was intended to further explore the dependence of the arthropod assemblages upon the sediment and algal cover of the pneumatophores, and was undertaken by monitoring the temporal changes in these assemblages after the pneumatophore cover was removed. Three experimental and three control plots each of 60 x 60 cm and around 3 m apart, were established. These contained pneumatophores occurring at densities of 300 - 400 pneumatophores per m^2. In the experimental plots, the sediment and algal cover was removed from all pneumatophores using abrasive Velcro material. Two samples of 10 pneumatophores each were randomly chosen from each experimental and control plot. The pneumatophores were cut at their bases, placed in bags and returned to the laboratory. The site was revisited after 1, 4, 12 and 25 weeks, to undertake further sampling. The samples were processed as described above. Samples were comparable in summed pneumatophore length (mean 148.3 ±SE 4.5cm), alleviating the need to correct for possible discrepancies arising from differences in habitat availability. Paired t-tests were used to compare abundance values between experimental and control plots ($N=6$ for each, $P<0.05$). The SPSS package ver. 9.0 (1998) was used throughout.

Results

Both sediment deposition and algal cover were negatively correlated with elevation along the pneumatophore. At the uppermost elevation, the mass of pneumatophore cover (sediment and algae) was less than five times that at the base. At each elevation, the ratio of fine sediment, to coarse inorganic sediment, to macroalgae was approximately 25: 5: 1 (Figure 1). Spearman=s rank correlation between the mass of the fine sediment and the coarse inorganic sediment was 1, indicating no differential deposition of the two sediment fractions at different elevations along pneumatophores. The total mass of sediment (the sum of the two sediment fractions) was therefore used in further correlations with arthropod distribution and abundance. There was also a strong correlation ($r_s = 0.925$) between the mass of the sediment and that of the macroalgae.

Abundances were remarkably variable among the taxa, ranging from the greatest mean abundance for a particular level (for 50 pneumatophores) of 533 individuals in the case of Tanaididae, to no individuals for the Ascidae and Ceratopogonidae (Table 2). The abundances of most taxa were negatively correlated with elevation, with the exception of the Ascidae, Halacaridae and Cecidomyiidae (Table 3). Although the most abundant taxon, the Tanaididae, showed a negative correlation with elevation, some samples gave extraordinary high abundance values at the uppermost pneumatophore level. All taxa that were significantly negatively correlated with elevation, were also significantly positively correlated with sediment deposition and algal growth (Table 3), suggesting that their abundances are related to variations in habitat availability along the pneumatophore length. The taxa that were positively correlated with elevation were all negatively related to the cover components, though the relationship was significant in only one case (Halacaridae). Total arthropod abundance was negatively correlated with elevation and positively correlated with sediment and algae (Table 3). The multiple regressions, however, showed that most of the variation in arthropod assemblage composition can be explained by considering elevation alone; only in one taxon (Empidoidea), and for total arthropod abundance was the amount of macroalgae the most important factor; and only one taxon (Uropodidae) yielded a significant value when regressed against the mass of sediment.

Experimental removal of the pneumatophore cover eliminated 90% of the arthropods (Figure 2). Although there was high temporal variability for the abundances in control plots, there was a general trend of recovery in the 25 week period considered. Total arthropod abundance on experimental pneumatophores after 25 weeks was almost ten times greater than the initial abundance following removal of cover, and 60% of the control abundance. The Halacaridae showed the most rapid recovery (there was no difference between experimental and control pneumatophores at 12 and 25 weeks), with complete recovery also seen for the Harpacticoidea and Ceratopogonidae, after 25 weeks. The most abundant taxon (the Tanaididae) showed relatively slow recovery (Figure 2).

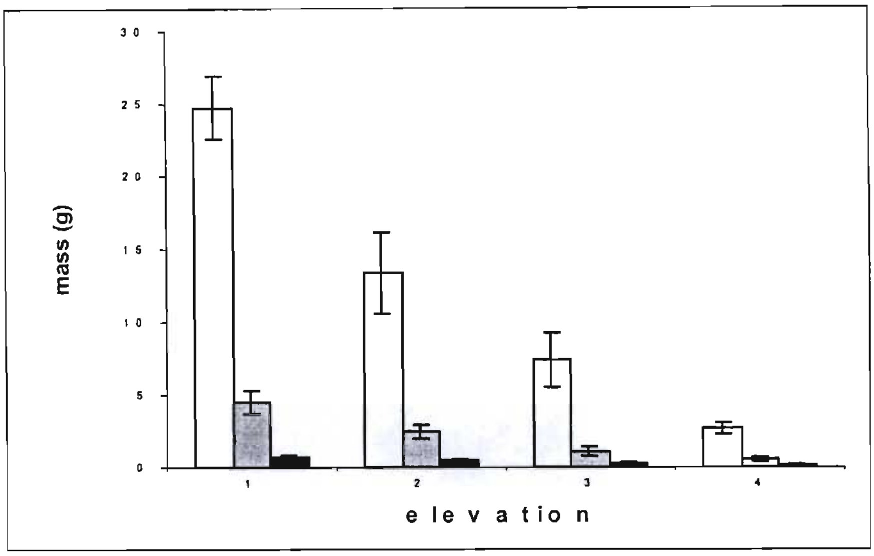

Figure 1. Variation of three microhabitat factors on mangrove pneumatophores: fine sediment (white), coarse inorganic sediment (gray) and macroalgae (black). The values represent grams of dry mass (for $N = 4$ sets of 50 pneumatophore segments each). The elevation levels indicated represent: 1: 0-5 cm; 2: 5-10 cm; 3: 10-15 cm; 4: 15-20 cm above ground.

Discussion

Pneumatophores provide ideal surfaces in estuaries for the attachment of sedentary biota, for example, algae and barnacles. The biota is considerably variable, taxonomically and ecologically (biomass and abundance), between mangrove stands and from one geographical region to the next. Whereas eucaryotic life growing on pneumatophores may comprise as little as finely structured filamentous algae, in other instances this contributes a biomass similar to that of the pneumatophores themselves. For example, epiphytic macrobiotic assemblages on pneumatophores are dominated by filamentous and lamellar algae in southern African estuarine systems (see Lambert et al., 1994; Phillips et al, 1994; 1996), by barnacles and oysters in some Australian bay systems (see Bayliss, 1993; Ross & Underwood, 1997), and by an array of

Table 2. Arthropod abundance values (mean ± SE, $N = 4$, per sets of 50 pneumatophores) at four levels of elevation on mangrove pneumatophores. All pneumatophores were longer than 15 cm, so the three lower levels represent abundances/ 50 pneumatophore segments, while the top level (15-20 cm) contained various numbers of segments (< 50).

	0-5 cm	5-10 cm	10-15 cm	15-20 cm
Ascidae	0.00 ± 0.00	3.50 ± 2.02	0.83 ± 0.83	9.05 ± 7.01
Uropodidae	9.00 ± 4.38	8.50 ± 2.99	2.78 ± 1.84	0.83 ± 0.83
Halacaridae	0.00 ± 0.00	22.75 ± 11.39	69.92 ± 35.16	149.44 ± 122.78
Cecidomyiidae	4.00 ± 2.12	4.00 ± 2.12	6.64 ± 3.61	13.71 ± 9.97
Empidoidea	57.50 ± 11.08	21.00 ± 10.30	5.56 ± 5.56	1.25 ± 0.80
Ceratopogonidae	101.00 ± 40.44	32.50 ± 9.54	0.83 ± 0.83	0.00 ± 0.00
Harpacticoidea	10.50 ± 7.79	14.75 ± 9.82	6.89 ± 4.67	4.89 ± 3.77
Metidae	80.00 ± 28.37	16.50 ± 12.35	2.03 ± 2.03	0.83 ± 0.83
Tanaididae	312.00 ± 73.52	375.00 ± 123.19	244.90 ± 115.69	533.60 ± 294.95
Total	574.00 ± 132.47	498.50 ± 133.93	340.39 ± 130.93	713.62 ± 384.85

Table 3. Spearman's rank correlation values for abundance of the arthropod taxa against 1) elevation level on the pneumatophores, 2) mass of sediment, and 3) mass of macroalgae. Asterisks indicate significant relationships (* $P < 0.05$; ** $P < 0.05$).

Taxon	Elevation	Sediment	Macroalgae
Ascidae	0.280	-0.227	-0.252
Uropodidae	-0.589*	0.760**	0.694**
Halacaridae	0.573*	-0.491	-0.517*
Cecidomyiidae	0.192	-0.183	-0.053
Empidoidea	-0.748**	0.777**	0.676**
Ceratopogonidae	-0.764**	0.787**	0.760**
Harpacticoidea	-0.209	0.149	0.052
Metidae	-0.789**	0.688*	0.618*
Tanaididae	-0.255	0.391	0.492
Total	-0.376	0.518*	0.526*

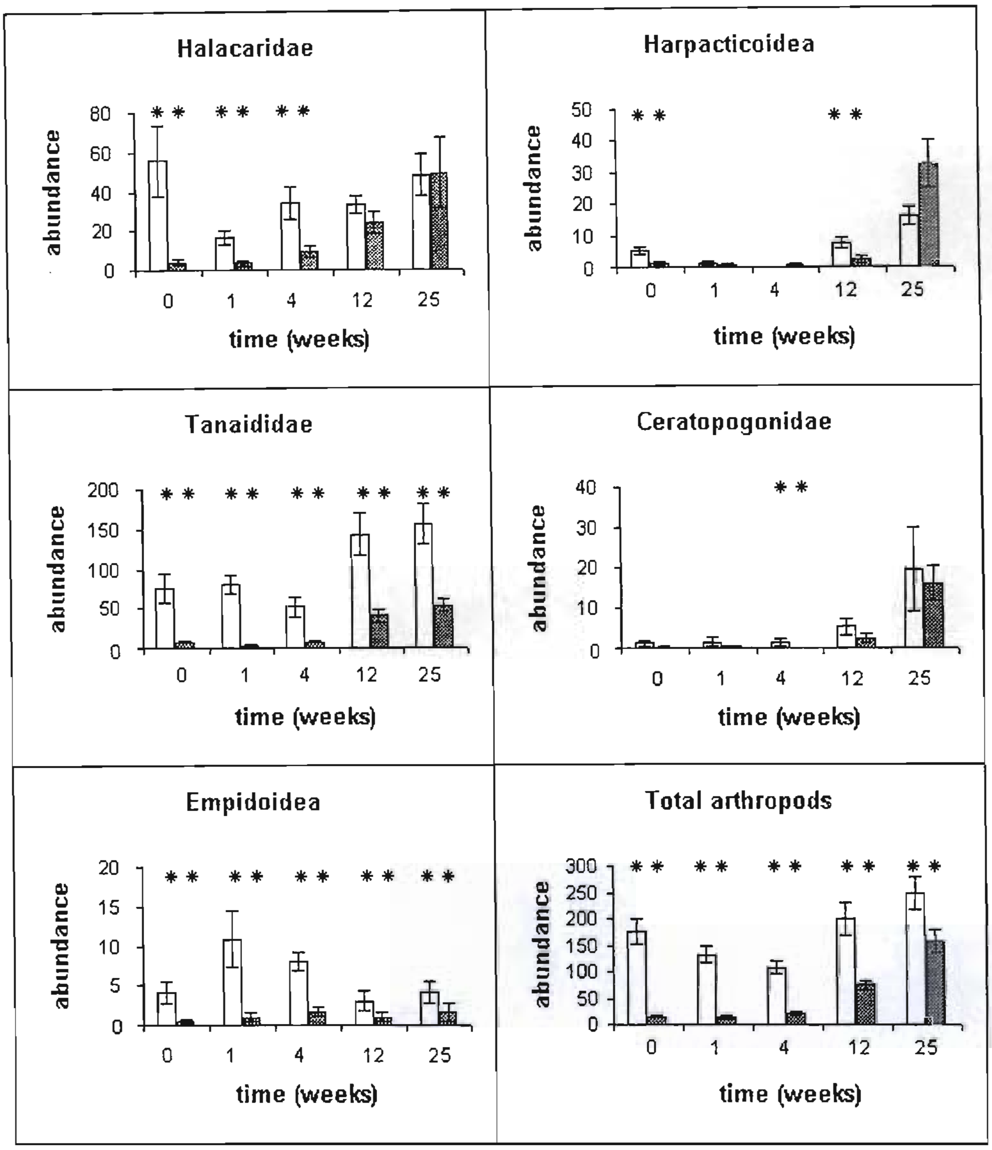

Figure 2. Variation in arthropods abundance (mean and SE, $N = 6$) for the most abundant five arthropod taxa and total arthropods in plots where pneumatophore cover was experimentally removed (gray bars) and in control plots (white bars). Pairs of asterisks indicate that abundance values for the control plots are significantly higher than for the experimental plots (t-paired test, $P < 0.05$).

Table 4. Multiple regressions of arthropod abundances and species richness against elevation, sediment, and macroalgal mass. Individual R values higher than 0.5 are marked by asterisks, while overall R values are given in the last column. The factor with the highest contribution to each multiple regression is shown in bold.

Taxon	Intercept	Coefficients			Overall R
		Elevation	Macroalgae	Sediment	
Ascidae	-11.20	**4.21**	0.19	2.27	0.42
Uropodidae	-0.39	-0.53	0.07	**12.87**	0.69
Halacaridae	-328.26	**111.64***	11.63	-149.68	0.56
Cecidomyidae	-17.89	**6.33***	0.05	18.36	0.47
Empidoidea	4.27	-5.19	**1.47**	16.38	0.87
Ceratopogonidae	110.20	**-32.77***	-0.48	27.71	0.69
Harpacticoidea	42.78*	**-8.74**	-1.09	10.94	0.40
Metidae	52.40	**-18.42**	0.28	30.90	0.69
Tanaididae	-1001.44*	**315.16***	30.80*	234.43	0.61
Total abundance	253.26	-29.26	**20.68**	-224.94	0.68
Species richness	8.10*	**-0.77**	-0.06	2.37	0.42

sponges, cnidarians, and ascidians in the open sea mangrove islands of Florida (Bingham, 1992; Bingham & Young, 1994). Depending on the nature of the biotic covering, in estuarine systems in particular, it potentially traps fine sediment. The algal and sediment covering of pneumatophores support a variety of motile meiofaunal arthropods, the distributions of which in southern African mangroves, have been the subject of recent investigations (Procheş & Marshall, 2001; Procheş et al., 2001).

Ecological distributions and species abundances, in general, are influenced by habitat suitability (physico-chemical conditions), biotic interactions, and life history patterns (Rozenweig, 1997). Species vertical distributions in the intertidal zone (particularly upper limits) are largely determined by tolerance of physical conditions relating to air exposure, such as desiccation (Underwood & Denley, 1984, but see Pugh & King, 1985, for Acari). While a previous investigation has shown that desiccation is important in structuring meiofaunal arthropod assemblages on pneumatophores (Procheş & Marshall, 2001), we show here that this also relates to habitat availability in some instances. Initial findings indicated that the primary habitat available to the meiofauna (comprising the algal and sediment cover) varies vertically along a pneumatophore in a manner of decreasing habitat with increasing elevation. This pattern probably relates to a desiccation-induced reduction in algal growth (Phillips et al., 1994; 1996; see Figure 3)

Arthropod abundance of some taxa (particularly, Uropodidae, Empodiodea, Ceratopogonidae and Metidae) corresponds with the reduction in habitat availability by decreasing along the vertical height of the pneumatophore. This pattern suggests a causal relationship between arthropod abundance and habitat availability (with reference to interstitial Uropodidae and Ceratopogonidae see Krantz, 1976; Linley, 1976). The other meiofaunal taxa showed either a significant positive relationship (in the case of the Halacaridae) or, were weakly positively or negatively related to habitat availability. Included among the numerous factors responsible for overriding the effects of habitat availability are those relating to biotic interactions (such as competition or predation). These are suggested by abundance correlations implied from this study and those determined in an earlier study (Procheş & Marshall, 2001) which showed that the two most abundant taxa (Halacaridae and Tanaidae) are similarly distributed on pneumatophores, and both are mainly negatively correlated with the taxa which closely track available habitat (Uropodidae, Empodiodea, Ceratopogonidae and Metidae; see Procheş & Marshall, 2001).

The low significance of algal and sediment mass regression values, as compared to the high predictive values held by elevation alone, suggests that in fact other factors, such as the direct influence of moisture, as well as biotic interactions among arthropods can be more important in determining vertical zonation patterns than the algal and sediment mass. However, the dependence of the arthropod assemblages upon the macroalgal and sediment covering, is shown clearly by the slow pace of recovery after clearing the pneumatophores.

The arthropod community had not completely recovered during the investigation period (25 weeks), with rate of recovery being vastly variable among taxa. Whereas abundances of some arthropod groups had recovered after twenty five weeks, the total arthropod abundance remained below that of the controls by this time (though this was largely due to the dominant Tanaididae). Extrapolation of the consistent temporal increase in our abundance data indicates that

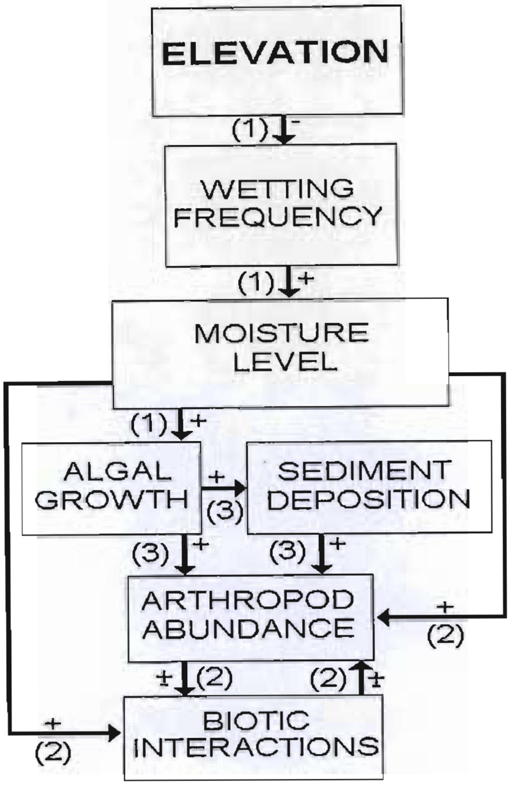

Figure 3. Interrelationships among physical and biotic components of the mangrove pneumatophore environment, based on Phillips et al., 1996 (1); Procheş & Marshall, 2001 (2); and the present study (3).

complete recovery should be affected by around fifty weeks. In another study, Eston et al. (1992) found epiphytic algal communities on pneumatophores to recover in four to eight months. The most rapidly colonising pneumatophore epiphytes include barnacles. Their recovery and colonisation, through the production of vast numbers of swimming larvae, happens within hours (Satumanatpan et al., 1999; Satumanatpan & Keough, 2000). Unlike the taxa we considered, barnacles are filter feeders and thus are unrelated to the algal and sediment habitat, but rather utilize pnuematophores as attachment surfaces only.

Intuitively it follows that taxa whose populations recover completely, prior to full recovery of the habitat, are more general in their utilization of habitat than those showing partial recovery. This situation was found to be applicable to the rapidly recovering Halacaridae (strongly negatively related to habitat availability) and the Harpacticoidea (weakly related to habitat), but not to the Ceratopogonidae (strongly correlated to habitat) (see Table 3 and Figure 1). These contrasting results indicate the effects on population and assemblage recovery of factors other than habitat utilization, for example, life history and dispersal characteristics of the taxa. The temporarily consistent increase in abundance of the Halacaridae suggests that their recovery relates to growth of the remnant population on the pneumatophores (as not all individuals were removed during the experiment), whereas harpacticoid copepods could recolonise from benthic sediments where they occur in relatively high abundance (Alongi & Sasekumar, 1992; Procheş et al., 2001). Insects (represented in our samples by larvae) have flying adults, enabling them to disperse effectively (Cheng & Frank, 1993), but not necessarily uniformly across available habitat. This may explain the variability in spatial and temporal distribution and abundance on pneumatophores of insects in general, and particularly, the Ceratopogonidae. With respect to the taxa showing poor recovery, the design of the current experiment does not permit inference regarding the extent to which their life histories versus habitat and niche availability and utilization, limit population growth.

Even though they offer considerable opportunities for ecological study, in that they can be readily quantified and their spatial patterns be easily identified, mangrove pneumatophore meiofaunas have been poorly explored. Whereas previously, the effects of desiccation and biotic interactions on their communities have been highlighted, the current study elucidates the effect of habitat availability on community structure. Utilization of the habitat comprising the algal and sediment pneumatophore cover, varies considerably among the species. In addition to habitat availability, development of the meiofaunal arthropod populations on pneumatophores depends on life history characteristics of the specific taxa as well as other factors (including biotic interactions). Given the diversity of mangrove systems worldwide, there is considerable scope for comparing the effects of pneumatophore cover on the ecology of meiofaunal arthropods, by considering other types of mangrove systems (which support vastly differing pneumatophore components) from other geographical regions (Lambert et al., 1994; Bayliss, 1993; Ross & Underwood, 1997; Bingham & Young, 1994).

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Chapter VIII

Arthropod distribution across spatial scales: patterns of diversity and abundance

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Abstract

Although most ecological variables are scale-dependent, few studies compare scale-related variations in abundance, species richness and assemblage structure. This study considers all of these parameters in the case of mangrove pneumatophore arthropod (Acari, crustaceans and insects), at seven spatial scales, from 10 cm to 100 km. Negative spatial autocorrelation in the abundance of common species was stronger at 10 km than at 100 km, while for rare species, the reverse was true. Spatial autocorrelation in species richness was found to decrease from 1 m (strong positive autocorrelation) to 10 km (strong negative autocorrelation), but was not significant at the 100 km scale. While these patterns largely reflect the patchy distribution of pneumatophores within mangrove forests, and that of the forests along the coast, an added effect of spatial fragmentation can be attributed to the poor dispersal abilities of the arthropods, in a highly dynamic environment. Variations in the abundance of common species, as well as the limited distribution of rare species caused differences in assemblage structure to increase with increasing distance, from 10 cm to 100 km. The 100 km scale clearly stood out as the most distinct, indicating biogeographical, rather than ecological, differences. The study highlights the need for combining univariate and multivariate approaches in investigating scale-dependent phenomena

Introduction

Understanding the structuring of an ecosystem can only be achieved when all the processes having a significant influence are considered, and these are likely to operate over a variety of scales (Dayton & Tegner, 1984; Levin, 1988; 1992; 1994; Menge & Olson, 1990, McCoy & Bell, 1991O'Neill et al, 1991; Legendre & Fortin, 1998; Koenig, 1999). Beyond pure theoretical interest, scale research proved to be of practical importance, especially in understanding human impact at local, regional and global levels, in defining critical habitat fragmentation and loss, and in planning corresponding conservation activities (With et al., 1997; Nagendra & Gadgil, 1999).

Marine science is one of the fields where scale research has been particularly productive (Bingham, 1992; Underwood & Petraitis, 1993; Bourget et al., 1994; Sournia, 1994; Saburova et al., 1995; Farnsworth & Ellison, 1996; Schoch & Dieter, 1996; Underwood & Chapman, 1996; 1998; Åberg & Pavia, 1997; Cosson et al., 1997; Lancaster & Belyea, 1997; Swadling et al., 1997; Guichard & Bourget, 1998; Eggleston et al., 1999; Fauchald et al, 2000). These studies indicate that the the type of substratum, from intertidal rock and Arctic ice to estuarine or deep-sea sediment, may greatly influence distribution patterns across scales, due to the action of different biotic and abiotic processes. It is however difficult, from the amount of knowledge accumulated so far, to assemble a detailed picture of scale-dependence in marine ecology. This is mainly because few habitats have been systematically surveyed, so as to consider large arrays of scales (but see Farnsworth & Ellison, 1996, Åberg & Pavia, 1997, Kunin, 1998). More often, the studies cover limited sets of distance classes, and as these differ from one habitat to the next, comparisons are not always possible.

A variety of methods have been devised for the analysis of spatial patterns (see reviews in Legendre & Legendre, 1983; Legendre & Fortin, 1989; Dutilleul, 1998; Gardner, 1998), but many of these have only been applied within a given distance class, within one or two orders of magnitude. For example, autocorrelograms (measuring self-correlation in the spatial distribution of single variables) are normally employed in depicting spatial patterns along series of evenly distanced samples. However, this method is applicable to samples separated by uneven distances, even when these differ by a few orders of magnitude. In this case, the method could provide a good deal of scale-dependence information. In the field of multivariate techniques, the method proposed by Underwood and Chapman (1998) is a relatively simple approach to analyzing cross-scale variations in community structure. However, it has not been applied in conjunction with univariate methods considering the distribution of single species.

The present study examines distribution patterns in a group of small-bodied animals over an array of spatial scales (seven, from 10 cm to 100 km, this being the one of the largest numbers considered so far in one sampling design). More specifically, it addresses the arthropods living on the pneumatophores of the mangrove tree *Avicennia marina*. The objective of the study was to identify the spatial scales at which most of the variation in individual species abundance, total abundance, species richness, and assemblage structure occurs, and to compare the results of these univariate and multivariate approaches. We show that abundance and richness of pneumatophore arthropods are positively autocorrelated over composition changes increasingly with increasing spatial scale. However, variation is not always highest for the largest scale (100 km). In the most abundant species, and also in total arthropod abundance, the 10 km scale holds the largest amount of variation, and this is suggested to be in relation with physical factors such as salinity, often more variable within, than between, estuarine systems.

Material and methods

Sampling program

Mangrove forests have a patchy distribution along the southern African coast, naturally occurring in open estuaries and bays (Macnae, 1963, Berjak et al., 1977, Ward & Steinke, 1982). The size of these patches varies from stands of a few square meters to hundreds of hectares, and adjacent patches are often tens of kilometers apart. The most abundant tree species in these forests is *Avicennia marina* (Forssk.) Vierh.. The pneumatophores of this species are pencil-like structures with a respiratory function (Tomlinson, 1986), emerging from the sediment of the mangrove forest floor at irregular intervals. Even in stands dominated by other tree species, *Avicennia* pneumatophores are present in high numbers, due to the broad distribution of subterranean roots. The pneumatophores occur at variable densities, from 0 to 1000/ m^2. Numerous studies have considered aspects related to their size, distribution, and the algal assemblages that usually cover them (Saifullah & Elahi, 1992, Phillips et al., 1994; 1996; Beck, 1998; 2000). Information is also available on the spatial distribution of the sessile fauna, with two studies actually considering spatial scale (Bingham, 1992; Farnsworth & Ellison, 1996). Much less is known about the motile arthropod fauna; although general characterizations of both small-scale (centimeters) and large-scale (hundreds of meters - kilometers) distributions exist (Procheş & Marshall, 2001a; 2001b; Procheş et al., 2001), no inter-scale study is available.

Sampling was done in three mangrove forests along the coast of KwaZulu-Natal (South Africa). The forest in Richards Bay covers an area of approximately 427.5 ha and is divided by a 'berm' (dam) wall between a southern wildlife sanctuary, and a northern harbour. The forests at Beachwood (c. 44 ha) and Bayhead (c.15 ha) are located within the Durban metropolitan area (Ward & Steinke, 1982). One transect was set in each of Richards Bay Harbour, Richards Bay Sanctuary, Beachwood and Bayhead. The distance between the former two, as well as the distance between the latter two, was approximately 10 km. The distance

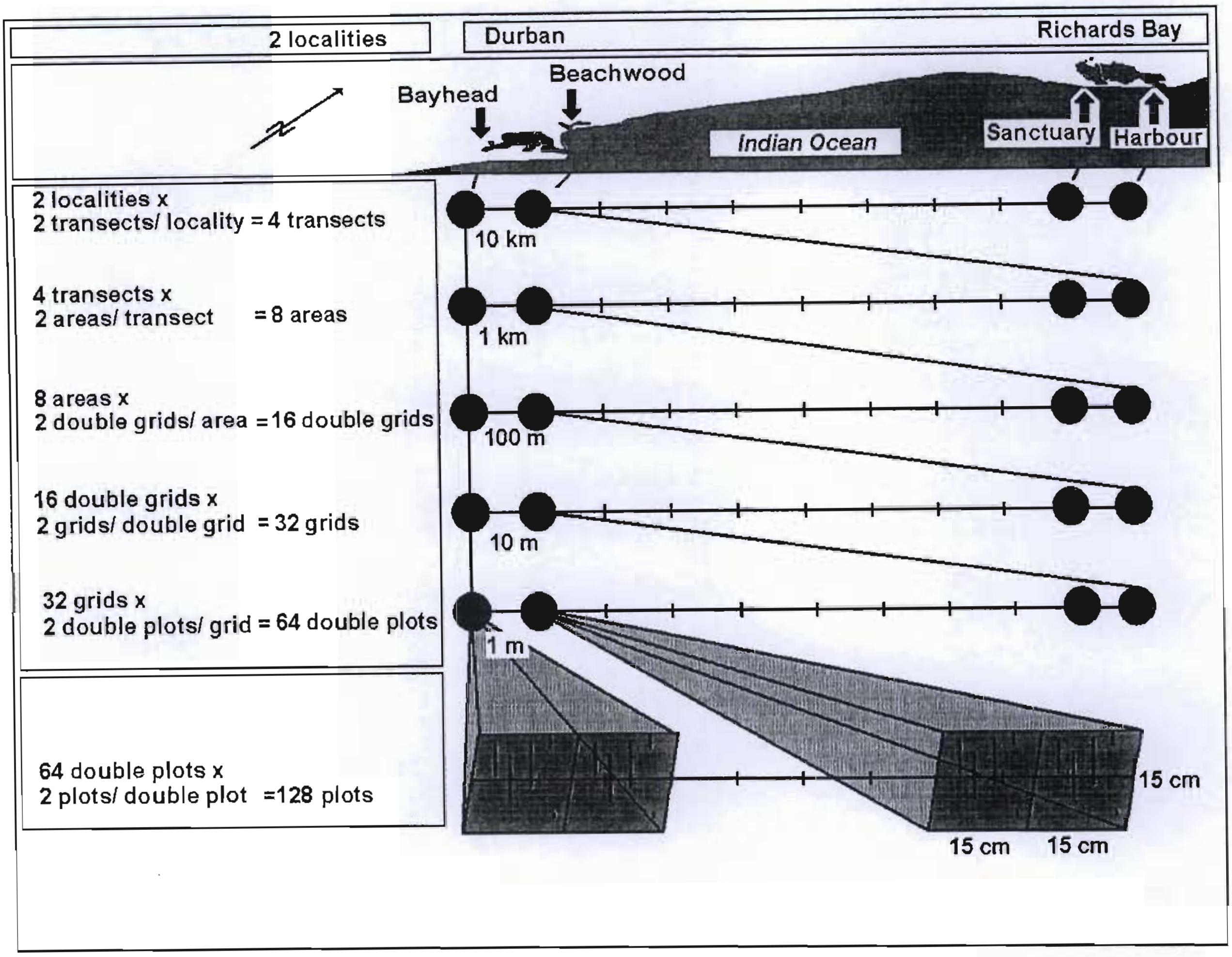

Figure 1. The sampling program. The 128 samples were collected from plots so arranged, as to allow assessing spatial relationships for species and communities at seven different spatial scales (localities 100km apart, transects 10km apart, areas 1 km apart, double grids 100m apart, grids 10 apart, double plots 1 m apart, adjacent plots).

between the two localities was 180 km, but for simplicity this will further be referred to as the 100 km scale. Five finer scales (1 km, 100 m, 10 m, 1 m, 10 cm) were considered in each transect, following a nested design based on that of Underwood & Chapman (1998) (Figure 1). This resulted in a total of 128 samples, allowing for comparisons at seven spatial scales. The environment within which sampling was conducted imposed some limitations on the sample layout, e.g. the distances between the sets of samples did not always represent the nominal values of their respective spatial scale. However, they did always represent between half and twice this value (e.g. double grids – nominally 100 m apart, were always between 50 and 200 m apart). The distance between the centers of the plots in a double plot, representing the 10 cm scale, was always 15 cm. The actual samples were represented by the arthropods on the *Avicennia* pneumatophores within each of the 128 plots.

Sample collection and processing

All the pneumatophores in a 15 x 15 cm sample quadrat were cut at ground level and returned to the laboratory. The pneumatophores were washed over a sieve to retain the algal and sediment covering, together with the arthropods larger than 0.15 mm. This was preserved in 25 ml sample bottles with 70% ethanol. The pneumatophores in each sample were dried and weighed, as a surrogate of habitat availability. The content of each bottle was then treated with hypersaline solution (as described in Fain & Hart, 1986), which resulted in the flotation of c. 90% of the arthropods. Floating specimens were identified and counted. The number of remaining arthropods was estimated by subsampling the mass of algae and sediment. This was brought to a 50 ml homogeneous solution; five subsamples of 5 ml each were then taken and arthropods in them counted until the total number of individuals belonging to one species surpassed twenty. A species represented by more than twenty individuals in a number of subsamples was not counted in the following subsamples. The average numbers of individuals from one species in the subsamples where this species was counted, was then multiplied by ten, to obtain an estimate for the 50 ml volume. c) the numbers of individuals belonging to each species in the two fractions were added to obtain the total value. Barnacles were counted separately.

Mangrove pneumatophore taxa

The arthropods inhabiting *Avicennia* pneumatophores are characterized by small size, generally low dispersal abilities, and high local abundance (Procheş et al., 2001). Efforts were made to identify all arthropods to 'morphospecies' level, however this was not possible for the harpacticoid copepods and the insect larvae, which were found (as slide-mounted specimens) to belong to numerous species, but were impossible to tell apart at the dissecting microscope. These two groups, representing respectively 16.86% and 10.16% of the total number of individuals were therefore excluded from our analyses. This left 21 species in the assemblage (14 Acari, 3 amphipods, 1 isopod, 1 tanaidacean, 1 barnacle, 1 collembolan). Morphospecies labeling was not always possible below family level; in fact among the Acari more than half the species are undescribed. The species considered in the study are listed in Table 1. Apart from the typical arthropod fauna of the mangrove forest floor (see Chapman, 1998; Procheş et al., 2001), rare taxa (e.g. Parasitidae, Cheyletidae, Erythraeidae, Nothridae), were also considered, in order to give correct estimates of species richness, and also to compare spatial patterns in common and rare species.

Table 1. Arthropod taxa from mangrove pneumatophores.

Acari	Mesostigmata	Parasitidae	Parasitidae sp.
		Ascidae	*Leioseius* sp.
		Uropodidae	*Uroobovella* sp.
	Prostigmata	Halacaridae	*Copidognathus caloglossae*
			Acarothrix umgenica
			Agauopsis sp.
		Tydeidae	Tydeidae sp.
		Tarsonemidae	Tarsonemidae sp.
		Cheyletidae	Cheyletidae sp.
		Erythraeidae	Erythraeidae sp.
	Oribatida	Nothridae	Nothridae sp.
		Oribatulidae	Oribatulidae sp.
			Pontiobates sp.
	Astigmata	Thyreophagidae	*Thyreophagus* sp.
Crustacea	Tanaidacea	Tanaididae	*Tanais philetaerus*
	Isopoda	Sphaeromatidae	Sphaeromatidae sp.
	Amphipoda		Amphipoda sp.
		Melitidae	*Melita zeylanica*
		Caprellidae	Caprellidae sp.
	Cirripedia	Balanidae	*Balanus amphitrite*
Hexapoda	Poduromorpha	Neanuridae	*Anurida maritima*

Statistical analysis

For univariate quantification of the effect of scale on species abundance, total arthropod abundance, and species richness patterns, spatial autocorrelation was conducted on each of these measures, using Bonferroni-corrected correlograms (with Moran's I as an autocorrelation measure, see Moran, 1950) on log-transformed data. The SAAP (Spatial Autocorrelation Analysis Program) package, ver. 4.3 (Wartenberg, 1989) was used. Correlograms are structure functions with autocorrelation values plotted on the ordinate, and distances among the sampling sites classed on the abscissa (Legendre & Fortin, 1989; Koenig, 1999). For describing spatial relations between samples, the rectangular co-ordinates system (Wartenberg, 1989) was employed. In defining distance classes for analyses, the unequal (customized) distance class option was used (see Wartenberg, 1989), in order to make each distance class represent one of the seven spatial scales considered. This resulted in 64, 128, 256, 512, 1024, 2048 and 4096 pairs, respectively, for the seven distance classes. According to Legendre & Fortin (1989), autocorrelation values in distance classes containing more than 1%

of the total numbers of pairs can be readily interpreted. This grants interpretable results for six of the seven distance classes in this study. The lowest number of pairs, 64, represented 0.8% of the total number (8128), however the results are considered for limited interpretation. Correlograms were used to illustrate autocorrelation in total abundance, species richness, and pneumatophore mass values. Autocorrelation values for individual species were given separately, as a table. To compare autocorrelation values in common and rare species, common species were defined as those present in more than 10% of the samples and representing more than 1% of the total number of individuals. Species present in only one sample were excluded from this analysis.

To compare the variation in community structure at different scales avoiding data non-independence, we used the method designed by Underwood & Chapman (1998). Bray-Curtis dissimilarity values were calculated for pairs represented by one individual sample and the centroid of one set of samples it belonged to. Sets of samples were selected to represent all of the distance classes considered (a sample was compared with the centroid of the samples found in the same double plot, grid, double grid, area, transect, locality, or the centroid of all 128 samples in the study). As 21 samples contained no arthropods, the total of 107 non-empty samples had to be used for comparison with seven distance classes without using the same sample twice. This gave a maximum of fifteen replicate dissimilarity values for each scale. The samples to be used for comparison at each scale were randomly chosen (Figure 2). Bray-Curtis dissimilarity values were computed using PRIMER 5 (Plymouth Routines in Multivariate Ecological Research) on 4th root transformed data (Clarke & Warwick, 1994), and then plotted against a distance axis. A one-way ANOVA, followed by a Student-Newman-Keuls test, was performed to compare the dissimilarity values for each spatial scale, using SPSS (ver. 9.0) for Windows.

Results

Univariate approaches: autocorrelation values of arthropod abundance and richness

Positive autocorrelations in species abundance were largely characteristic to fine scales (10 cm, 1 m, 10 m, 100 m), and negative autocorrelations, to large scales (10 km, 100 km). In the intermediate scale of 1 km, the abundances of some species were positively, and those of other, negatively autocorrelated. Generally, autocorrelation values decreased continuously with increasing distance, exceptions occurring for the lowest and highest scales (Table 2).

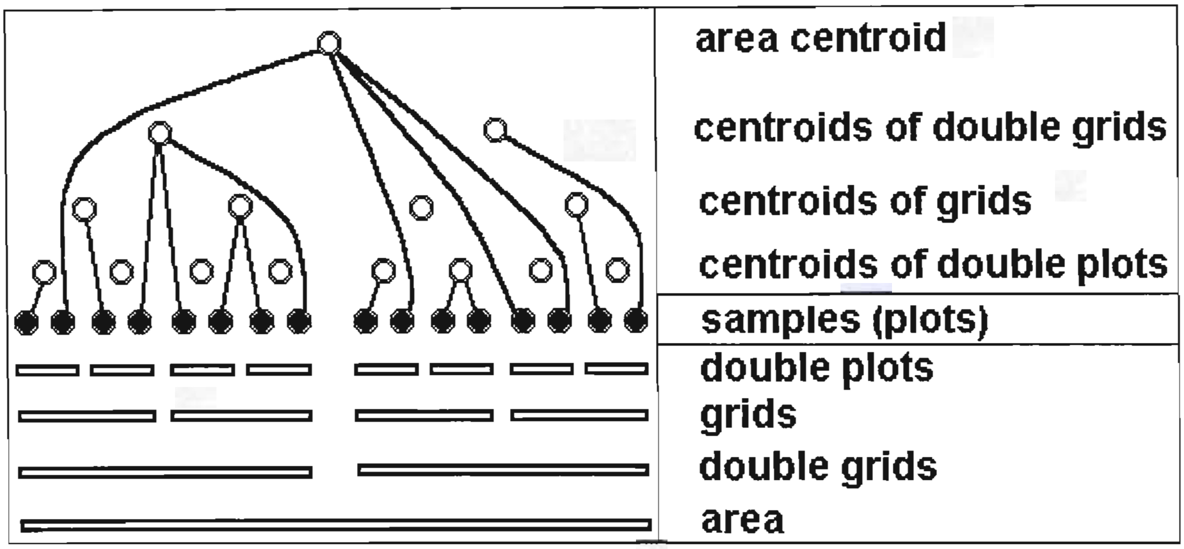

Figure 2. The method for evaluating variations in community structure at different spatial scales designed by Underwood & Chapman (1998). Circles represent samples or centroids for subsets of 2, 4, 8, and 16 samples. Links represent randomly selected sample-centroid pairs for which dissimilarity values are calculated. A sample is always compared to the centroid of the set it belongs to, and equal numbers of dissimilarity values are calculated for sets from each spatial scale. The example in this figure illustrates how this method is applied to a set of 16 samples. In our study, the method was applied to a set of 128 samples.

Unusual patterns appeared in *Balanus amphitrite* and *Agauopsis* sp. In these two species, the positive values for the 100 m scale were higher than both the 10 m and the 1 km scales. In *Leioseius* sp., an unusually high value occurred in the 1 km class, as compared to the 100 m class (Table 2). The highest positive autocorrelation was at the 10 cm scale for eight species, and in the 1 m class for six species. The lowest negative correlation was at the 100 km scale for five species, at the 10 km scale for another five species, and at the 1 km scale for *Uroobovella* sp (only significant values counted). Abundant and widely distributed species showed more significant values than rare and localized species (Table 2). Positive autocorrelation at low scales was high in common species, and lower in rarer species. For common species, the highest positive autocorrelation value was most often at the 10 cm scale, and the lowest negative value at 10 km, whereas in rare species the extreme values occurred more often at 1 m and 100 km, respectively (Table 2).

Autocorrelation of total arthropod abundance closely followed the curve for the dominant species, *Tanais philetaerus* (Figure 3, cf. Table 2). Species richness showed a

Table 2. Autocorrelation vales (Moran's I) for arthropod species from mangrove pneumatophores at seven spatial scales. Bonferroni-corrected overall significance values are also given for the correlogram of each species. Significance: * $P< 0.050$; ** $P< 0.001$. The lowest significant negative values for each species is given in bold, while the highest positive significant value is underlined. The species area arranged in decreasing order of abundance, and species present in only one sample were excluded.

Species	Total abundance	Samples present	10 cm	1m	10 m	100 m	1 km	10 km	100 km	Overall significance
Common										
Tanais philetaerus	9362	81	0.95**	0.88**	0.79**	0.74**	0.27**	**-0.53****	-0.01	0.001
Copidognathus caloglossae	1139	18	0.98**	0.87**	0.90**	0.11**	0.14**	**-0.11****	**-0.11****	0.001
Balanus amphitrite	772	45	0.87**	0.83**	0.20**	0.46**	-0.02	**-0.24****	-0.01	0.001
Leioseius sp.	244	56	0.53**	0.59**	0.39**	0.03	0.22**	**-0.14****	-0.05**	0.001
Acarothrix umgenica	144	22	0.70**	0.55**	0.11*	-0.01	0.10**	-0.04*	**-0.05****	0.001
Rare										
Thyreophagus sp.	74	9	0.33**	0.46**	0.30**	-0.03	0.11**	**-0.05****	**-0.05****	0.001
Melita zeylanica	57	10	0.11	0.38**	-0.01	0.03	-0.06*	-0.02	-0.01	0.001
Agauopsis sp.	33	4	0.65**	0.41**	-0.03	0.14**	-0.03	-0.03	**-0.03****	0.001
Tarsonemidae sp.	30	4	0.13*	0.22**	-0.02	-0.02	-0.02	-0.02	-0.01	0.001
Uroobovella sp.	25	9	0.75**	0.69**	0.74**	-0.07	**-0.07***	-0.04*	-0.05**	0.001
Tydaeidae sp.	16	7	-0.04	0.14*	0.08*	-0.03	0.03*	-0.02	-0.02	0.002
Pontiobates sp.	16	4	-0.02	0.08*	0.03	-0.02	0.01	-0.01	-0.01	0.103
Spheromatidae sp.	9	4	0.63**	-0.03	-0.03	0.01	0.08**	-0.03	**-0.03****	0.001
Anurida maritima	4	3	0.70**	-0.02	-0.02	-0.02	-0.02	-0.02	-0.01	0.001

similar curve, but with a relatively smoother slope, while correlation in total pneumatophore mass was less regular, but still generally decreasing with distance (Figure 3).

A multivariate approach: differences in community structure

At all scales but 100 km, some samples were highly similar to the centroids of their respective sample sets, while other were dissimilar, causing a wide scatter of the Bray-Curtis dissimilarity values within each scale. Even so, averaged dissimilarity values significantly increased with spatial scale (Table 3, Figure 4). The 100 km scale was the most distinct, as the highest, and also the most homogeneous dissimilarity values occurred at locality level. Among the other scales, the 10 cm scale was quite distinct, with very low averaged dissimilarity, and the 1 m scale appeared as intermediate between the 10 cm scale and larger scales (Table 3, Figure 4).

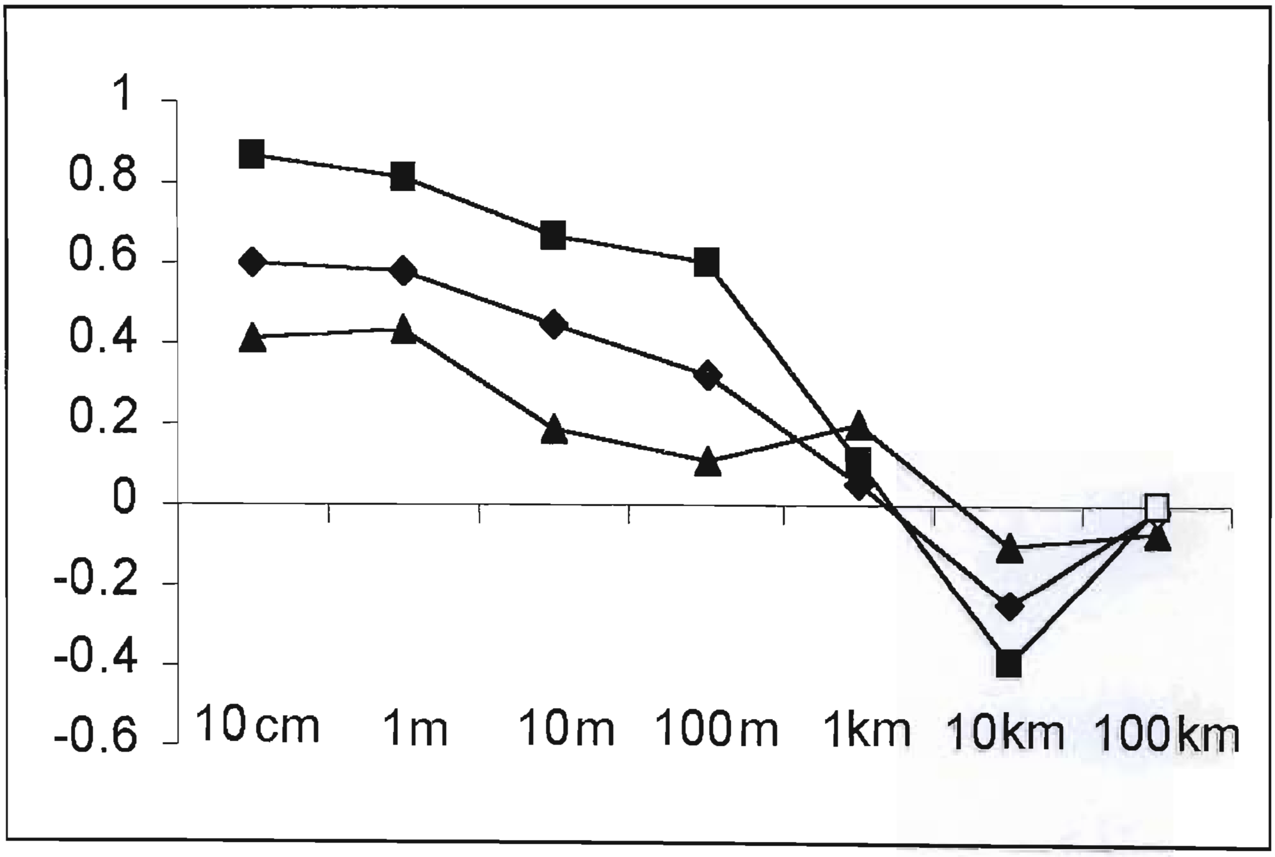

Figure 3. Bonferroni-corrected correlograms for total arthropod abundance (squares), species richness (diamonds), and total pneumatophore mass (triangles) at seven scales. Significant values are represented by closed symbols.

Table 3. One-way ANOVA and Student-Newman-Keuls test comparing the Bray-Curtis dissimilarity values between individual samples and the centroids of the sets they belong to, at seven scales.

ANOVA	SS	df	MS	*F*	*P*
Between scales	30927.674	6	5154.612	9.168	0.001
Within scales	55097.893	98	562.223		
Total	86025.567	104			

SNK test	10 cm	1 m	10 m	100 m	1 km	10 km	100 km
Average	24.26	37.00	45.35	57.00	58.45	59.81	81.98
Standard error	5.08	5.39	5.96	6.89	7.59	7.14	3.98
Subset	a	a/b	b	b	b	b	c

Significance of the subsets ($\alpha=0.05$): a, 0.141; b, 0.074, c, 1.000

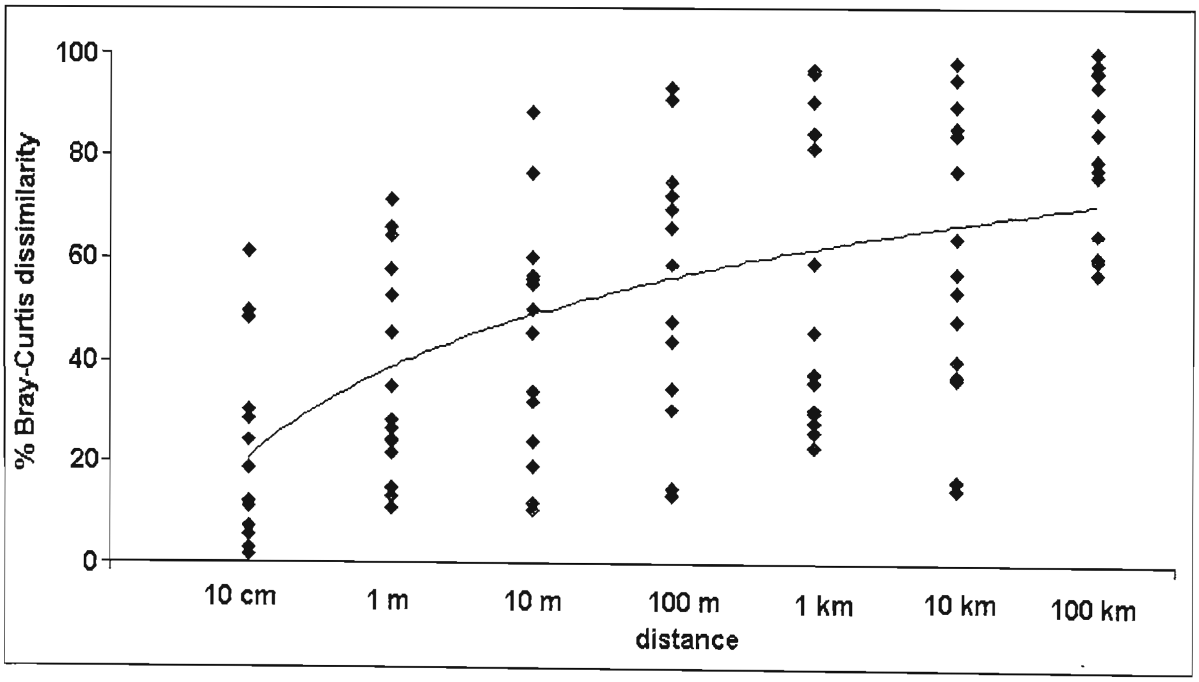

Figure 4. The relationship between Bray-Curtis dissimilarity (among samples and sample centroids), and spatial scale. (See Materials and Methods for a full explanation.)

Discussion

Environmental patchiness

The distribution of populations and assemblages is often limited to suitable patches of habitat. In a spatial perspective, the distribution of organisms is likely to be most uneven at the scale where environmental patchiness is most pronounced (Pielou, 1977; Maurer, 1990; Cosson et al., 1997). For a given population or assemblage, the size and spacing of suitable patches determines the level of habitat availability (Wiens, 1976; Levin & Buttel, 1987; Swadling et al., 1997). At the same time, the existence of non-inhabited patches can impose barriers resulting in local isolation. In a dynamic environment, each patch is characterized by its own processes of colonization, population growth, and extinction, leading to differences among patches (MacArthur & Wilson, 1967; Rosenzweig, 1997). In the presence of an environmental gradient, these differences will tend to increase with increasing distance. Even if abiotic gradients are absent, biotic gradients derived from patch history will cause similar effects, at least over small scales (Levin, 1992; 1994).

Patchiness of arthropod distribution in mangrove pneumatophore habitats arises from at least three effects: 1) aggregation of individuals on a pneumatophore; 2) aggregations of pneumatophores within a mangrove forest; and 3) distribution of forest patches along the coast. The first level of patchiness is not covered by the present study, but has been partly addressed elsewhere (Procheş & Marshall, 2001b). While it is preferable, especially in fine scale studies, to consider distances between individual animals rather than samples lumping together their coordinates (Gardner, 1998), the small size of pneumatophore arthropods negates this procedure.

The third level of patchiness was purposefully eliminated from the study, by sampling only in mangrove forests, and not outside them. Yet, it could be expected that the relative isolation of the faunas in different forests, together with the specific characteristics of the estuaries and bays where they were located, should cause spatially-related differences among forests. The size of forest patches considered here ranges between the 1 km and 10 km scales, and the distance between two patches is in the region of 10 km – 100 km.

Most of the spatial distribution patterns depicted here for pneumatophore arthropods should relate to the second level of patchiness, and therefore the dry mass of pneumatophores has been used as a surrogate of habitat availability. Variations in the density and size of pneumatophores occur at all scales, from 10 cm to the size of the forest patch (see Saifullah & Elahi, 1992). In the present study, pneumatophore mass was negatively autocorrelated in the

10 km and 100 km scales (Figure 3), which suggests that variations also exist among mangrove forests. This means that the availability of small-scale habitat patches (the pneumatophores) differs among large-scale habitat patches (the mangrove forests). Arthropod abundance, if strictly determined by habitat availability, should follow a similar pattern. Species richness is also expected to follow a similar pattern, as larger numbers of species are likely to inhabit larger habitat patches (see species-area curve theory in Rosenzweig, 1997). And indeed, similar to pneumatophore mass, arthropod abundance and species richness show a decline in autocorrelation from finer, to larger scales (Figure 3).

Habitat utilization and population dynamics

Mangrove arthropods are unlikely to fully exploit the available pneumatophore habitat. *Avicennia* pneumatophores are not long-lived structures (Tomlinson, 1986), and are often affected by the various disturbances characteristic to mangrove forests (lightning, tree extraction, pollution, flooding; see Berjak et al., 1977; Begg, 1978; Ellison & Farnsworth, 2000). Colonization of new pneumatophores is a must for population survival. Furthermore, finding a partner and a suitable microhabitat for reproduction, are unlikely events considering that, for most species, the average abundance per penumatophore was below one. While many marine organisms have swimming larvae enabling long distance dispersal (Morgan, 2001; Underwood & Keogh, 2001), among pneumatophore arthropods this feature is rare (it occurs in barnacles (Satumantpan et al., 1999; Satumanatpan & Keough, 2000), but is absent in mites and most crustaceans). Therefore, a local population can generally spread only across small distances. The improbability of long-distance dispersal explains why spatial dependence in arthropod species richness was more pronounced, as compared to that of habitat availability (pneumatophore mass), with stronger positive autocorrelation at finer scales, and stronger negative autocorrelation at larger scale (Figure 3). Spatial dependence was even more pronounced in the case of arthropod abundance, this being largely dependent on local population size, in turn determined by the probability of the recruits finding a mate and suitable microhabitat for reproduction.

Further differences appear at species level. Depending on their body size, mobility and life history, different species utilize the available habitat to different degrees (Morse et al., 1985; Zwölfer & Brandl R, 1989; Hansen, 2000). Although the abundance autocorrelation for most species showed decreasing trends towards larger scales, similar to that of habitat availability (pneumatophore mass), the precise shape of the latter (with top positive autocorrelation values at 1 m and 1 km scales; compare Figure 3 and Table 2), was only followed by one arthropod species: the ascid mite, *Leoseius*. This is not surprising, as *Leioseius*, a predator of terrestrial affinities (see Krantz, 1978) is the only pneumatophore species that fully exploits the entire surface of the pneumatophores, irrespective of microhabitat conditions (Procheş & Marshall, 2001b; Procheş et al., 2001). Other types of patterns in cross-scale autocorrelation are noted in the other arthropod species. The uropodid mite, *Uroobovella*, is characterized by a positive peak at 10 m and a negative peak at 1 km. This species is strictly dependent on a specific microhabitat with dense algal growth and sediment deposition (Procheş & Marshall, 2001a; 2001b), and its spatial distribution patterns may reflect the distribution of this microhabitat. As the algal growth is dependent on particular sunlight levels, the 10 m peak could be explained as the typical spacing of mangrove trees or canopy gaps. Another pattern, with high autocorrelation in the 100 m class occurred in the barnacle, *Balanus* and the mite, *Agauopsis*. This is likely to indicate good intra-estuarine dispersal, and is easy to explain in the case of the barnacle, which has swimming larvae, but not in the case of the mite, which lacks them. The most common pattern (all other species, see Table 2), is a relatively smooth decrease in autocorrrelation with scale, the highest positive value being either at 10 cm, or at 1 m, and the lowest negative, at 10 or 100 km. No specific explanation for this pattern can be suggested, but it may simply depict the general spatial pattern for a population characterized by extinction and subsequent colonization from adjacent patches.

Common and rare species

Further differences in spatial distribution exist among common and rare species (Gaston, 1994; McGeoch & Chown, 1997). In this study, the highest positive autocorrelation for rare species occurred at 1 m, rather than 10 cm, generally indicating that two adjacent individuals are more often 1 m apart. Also, rare species were characterized by strongest negative autocorrelations at 100 km, as most of them only occur in only one of the two localities (either Durban or Richards Bay). Such faunistic differences along the KwaZulu-Natal coast have been observed by Macnae (1963), and should be considered a biogeographical, rather than ecological, effect (see Cornell, 1985; Ricklefs, 1987; Cornell & Lawton, 1992). It is less obvious why common species should have the strongest negative autocorrelation at 10 km. A possible explanation, is that the harbours in both Durban and Richards Bay have a natural regime of tidal flushing, normally keeping salinities above 30 (Begg, 1978). This insures an input of arthropod recruits, especially in the form of crustacean larvae (see Ross & Underwood, 1997; Satumanatpan et al., 1998). On the other hand, the estuarine waters in Beachwood are known to have salinities often as low as 12 (Phillips et al., 1994; 1996). The situation is similar in the Sanctuary in Richards Bay, completely closed to tidal flushing at the time when we collected. *Tanais philetaterus*, the most abundant species in both harbours, was represented in low numbers in Beachwood and Richards Bay Sanctuary, and this species has been shown to be negatively influenced by low salinities (Procheş et al., 2001). Such differences in the values of physical factors, more prominent within than among localities, can account for the stronger negative autocorrelations at the 10 km scale.

Community structure

Community structure is the result of both species diversity and abundances (Clarke & Warwick, 1994), therefore spatial variation in community structure combines all the single factors discussed above. If some of these varied most at 10 km and others at 100 km, community structure clearly varied most at 100 km. At all scales but 100 km, there was a broad scatter of the dissimilarity values, indicating mixed (smaller and larger) variations in assemblage structure, while in the 100 km scale, these were consistently large (Figure 4). Three different classes of distances are separated by the ANOVA procedure (Table 3). These can be defined as scales below alpha diversity (10 cm – 1 m), alpha diversity (1 m – 10 km), and beta diversity (100 km) for mangrove pneumatophore arthropods (*sensu* Whittaker, 1970). This means that the 'point diversity' for these assemblages is reached around the 1 m scale, while biogeographical species replacement characterizes scales larger than 100 km.

Pneumatophore arthropod assemblages contain species of both marine and terrestrial ancestry, and are influenced by physical factors from both environments. It is expected (Ricklefs, 1990; Levin, 1994) that different patterns would occur between typical marine and terrestrial ecosystems, as indicated by a number of available studies (e.g. Cornell, 1985; Underwood & Chapman, 1996). However, to fully certify this, studies using standardized nested hierachical schemes, similar to the one presented here, would be necessary.

In conclusion, this study brings together univariate and multivariate methods, to investigate the patterns of spatial variation in arthropod assemblages. It points out the fact that these methods can partly confirm one another, but also complete one another, and their combination is likely to produce more accurate ecological interpretations.

Acknowledgements

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Chapter IX

Summary and discussion

Ecological and biogeographical patterns of secondary marine organisms are generally constrained by their terrestrial links (Vermeij & Dudley, 2000). Chapter II shows that the taxa that are in one way or another land-dependent (those land-dependent for most of their life cycle, such as the mangrove trees, or at least during the reproductive season, as the seabirds, seals and marine reptiles) have global distribution ranges largely corresponding to three climatic belts. Some genera are strictly tropical in distribution, while others are restricted to either northern, or southern cold waters. Very few are distributed across all latitudes. This results in the existence of three distinct species assemblages, one northern, one tropical and one southern, and also in an atypical latitudinal pattern of species richness, with three peaks in the three species-rich latitudinal bands, and two lows in the warm temperate regions of each hemisphere.

Both the existence of three different faunas, and the bimodal distribution of species richness in each hemisphere is confirmed (Chapter III) for at least one group of marine mites, the Ameronothroidea (Oribatida), for which records from the cold-climate regions of both hemispheres are quite reliable. While records from tropical regions are scarce, these represent entirely different families, and suggest much higher species richness. The Ameronothroidea, together with the astigmatid family Hyadesiidae, are shown to represent an ecological group characterized by worldwide intertidal distributions and high numbers of species per genus. In this context, their low fecundity and limited dispersal possibilities, suggest long evolutionary associations with the marine environment. However, their diversity is still relatively low, as compared to that of typically marine (and not strictly intertidal) mites in the family Halacaridae (Prostigmata). Also, the latter family is cosmopolitan and seems to have unimodal latitudinal distribution patterns, as suggested by Bartsch's (1989) review.

Chapter IV reviews the available literature on southern African marine intertidal mites, and at the same time presents original results from a bioegeographical survey on the region's rocky shores. The complete list of southern African mites contains eighty two species, but this is likely to be an underestimation, given the absence of collections from habitats such as coral reefs, sandy beaches and salt marshes. The bulk of the southern African intertidal mite fauna (forty eight species) is contained in the family Halacaridae. Seventeen other species represent the Ameronothroidea and Hyadesiidae. In both these ecological groups, the west coast is species-poor, while the south and east coast are species-rich (the total number of species per locality being about double, as compared to the west coast). These three provinces, defined for other southern African marine biota, are confirmed here as having different marine mite faunas. The pattern of species richness for intertidal mites is also similar to that already observed for other intertidal rocky shore faunas, and different from that characterizing coral reef faunas. (The coral reef element is essential in determining the patterns of species richness in fishes and echinoderms, both of these having much richer faunas on the east coast, as compared to both the west and south coast.)

The following chapters represent a series of investigations into the ecology of mangrove pneumatophore arthropods. Chapter V indicates that in this environment, species richness is evenly distributed between primary and secondary marine species. However, the two groups greatly differ in abundance, with primary marine arthropods being about one order of magnitude more abundant that their secondary marine counterparts. Another difference appears when considering assemblage composition along a salinity gradient, with primary marine species apparently being more sensitive to low salinity, though this needs to be tested experimentally. However, species from both groups are more abundant along forest fringes, than in other habitats, and both groups appear to have summer peaks in abundance (though the latter needs to be confirmed by multi-annual studies).

Further differences between primary and secondary marine arthropods are highlighted in Chapter VI, concerning vertical distribution along the pneumatophores, and species interactions. Typical primary marine species from this environment are more abundant at higher elevation levels, while species with close terrestrial ancestry are more abundant at lower levels. When considering the halacarid mites (that have long marine associations) together with the primary marine group, differences in vertical distribution between the two groups are highly significant. Correlation values among species abundances within each of the two groups are always positive, while correlations between species from different groups are either positive or negative. Environmental factors, especially desiccation, which increase with both elevation and exposure to sunlight, affect both groups, causing their abundances to co-vary.

Chapter VII suggests that desiccation affects penumatophore arthropods not only directly, but also by reducing algal growth. Algal mass is shown to increase sediment deposition, thereby accommodating more interstitial arthropods. Correlations between arthropod abundance and the dry mass of the algae/sediment are significantly positive for both primary and secondary marine species. No clear differences between the two groups could be observed in terms of population recovery after pneumatophore defaunation, which can be explained by pneumatophore meiofaunal species in general lacking swimming larvae, and therefore having limited dispersal capacities.

Patterns of variation in pneumatophore arthropod distribution across spatial scales are described in Chapter VIII, showing that levels of similarity in assemblage composition and species abundance decrease with increasing scale. No differences in cross-scale distribution were observed between primary and secondary marine species, possibly relating to the fact that both categories include widespread and localized species, occurring in low and high abundance.

While logistic constraints imposed a limit on the number of factors considered in each mangrove pneumatophore ecology chapter, by putting all these chapters together, a consistent picture takes shape, indicating a strong dependence of the arthropod assemblages on the availability of suitable habitat. This in turn is dependent upon both the density and size of the pneumatophores, but only where sunlight and elevation conditions are suitable. Where the microclimate is not appropriate, the arthropod assemblages are absent or scarce, irrespective of pneumatophore availability. No definitive answers are provided regarding the nature of biotic interactions within these assemblages, although such interactions are shown to be present, and to some extent different between primary and secondary marine organisms.

Previously unreported patterns emerge from the thesis with respect to biogeography. Differences are shown to occur between the distributions of primary and secondary marine organisms, as long as secondary marine organisms maintain links with terrestrial habitats (as in the case of seabirds and ameronothroid mites), but disappear in the case of land-independent species (such as cetaceans and halacarid mites). Also, these differences are clear at global scale, but become difficult to assess at regional scale, as the small number of species (e.g. southern African ameronothroid mites) does not allow for proper statistical treatment.

There remain many interesting unanswered questions, relating to both ecology and biogeography. For example, how do abundance and species richness ratios between secondary marine arthropods vary among habitats and geographical regions? From the little available information, it appears that geographical variation in this respect is relatively small, when compared to variation among habitats. Values around ten primary to one secondary marine individuals, as documented for mangrove pneumatophores (Chapter V), have also been reported for sand deposits, lower rocky shores (Bartsch, 1989), as well as sea-grass beds

(Sánchez-Jerez et al., 1999). A much better representation of secondary marine species (up to 90% of the total arthropod abundance) is encountered in the upper littoral of rocky shores (Bartsch, 1989; Mercer et al., 2000). There is however a dearth of understanding as to what are the factors determining these differences. Variations in species richness also appear to be mainly habitat-determined. Rocky shores in most regions of the world, as well as in most southern African localities, harbour a hyadesiid fauna of two to three species (chapters III, IV). This taxonomic group could provide an excellent model for studying niche separation mechanisms, in terms of feeding and tolerance to physico-chemical factors.

An interesting pattern not previously discussed in the thesis is the high ratio of secondary marine to primary marine arthropod species on mangrove pneumatophores. It is shown here that this ratio is around 1:1. Although few cases for comparison are available, the value of 1:15 (for British subtidal hard substrata; Gee & Warwick, 1996) is more likely to be a typical one. A reason for the high ratio in mangrove habitats may relate to the small ecological distance between the typical soil environment of mites and insects, and the mangrove sediments. This may suggest the center of origin for secondary marine arthropods to be in tropical regions, where mangroves are prevalent. However, it would be simplistic to suggest a that a single or predominant effect has prevailed in the origin of these arthropods. For example, the ameronothroid mite *Halozetes* and the hyadesiid mites are restricted to rocky shore environments. It is probable that these mites originated independently of the mangrove environment, most likely as a result of glaciation at higher latitudes, and this resulted in specialized attributes for a rocky shore existence. Although these ideas are given in different perspectives for different organisms in chapters II and III, there is still considerable scope for further study in this respect.

In the context of the growing concern for the loss of biodiversity, and its potential effects on ecosystem functioning, further interest should be taken in the animal groups considered here. Secondary marine arthropods constitute a major percentage of the total marine biodiversity, and could therefore be used in assessing conservation priorities for marine protected areas. Studies on these organisms are especially relevant in view of the recently recognized importance to document the biodiversity of "coastal transition zones" (CTZs), which form the interfaces among soils, freshwater sediments and marine sediments (Levin et al., 2001; Wall et al., 2001).

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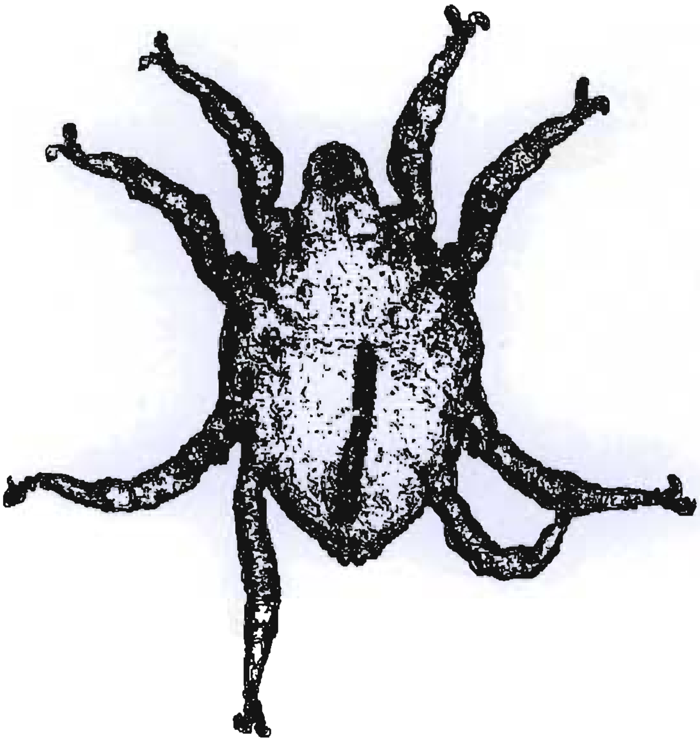
Appendix



Part I

Halacaropsis praecognita n. sp. (Acari: Halacaridae) from southern Africa

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Abstract

The marine halacarid mite genus *Halacaropsis* Bartsch, 1996 (Acari: Halacaridae) currently comprises four species from the Mediterranean, northern Atlantic, and Australia. A new species, *Halacaropsis praecognita* n. sp. (Acari: Halacaridae) is described from the rocky shores of southeastern Africa (Eastern Cape and KwaZulu-Natal). This species possesses the characteristic peg-like setae on leg I and enlarged median claws, but is distinguishable from the other *Halacaropsis* species by not having toothed median claws on any of the legs.

Introduction

The family Halacaridae (Acari: Prostigmata) is mainly represented by marine species, living in habitats ranging from the littoral fringe to deep-sea trenches (Bartsch 1989). Despite a review (Bartsch 1972) and a few additional articles (Bartsch 1974, 1986, 1987, 1992), the southern African fauna remains poorly known, with less than twenty species described from the region. The current paper describes a new species, the largest known to date.

The genus *Halacaropsis* Bartsch, 1996 is based on the '***hirsuta*** group' of the genus *Agauopsis*, and combines characters of both *Agauopsis* (chaetotaxy of tibia I) and *Halacarus* (chaetotaxy of tarsi I and II). It is represented by *H. hirsuta* (Trouessart, 1889), from the Mediterranean and the northern Atlantic, *H. warringa* (Otto, 1993), from southeastern Australia, *H. capuzina* Bartsch, 1996, from south-western Australia and *H. nereis* Otto, 1999, from the Coral Sea. An undescribed species from southern Africa has been reported by Bartsch (1986, 1996).

Material and methods

The southern African material comprised six specimens, which were cleared in lactic acid and mounted in Hoyers medium. Three specimens of *H. nereis* Otto were examined for comparison. Drawings were prepared from light-micrographs. Abbreviations used in description: AD, anterior dorsal plate; AE, anterior epimeral plate; PE, posterior epimeral plate; GA, genito-anal plate, OC, ocular plate; PD, posterior dorsal plate; ds, dorsal setae; ae, anterior epimeral setae, P-2, P-3, P-4, second, third and fourth palpal segments, staring from the base. All setae numbered from anterior to posterior. Legs numbered I to IV.

Halacaropsis praecognita n. sp.

Holotype: male, South Africa, KwaZulu-Natal, Park Rynie, 29 VI 1999, leg. Ş. Procheş, from mid-littoral algae. Paratypes: 1) male, South Africa, KwaZulu-Natal, Park Rynie, 1 IX 1999, leg. Ş. Procheş, from *Cheilosporum* and *Jania* algae; 2) male, South Africa, Eastern Cape, Preslies Bay, 29 V 1999, leg. D.J. Marshall, from lower littoral coralline algae; 3) female, South Africa, Eastern Cape, Sardinia Bay, 8 VIII 1998, leg. D.J. Marshall, from Porphyra algae; 4) female, South Africa, Eastern Cape, Sardinia Bay, 8 VIII 1998, leg. D.J. Marshall, from mixed red algae; 5) deutonymph, South Africa, Eastern Cape, Sardinia Bay, 8 VIII 1998, leg. D.J. Marshall, from mixed red algae. The holotype and paratypes are deposited at the Natural History Museum in London (accession number BMNH(E)2001-13).

Male. Idiosoma 575 - 660 µm long and 510 - 565 µm wide.

Dorsum. AD 180-210 µm long and 175 - 190 µm wide, with ds-1 situated on a small prominence, frontal spine with small lateral lobes. OC 125-130 µm long and 70-75 µm wide, with two corneae. PD 235-240 µm long and 150-190 µm wide, very thin and with ds-5 in its posterior margin. Setae ds-2, ds-3 and ds-4 large, on platelets in the striated integument (Fig. 1A).

Venter. AE 205-215 µm long and 510 µm wide, carrying ae-1, ae-2 and ae-3. PE 280-310 µm long and 150-165 µm wide with one dorsal and three ventral setae. GA 255-330 µm long and 180-230 µm wide, with genital opening placed centrally and the seventh pair of ventral setae on in the anterior part (Fig. 1B). 5-6 pairs of perigenital setae on the inner circle and 18-21 on the outer one. Genital opening with six pairs of subgenital setae, of which the fourth is thicker than the other (Fig. 1I).

Gnathosoma 225-230 µm long and 165µm wide, rostrum slightly longer than gnathosomal base. Basal pair of maxillary setae long, terminal pair short, two short pairs of rostral setae present. Palps longer than rostrum, P-2 with a long seta, P-3 with one short, spiny-tipped seta, P-4 with two proximal setae, one longer than the segment, and four distal sub-apical setae (Fig. 1C).

Legs long and robust. First pair longer than the other, with ventral peg-like setae. Two ventral, denticulate setae are present on tibia II, one on tibia III, two on tibia IV. Chaetotaxy

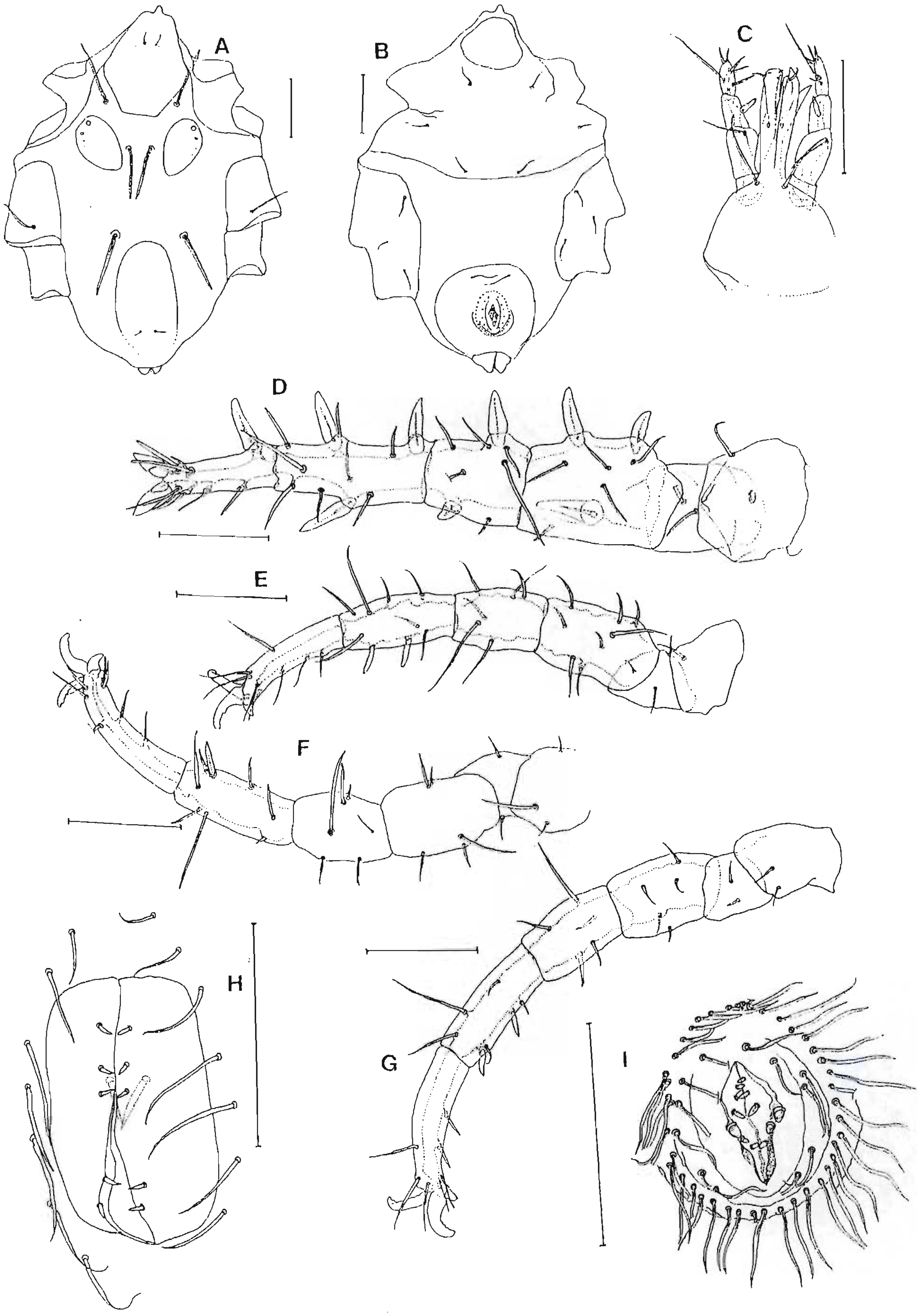

Figure 1. *Halacaropsis praecognita* n. sp.; A idiosoma (dorsal), male; B idiosoma (ventral), male; C gnathosoma (dorsal), male; D leg I, male; E leg II, male; F leg III, male; G leg IV, male; H female genital opening; I male genital opening. All bars: 100µm.

summarized in Table 1, and shown in Figs. 1D-1G. Lateral claws smooth, median claws of all legs lacking accessory teeth.

Table 1. *Halacaropsis praecognita* n. sp.; Chaetotaxy of the legs. Tarsal counts do not include solenidia and parambulacral setae. The number following "+" in leg I represents the number of peg-like setae.

	Leg I	II	III	IV
Trochanter	1	1	3	1-2
Basifemur	2-3	3-4	2	2
Telofemur	5+3	7-8	5	5
Genu	5-6+2	6-7	6	5-6
Tibia	7-8+3	9-10	7-8	7-8
Tarsus	7+1	6	5	5

Female. idiosoma 680-820 μm long and 470-580 μm wide.

Dorsum. similar to the male, AD 205-215 μm long and 195-225 μm wide. OC 150-165 μm long and 80-95 μm wide. PD 295 μm long and 170-180 μm wide.

Venter. similar to the male, AE 230-245 μm long and 510-520 μm wide. PE 310-315 μm long and 170-180 μm wide. GA 235 μm long and 180-190 μm wide, with genital opening placed slightly posterior the center and the seventh pair of ventral setae on in the anterior part. Seven pairs of perigenital setae, five pairs of short, thick subgenital setae, and one pair of prominent spiniform endogenital setae, along with smaller indistinct ones (Fig. 1H).

Gnathosoma 240-290 μm long and 120-170 μm wide.

Deutonymph. Idiosoma 490 μm long and 410 μm wide. AD 160 μm long and 160 μm wide. OC 115 μm long and 110 μm wide. PD 210 μm long and 95 μm wide. AE 225 μm long and 410 μm wide. PE 220 μm long and 130 μm wide. Genital (60 μm long and 80 μm wide) and anal (75 μm long and 125 μm wide) shields discrete. Gnathosoma 175 μm long and 100 μm wide.

Etymology: The name *praecognita* refers to the knowledge of a southern African *Halacaropsis* before its actual description (Bartsch 1986, 1996).

Table 2. Characters of taxonomic significance in the genus *Halacaropsis*.

Species	*H. hirsuta*	H. warringa	*H. capuzina*	*H. nereis*	*H. praecognita*
Description	Trouessart, 1889	Otto, 1993	Bartsch, 1996	Otto, 1999	Present paper
Lateral lobes at the anterior tip of AD	-	+	+	+	+
Denticulate postero-ventral seta on tibia I	+	+	+	-	+
Lateral claws denticulate	+	+	+	-	-
Accessory tooth on median claw I	+	+	+	+	-
Accessory tooth on median claw II-IV	+	+	+	-	-
Rostrum slightly longer than gnathosomal base	-	-	+	-	+
Spines at tip of P-3 seta	+	+	-	+	+

Discussion

H. praecognita sp. nov. is closest related to *H. nereis* Otto. The two species have in common the smooth lateral claws, and the lack of the accessory tooth on median claws II-IV, characteristics which distinguish them from all other *Halacaropsis* species (Table 2). However, the absence of an accessory tooth on the median claw of leg I, the presence of a denticulate postero-ventral seta on tibia I, and the rostrum, slightly longer than the gnathosomal base, separate *H. praecognita* sp. nov. from *H. nereis* Otto.

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Part II

New species of Copidognathinae (Acari: Halacaridae) from southern Africa

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Abstract

Three new species of Copidognathinae (Acari: Halacaridae) are described from the eastern coast of southern Africa (Mozambique; South Africa: Eastern Cape and KwaZulu-Natal). *Copidognathus caloglossae* sp. nov. and *Acarothrix umgenica* sp. nov. were collected in mangrove habitats, whereas *Copidognathus xaixaiensis* sp. nov. was collected on a rocky shore. *Acarothrix umgenica* represents the first record of the genus *Acarothrix* Bartsch 1990 from the African continent.

Introduction

The subfamily Copidognathinae comprises the largest halacarid genus (*Copidognathus* Trouessart, 1888, which has c. 300 species described) along with *Acarothrix* Bartsch, 1990, *Arrhodeoporus* Newell, 1947, *Copidognathides* Bartsch, 1976, *Phacacarus* Bartsch, 1992 and *Werthella* Lohmann, 1907. Characteristics of the subfamily are: adult anterior epimeral plate with one pair of pores, palp with one seta on the femur and none on the patella, leg genua shorter than both telofemora and tibiae, chaetotaxy of tibiae I and II similar, solenidia dorsolateral in tarsi I and II (Bartsch, 1997a).

To date, only one species from this subfamily, *Arhodeoporus kunzi* Bartsch, 1987, has been recorded in the subtropical waters stretching from eastern South Africa to southern Mozambique (Bartsch, 1987). Three new species of Copidognathinae from this region are described here.

Methods

The mites described here were collected during the last few years by D. J. Marshall of the University of Durban-Westville and the author in a few localities along the eastern coast of southern Africa (Figure 1). Specimens were cleared in lactic acid and mounted in Hoyers medium. All measurements were taken on slide-mounted material and drawings were prepared from light micrographs. The type material is deposited at the Natural History Museum, London, United Kingdom.

Abbreviations used in description and figures: AD, anterior dorsal plate: AE, anterior epimeral plate; AP, anal plate; GA, genito-anal plate; GP, genital plate; OC, ocular plates; PD, posterior dorsal plate. Dorsal setae numbered ds-1 to ds-6 (not including the dorsal seta on PE). Legs numbered I to IV.

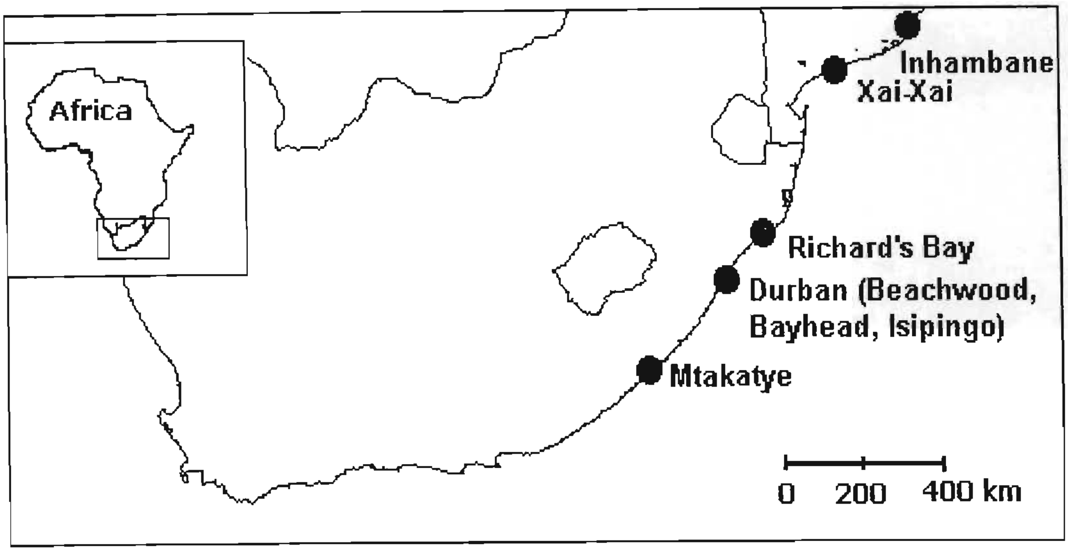

Figure 1. The collection localities.

Taxonomic descriptions

***Copidognathus xaixaiensis* sp. nov.** (Figure 2)

Material. One male (holotype, accession number BMNH(E)2001-14), from the middle littoral rocks on the breakwater wall facing the resort in Xai-Xai (Mozambique), collected in December 1997, leg. D.J. Marshall.

Male. Idiosoma 265 μm long and 160 μm wide.

Dorsum. All plates with polygonal reticulation. AD 50 μm long and 60 μm wide, with ds-1 positioned posterior of center; reticulation restricted to the central-posterior part. Anterior margin of AD rounded. OC 45 μm long and 40 μm wide, with one large cornea and ds-2 at the anterior end; the existence of a second cornea is not obvious. The posterior end of OC protruding and reaching to the trochanter of leg III; reticulation restricted to the anterior half. PD 175 μm long and 100 μm wide, not extending beyond the anterior margin of OC. ds-3 to ds-5 evenly placed along each median costa; lateral costae not obvious. The reticulation covers the whole surface, although more pronounced in the anterior third, where the pattern is generally hexagonal. In the posterior part the polygons have various shapes, but are

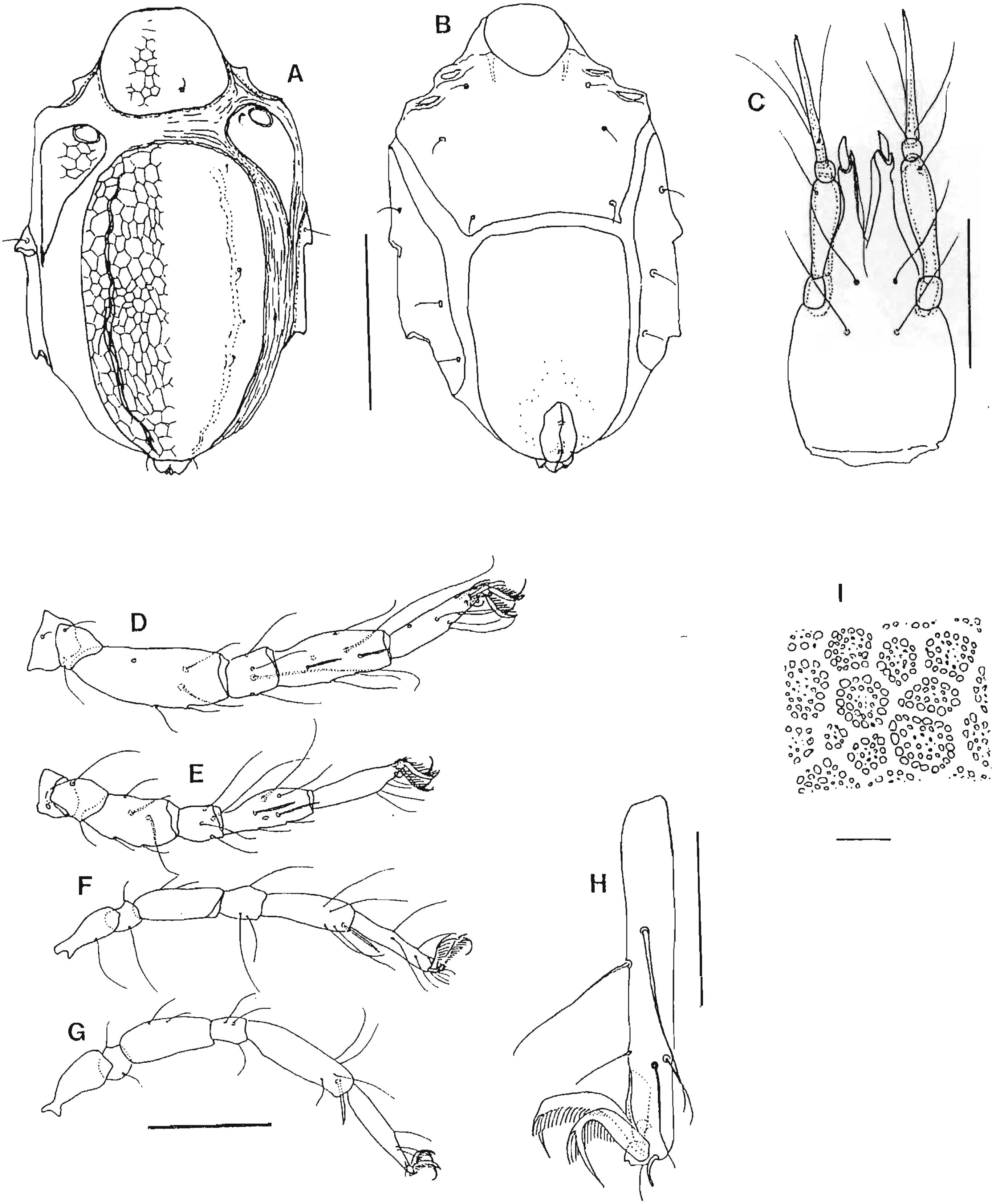

Figure 2. *Copidognathus xaixaiensis* sp. nov. (male), A) idiosoma, dorsal view, B) idiosoma, ventral view (bar: 100 μm), C) gnathosoma, dorsal view, (bar: 50 μm), D) leg I, medial view, E) leg II, medial view, F) leg III, lateral view, G) leg IV lateral view (bar: 100 μm), H) tarsus III (bar: 50 μm), I) reticulation from the anterior third of AD (bar: 10 μm).

generally more elongated (Figure 2A). Meshes of reticulation not subdivided, size 4-10 µm (Figure 2I).

Venter. All plates smooth. AE 100 µm long and 125 µm wide, with three pairs of ventral setae. PE 125 µm long, with one dorsal and three ventral setae. GA 120 µm long and 90 µm wide (Figure 2B).

Male genitalia. Located at the posterior extremity of GA, surrounded by numerous perigenital setae (extremely fine and difficult to count). Genital opening with four pairs of fine sub-genital setae, two anterior and two posterior.

Gnathosoma. 110 µm long and 55 µm wide, with smooth cuticle. Rostrum triangular, palpi strongly elongated. Distal palp segment with a whorl of three long basal setae; no apical setae were identified (Figure 2C).

Legs. Leg I longer and more robust than other legs. Chaetotaxy, from trochanter to tibia: leg I, 1, 2, 5, 4, 7; leg II, 1, 2, 5, 4, 7; leg III, 1, 2, 2, 3, 5; leg IV, 0, 2, 2, 3, 5. Medial setae on tibiae (two on legs I, II, one on legs III, IV) thickened, but not clearly bipectinated. Lateral setae on genu and tibia II long, on genu and tibia I extremely long, longer then corresponding tarsi (Figure 2D-G). Claws with a well-developed comb and long, pointed tips (Figure 2H).

Female and juvenile stages. Unknown.

Etymology. This species is named after the collecting locality, Xai-Xai (pronounce Shye-Shye) in Mozambique.

Remarks. This species belongs to the *Copidognathus tricorneatus* group, which has been reviewed by Bartsch (1997b). Among the species of the group, it is similar to *Copidognathus tricorneatus* (Viets, 1938) in having large meshes in the reticulation of PD, medial costae not reaching the anterior margin of this plate, and triangular rostrum, with rostral sulcus extending to the base of the second palp segment. It has however a very characteristic OC, with no obvious second cornea, and ds-1 in the inner corner. Unlike in any species of this group, the lateral setae on the genu and tibia of leg I are unusually long. A similar feature occurs in the unrelated species *Copidognathus venustus* Bartsch, 1977.

***Copidognathus caloglossae* sp. nov.** (Figure 3)

Type material (accession number BMNH(E)2001-13). Holotype: male, South Africa, Eastern Cape, Mtakatye Estuary, May 1999, leg. Ş. Procheş. Paratypes: one male, two females, and one protonymph, data as in holotype; one protonymph, and two larvae, from

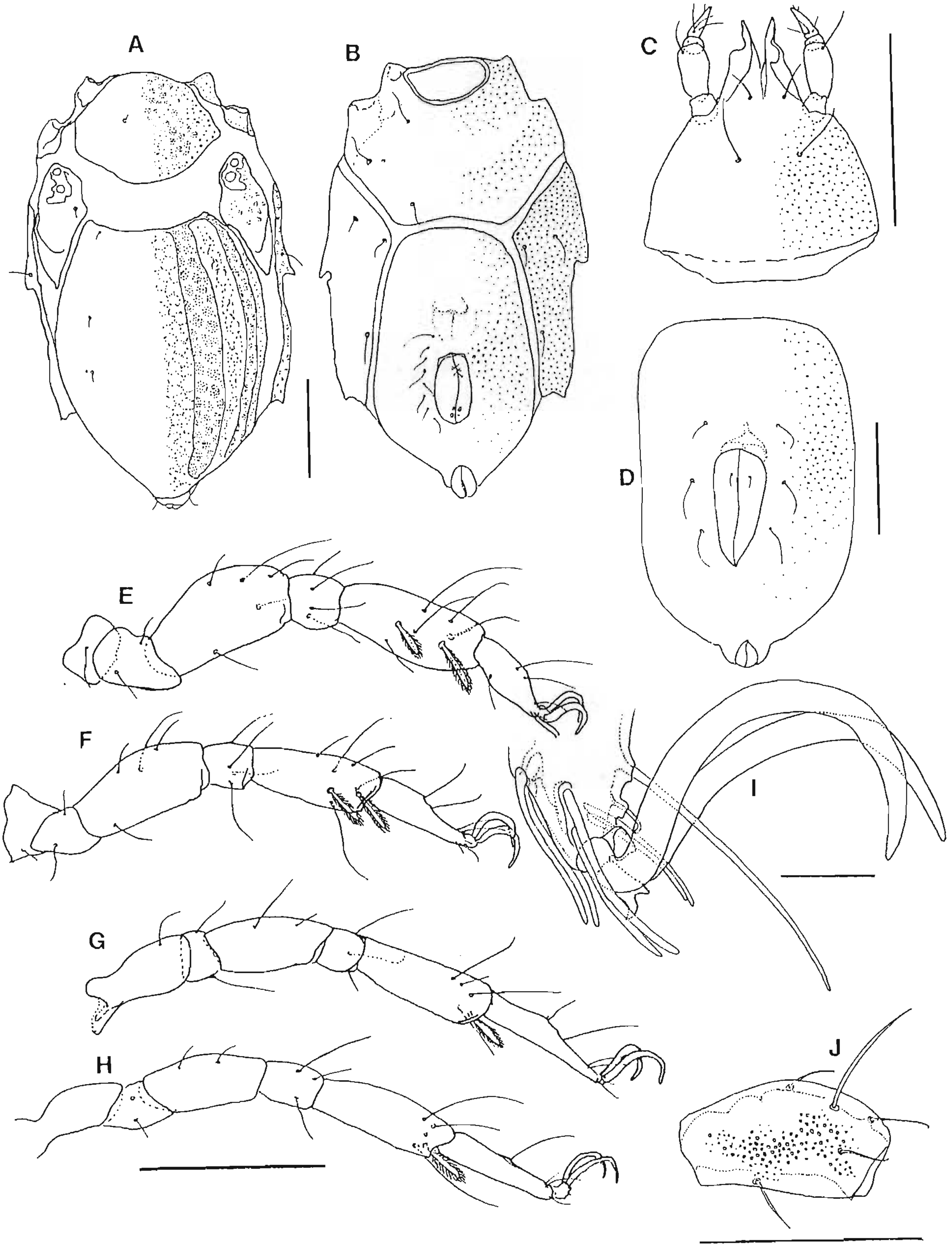

Figure 3. *Copidognathus caloglossae* sp. nov. A) idiosoma, dorsal view, B) idiosoma, ventral view, C) gnathosoma, dorsal view, D) female ano-genital plate, E) leg I, medial view, F) leg II, medial view, G) leg III, lateral view, H) leg IV, lateral view, I) tip of tarsus I, J) telofemur I, lateral view. All drawings, except D) based on male individuals. All bars: 100 μm, except I), where 10 μm.

South Africa, KwaZulu-Natal, Bayhead Lagoon in the Durban Harbour, July 1999, leg. Ş. Procheş. Other material (30 more individuals examined) comes from Richards Bay, Isipingo and Beachwood mangrove forests in KwaZulu-Natal, as well as from Inhambane (Mozambique). All individuals were collected from the algal association known as 'Bostrychietum', covering the pneumatophores of the mangrove-tree *Avicennia marina* (Forsk.) Vierh..

Male. Idiosoma 370 - 425 µm long and 275 - 300 µm wide.

Dorsum. AD 115 - 135 µm long and 140 - 150 µm wide, with ds-1 in the anterior half. Three prominent porose areolae present, one oblong, anterior and two rounded, centro-lateral, all with groups of five to ten pores. Other pores are present on all edges of the plate, without forming clearly defined fields. OC 90 - 125 µm long and 60 - 80 µm wide, with centro-lateral porose areolae, one seta and two corneae. A ridge separates the postero-lateral end of OC by from the rest of the plate. PD 230-260 µm long and 220 - 230 µm wide, with four large costae covered with groups of 10-15 pores; the space between the costae with an indistinct canalicular reticulation (Figure 3A).

Venter. AE 120 - 155 µm long and 240 - 260 µm wide, with the first three pairs of ventral setae. Canaliculi mainly in two transverse bands, joining the origin of legs in pairs I and II, respectively. PE 160 - 180 µm long, with evenly distributed canaliculi, carrying one dorsal and three ventral setae. GA 175 - 210 µm long and 150 -180 µm wide, with genital opening placed behind the middle. Five to nine pairs of perigenital setae, generally disposed in one circle; sometimes the posterior ones are more outwardly placed than the anterior ones. Genital opening with four pairs of sub-genital setae, two anterior and two posterior (Figure 3B).

Gnathosoma. 130 - 135 µm long and 115 - 125 µm wide, rostrum slightly shorter than gnathosomal base, palpi longer than rostrum. Gnathosomal base with evenly arranged canaliculi. Distal segment of palpus with a whorl of three long basal setae and a few small terminal setae (Figure 3C).

Legs. First pair shorter and more robust than other legs. Claws smooth, no accessory process was identified (Figure 3I). Canaliculi present, especially in the femora and tibiae of legs I and II. Chaetotaxy, trochanter to tibia: leg I, 1, 2, 5, 4, 7; leg II, 1, 2, 4, 4, 7; leg III, 1, 2, 2, 3, 5; leg IV, 0, 2, 2, 3, 5. Medial bipectinated setae on tibiae: two on legs I and II, one on legs III and IV (Figure 3E-H). Ventral setae on telofemora I and II, as well as on all basifemora very short (Figure 3J). Dorsal setae on tarsus I and II located in the middle of the segment.

Female. Idiosoma 410 - 450 µm long and 305 - 335 µm wide.

Dorsum. Similar to the male, AD 115 - 120 µm long and 155 - 160 µm wide. OC 105 - 120 µm long and 80 - 105 µm wide. PD 260 - 335 µm long and 215 - 230 µm wide.

Venter. AE 160 - 165 µm long and 270 - 275 µm wide. PE 170 - 180 µm long. GA 200 - 205 µm long and 150 - 175 µm wide, with genital opening placed slightly behind the middle. Three pairs of perigenital setae (Figure 3D).

Gnathosoma. 130 - 160 µm long and 100 - 130 µm wide.

Protonymph. Idiosoma 275 - 410 µm long and 225 - 310 µm wide. Plates smaller than in adults, as compared to total body length, leaving large areas of striated integument. AD 60 - 75 µm long and 90 - 95 µm wide. OC 50 - 60 µm long and 45 - 50 µm wide, with two corneae located on a protuberance; however, the posterior ridge present in adults is absent. PD 130 - 145 µm long and 155 - 195 µm wide. AE 85 - 95 µm long and 160 - 220 µm wide. PE 125 - 130 µm long. Genital and anal plates separate; genital 45 - 60 µm long and 50 - 60 µm wide, anal 50 µm long and 75 - 80 µm wide.

Gnathosoma relatively small, 125 - 130 µm long and 45 - 90 µm wide.

Legs significantly smaller than in adults, basifemur and telofemur IV merged in one femoral segment.

Larva. Idiosoma 270 - 280 µm long and 195 - 210 µm wide; plates small, large parts of the integument are not striated, but have irregular folds. AD 50 - 55 µm long and 55 - 60 µm wide. OC 25 - 30 µm long and 30 - 35 µm wide. PD 75 - 85 µm long and 95 - 100 µm wide. AE 75 - 85 µm long and 160 - 170 µm wide, with large, clearly visible pores. PE 65 - 75 µm long. Genital and anal plates separate; genital 25 - 30 µm long and 35 - 40 µm wide, anal 40 - 45 µm long and 70 - 75 µm wide.

Gnathosoma 105 - 110 µm long and 40 - 80 µm wide.

Femoral segments merged in all *legs*.

Etymology. The name *caloglossae* refers to the alga *Caloglossa leprieurii* (Mont.) J. Ag., one of the components of the algal association from which the mites were collected.

Remarks. One uncommon feature found in *C. caloglossae* sp. nov. is represented by the completely smooth claws. It has been suggested that in the halacarid sub-family Rhombognathinae, smooth claws are associated with species from habitats exposed to little wave action, while claw combs are used for securing the mite to substrates exposed to strong wave action (Pugh *et al.,* 1987). As southern African mangroves are an estuarine feature, the wave action is low, favoring similar features in *C. caloglossae* sp. nov. (subfamily Copidognathinae). Other characters which, combined, are useful in defining this species are the four dorsal costae covered with groups of pores, short mouthparts, the short ventral setae on telofemora I and II, as well as on all basifemora, the medial position of dorsal setae on tarsi I and II.

An aspect worth noting is the presence of this species in the Isipingo Estuary, where salinity is close to zero. Five other species of *Copidognathus* have been recorded from similar low-salinity habitats (Bartsch 1996).

***Acarothrix umgenica* sp. nov.** (Figure 4)

Type material (BMNH(E)2001-13). Holotype: male, South Africa, KwaZulu-Natal, Beachwood mangroves in Durban, 18 August 1999, leg. Ş. Procheş. Paratypes: one male, same data as for holotype; two females, two protonymphs, and one larva, same locality as the holotype, 26 October 1999, leg. Ş. Procheş. Other material was collected in Richards Bay (South Africa, KwaZulu-Natal). In all, around 30 specimens were examined, all of which were collected in sediment or algae covering the pneumatophores of the mangrove-tree *Avicennia marina*.

Adults. Sexes very much alike; no significant difference in body or plate sizes. Idiosoma 325 - 385 µm long and 230 - 300 µm wide.

Dorsum. All plates thin, apparently smooth, although high magnifications reveal complex cuticular patterns. AD 80 - 90 µm long and 100 - 105 µm wide, with a posterior transversal strip-shaped part where a reticulation is visible. OC 105 - 130 µm long and 85 - 105 µm wide, with two corneae, one anterior seta and, locally, unclear reticulation. ds-3 could not be located. PD 220 - 230 µm long and 105 - 115 µm wide, with three pairs of setae: ds-4 and ds-5 placed centrally, equally distant from a pair of gland pores; ds-6 ventral, close to anal opening, next to a pair of small gland-bearing cones, indistinct in some individuals. A central pattern of canalicular polygons is more visible in the anterior half of PD; in many individuals, particularly if well cleared, this plate appears to be completely smooth (Figure 4A).

Venter. All plates with fine, evenly arranged canaliculi. AE 150 - 155 µm long and 210 - 255 µm wide, with three pairs of ventral setae and a pair of large pores. PE 170 - 220

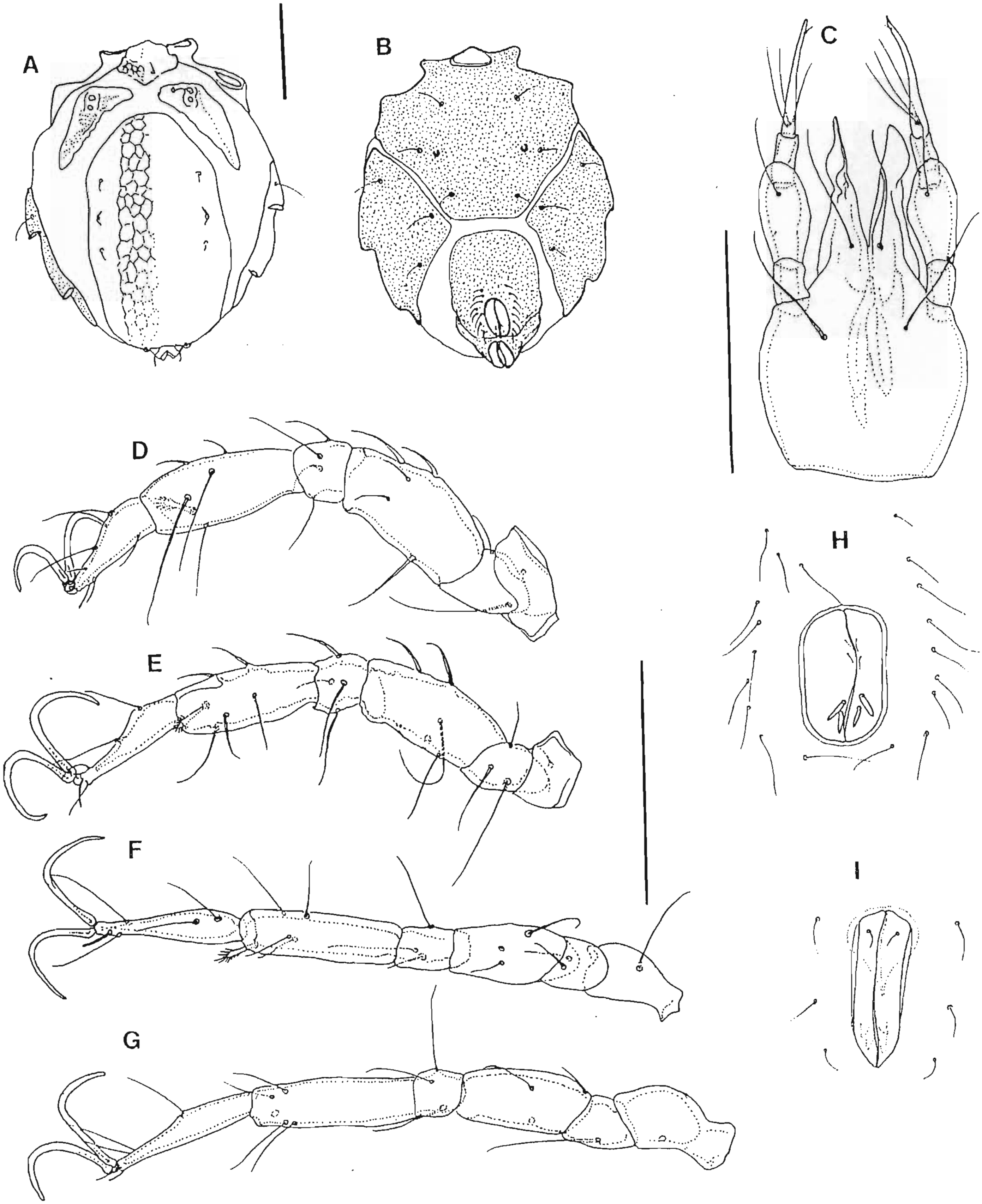

Figure 4. *Acarothrix umgenica* sp. nov., male: A) idiosoma, dorsal view, B) idiosoma, ventral view, C) gnathosoma, dorsal view, D) leg I, lateral view; E) leg II, lateral view, F) leg III, dorsal view, G) leg IV, lateral view, H) male genitalia, I) female genitalia. All drawings except I) based on male individuals. All bars: 100 μm.

μm long, with one dorsal and three ventral setae. GA 155 - 175 μm long and 120 -160 μm wide, with a fold between the genital part and the anal part (Figure 4B).

Male genitalia. Eight to ten pairs of perigenital setae, sometimes asymmetrically disposed. Subgenital setae: two pairs setiform and two spur-like. Behind the last spur-like setae, a pair of genital acetabula can sometimes be observed (Figure 4H).

Female genitalia. Three pairs of perigenital setae surround the genital opening; and one pair of anterior subgenital setae (Figure 4I).

Gnathosoma. 125 - 170 μm long and 55 - 90 μm wide, palpi longer than rostrum. Gnathosomal base with evenly arranged canaliculi. Distal palp segment with a whorl of three long basal setae and one short subterminal seta (Figure 4C).

Legs. First pair more robust, the other pair long and slender. Chaetotaxy of legs, from trochanter to tibia: leg I, 1, 2, 5, 4, 6; leg II, 1, 3, 5, 4, 6; leg III, 1, 2, 3, 3, 5; leg IV, 1, 1(?), 3, 3, 5. Claws very long, especially in legs II, III, IV, almost smooth, dent of accessory process indistinct (Figure 4D-G).

Juvenile stages. Plates very thin, with poorly defined limits. The integument is generally smooth. *Protonymph. Idiosoma* 245 - 320 μm long and 200 - 235 μm wide.

Gnathosoma 120 - 155 μm long and 80 - 85 μm wide.

Legs: basifemur and telofemur IV merged in one femoral segment.

Larva. Idiosoma 235 - 265 μm long and 175 - 205 μm wide.

Gnathosoma 110 - 120 μm long and 40 - 60 μm wide.

Femoral segments merged in all *legs*.

Etymology. The name *umgenica* refers to the river Umgeni (alternative spellings: Mgeni, mNgeni, uMngeni), from whose estuary the specimens were collected. According to Begg (1978), the name means in Zulu 'the river that flows among thorny trees (*Acacia*)'.

Remarks. *Acarothrix umgenica* sp. nov. differs from the other two species of *Acarothrix* (compare Bartsch, 1990, 1997a) in the relative size of the dorsal plates: in the new species AD is much smaller and PD is larger. The shape of OC is also different, with longer posterior tips. The fold separating the anal and genital parts of AG, present in slide-mounted males and females, indicates a strong convexity of the genitalia, not noted in the other *Acarothrix* species. The reticulation present on PD is similar to that illustrated by Bartsch (1990) for *A. palustris* protonymphs, but in the new species this could only be observed in adults. No canalicular punctuation on the ventral plates has been described in either *A. palustris* Bartsch, 1990 or *A. longiunguis* Bartsch, 1997.

This is the first mention of the genus *Acarothrix* from the African continent. Previously, the genus was known from southern China and northern Australia (Bartsch, 1990, 1997a). This distribution is possibly congruent with that of Indo-West Pacific mangrove forests.

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