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ENDEMISM: ORIGINS AND IMPLICATIONS

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ENDEMISM
CLADISTICS

ABSTRACT. – All taxa are endemic and occur in nested distributions at a range of spatial scales. Distinguishing endemics as either neoendemics or palaeoendemics may not be of practical value in analytical biogeography, but distinguishing extinction mediated endemics (cryptoendemics) from endemics which never had a significantly wider range (euendemics) would be useful for interpreting the history of geographic areas. Only cladistic phylogeny provides a tool for distinguishing these two types of endemic.

ENDÉMISME
CLADISTIQUE

RÉSUMÉ. – Tous les taxons sont endémiques et présentent des répartitions emboîtées selon les échelles spatiales considérées. La distinction de néoendémiques et de paléoendémiques parmi les endémiques peut ne pas avoir de valeur pratique en biogéographie analytique; en revanche, distinguer les endémiques dus à des extinctions (cryptoendémiques) par rapport aux endémiques qui n'ont jamais présenté de distribution significativement plus large (euendémiques) pourrait être utile pour interpréter l'histoire des aires géographiques. Seule, la phylogénie cladistique fournit un outil permettant de distinguer ces deux types d'endémiques.

ENDEMISM IN BIOGEOGRAPHY

Endemism has long been a central theme in biogeography, but it is often misinterpreted as referring only to "narrow" distributions, inferring that only some taxa are endemic. Hengeveld (1990) for example notes "it is hard to distinguish between endemic species and "wides"...". Lincoln *et al.* (1982) define an endemic as "restricted to a particular geographical region", a definition which can be seen to apply, quite correctly, to all organisms.

Since all taxa are endemic, it becomes necessary to categorise them on the basis of their range (extensive or restricted) and of their disjunction. Both range and disjunction are continua and depend upon the spatial scale (Table I, Fig. 1). The ranges of taxa vary from cosmopolitan through continental or ocean basin scales, to single sites. They all show some degree of disjunction, since populations, species and higher taxa are all separated from one another at some spatial scale. A taxon occurring uniquely in a local area might not be considered to have a disjunct distribution at a global scale. On the other hand it clearly could be considered to have a disjunct distribution on a local spatial scale. The decapod crustacean genus *Fredius* Pretzman, for example, is found only in the Guianan lowlands of South America. When considered globally, this is not a disjunct distribution. Within the Guianan lowlands, however, the species are separated into four major basins, the Orinoco basin, the Essequibo-Cuyuni basin, the Atlantic basin and the Amazon basin (Rodriguez & Campos 1998), a clearly disjunct distribution. Disjunction can come about either through a vicariant event, or through jump dispersal. Vicariance may result from tectonic activity (plate movement, or orogeny), from eustasy or from local climate changes (often linked to tectonic and eustatic events). Jump dispersal occurs when propagules cross an intervening uninhabitable terrain to colonise a new area. This is difficult to discern as a naturally occurring event due to its relative rareness coupled with the short period of time over which scientific records have been kept. It may also be obscured by the frequency of human mediated transport (anthropochore dispersal).

Endemics then, can be classified hierarchically, consisting of a series of nested sets of areas of occupancy by taxa, the largest set of which, under current knowledge, is the entire world. If the biogeographic patterns resulting from multiple nested distributions can be shown to be statistically non-random, they demand a biogeographic interpretation. Some areas can be shown to have greater densities of species which are endemic to

Table I. – Classification of endemics with examples.

Range	Characteristics	Explanation	Example
Global (Holendemic)	Unlimited biogeographically, limited only by ecological and physiological tolerances.	Taxon with good powers of dispersal and colonisation (high competitive advantage) and with sufficient time for establishment.	*Gnathophyllum* (Fig. 1)
Conjunct broad (Euryendemic)	Broad, more or less continuous or contiguous distribution, limited by biogeographic barriers	Taxon expanding or contracting its range(s), or in quasi stasis or regressive (aging) taxon beginning to contract its range(s), or in quasi stasis	*Periclimenella* (Fig. 2)
Conjunct narrow (Stenoendemic)	Restricted more or less continuous or contiguous distribution limited by biogeographic barriers	Progressive taxon recently evolved yet to expand its range, or evolved *in situ* (phylogenesis) from a clade constrained historically by biogeographic barrier(s), or relict (old) taxon.	*Macrohectopus* (Fig. 2)
Disjunct (Rhoendemic)	Two or more widely disjunct distributions.	1. Vicariated taxon	
		a) Euendemics, isolated by tectonic changes in geography	*Globosolembos francanni* Reid Amphiatlantic (Cape Verde and Florida)
		b) Cryptendemics, isolated by extintion of intervening populations or taxa	Iguanidae New World + Madagascar/Fiji. Extinct in Africa
		2. Taxon jump-dispersed across a biogeographic barrier.	
		a) Natural	*Bubulcus ibis* (L.) jump dispersed from Africa to South America in 1920's
		b) Anthropochore	*Elminius modestus* Darwin Spread in 20th century from New Zealand, ? Australia to Europe and South Africa

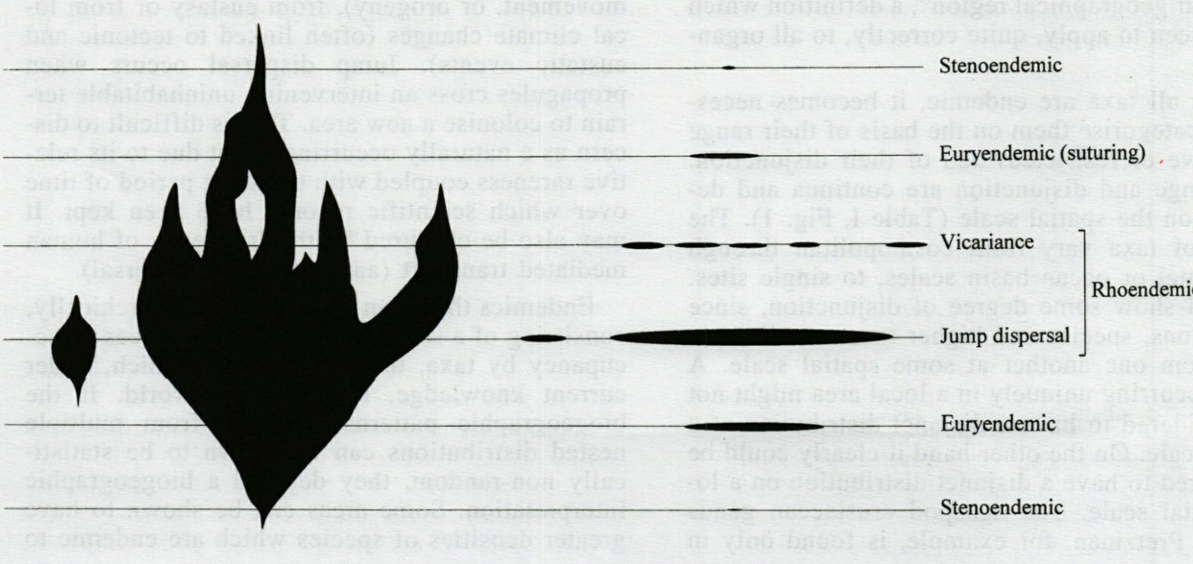

Fig. 1. – Schematic representation of the formation of endemic types.

Fig. 2. – The distribution of the shrimp genus *Gnathophyllum* Latreille, a holoendemic.

themselves than have others. These have been described as "areas of endemism" and have formed the nucleus of much biogeographic classification. Areas of endemism are interpreted as areas of high endemicity separated from other such areas by a decided gap. The gap may be defined as an area of low endemicity between the two areas of high endemicity e.g. the Sinaloan gap between the Cortez and the Mexican marine Provinces. Alternatively it may be defined as the region of co-occurrence of endpoints in species distributions (Hastings 2000).

The first biogeographer to employ endemism as an analytical, rather than a descriptive tool, was probably Wallace (1876) who used the numbers of endemics as a measure of island age. He hypothesised that the more endemic species that occurred on an island, the more archaic that island was likely to be, the assumption being that older islands had experienced a longer period of time for the occurrence of phylogenesis.

Croizat (1958), developed a biogeographic methodology (panbiogeography) for transforming the recorded distributions of individual taxa into simplified pathways (tracks) and then combining several of these individual pathways into a summary (generalised track) which could be used to hypothesise the historical evolution of the biota concerned. This method has been further refined or applied by Page (1987), Craw (1989), Morrone & Lopretto (1994) and others. Meanwhile, Hennig (1966) developed a method for reconstructing phylogenies based on evolutionary descent. It was left to Nelson & Platnick (1981) to synthesise these two methods in their seminal book on cladistics and vicariance. The use of cladistic methodology to answer biogeographic questions has been further developed in recent years by several authors, notably Humphries & Parenti (1986, 1999).

In cladistic biogeography, a phylogeny is first determined, after which, known distributions of the taxa in the phylogeny are superimposed upon the terminal nodes of the cladogram. It is the ancestor-descendent branching of a clade which indicates the sequence (although not the timing) of vicariant events and hence the relationship (and relative age) of each area. Areas of endemism are not a primary component of any data set analysed in cladistic biogeography and the number of endemics in a given area (*cf.* Wallace above) is irrelevant to any hypotheses of area relationships. In contrast, endemics have been used as the primary biogeographic data set in parsimony analysis of endemicity (PAE) devised by Rosen & Smith (1988). PAE uses a cladistic method, but bypasses the requirement for a prior phylogenetic analysis. Taxa are treated as equivalent to characters and their distributions are the equivalent of character states. In cladistic terminology, taxa which occur in one place only are equivalent to autapomorphies, those occurring in all of the studied sites are equivalent to plesiomorphies and as in phylogenetic cladistics, neither have information content and are accordingly omitted from the analysis. Taxa occurring in some but not all of the areas under study (equivalent to synapomorphies) and which also lack an extrinsic distribution, are the only ones considered to have biogeographic information content in this method. The assumption in PAE is that two (or more) areas sharing endemic taxa are in

Fig. 3. – The distribution of the euryendemic shrimp genus *Periclimenella* Bruce (closed circles) and of the stenoendemic amphipod genus *Macrohectopus* Stebbing (closed square).

some way more "related" to each another, as a result of a lack of historical biogeographic barriers between them, than either is to any other area that does not share with them those same taxa. Humphries (2000), it should be noted, strongly criticises this method, asserting that, by bypassing taxic homology, it has corrupted the meaning of area homology. In PAE, the taxa are derived character states (synapomorphies) of the areas. Because PAE makes the inference that areas uniquely sharing taxa are more related one to another than to areas lacking these same taxa, it depends upon an assumption that extinction has not significantly modified the distribution patterns.

If a biogeographic analysis based on endemics is to be meaningful, it is necessary to distinguish between on the one hand, absent having never been present in the area (equivalent to symplesiomorphic in phylogenetic cladistics) and on the other hand, lost from the area i.e. extinct (equivalent to synapomorphic). Any analysis of endemics needs to be based entirely upon "synapomorphies", which include both "present now" and "present once but now extinct". Iguanid lizards, for example, occur among other places, in Madagascar and South America, but not in Africa. Few biogeographers would posit a closer ancestral relationship between Madagascar and South America than between Madagascar and Africa. Iguanids almost certainly did occur in Africa but became extinct there (presumably through competition with more advanced agamid lizards). Thus, in cladistic terms, iguanids do occur in Africa but in modified form (they have been lost rather than having never been present). It could be argued that the same assumptions about "loss" are made in phylogenetic cladistics with regard to missing character states. However, data for falsifying a given hypothesis are more readily called upon in phylogenetic analysis. In a phylogenetic analysis, characters may be polarised by outgroup analysis, thus facilitating the identification of lost (rather than never evolved) states. PAE is not amenable to outgroup analysis. Clearly the outgroup would have to be an area outside the area of study which by the criteria set in PAE could exist only in the state "absent". In addition, in phylogenetic cladistic analyses a number of unrelated character types may be analysed, allowing multiple corroboration, whereas PAE uses only one character type, the taxon.

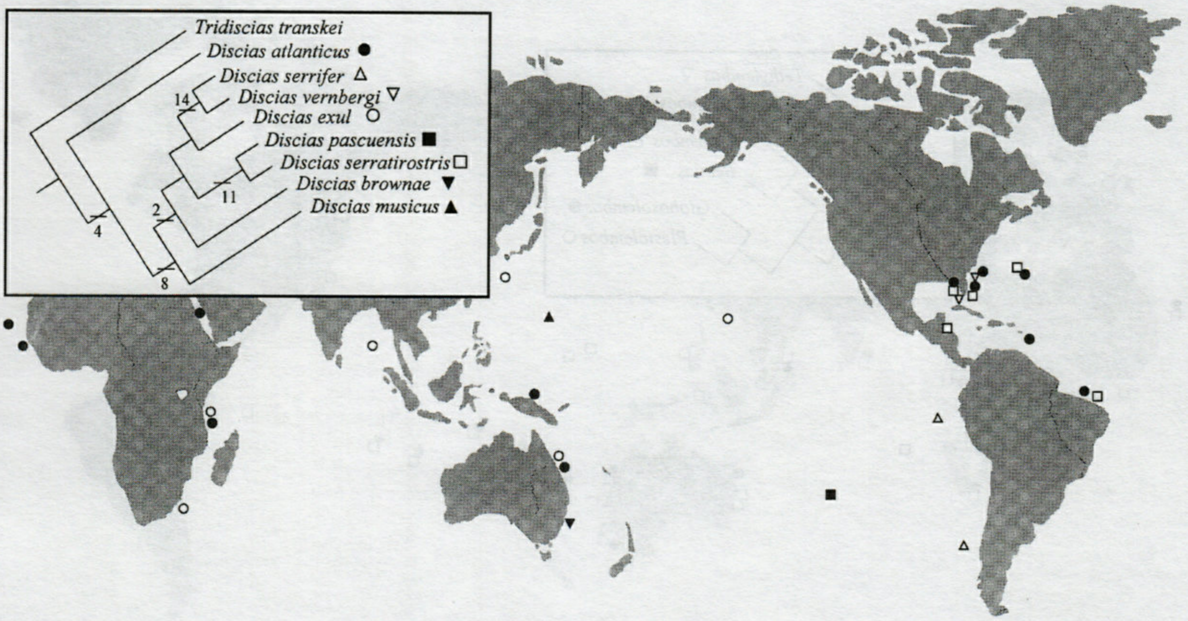

Fig. 4. – The distribution and phylogeny of the shrimp genus *Discias* Rathbun (for character matrix see appendix 1).

Vicariance biogeography then, based on phylogenetic cladistics, provides the most robust biogeographic technique, with the fewest assumptions. However, it requires well founded phylogenies which at this stage are missing for the vast majority of taxa. PAE may be flawed by its lack of an underlying phylogeny, but it can, if the signal is greater than the background noise, provide, in the absence of a sound phylogeny, a "rough and ready" technique for highlighting vicariant events, particularly when more than one level of the taxonomic hierarchy is used (see for example Myers 1991). The use of more than one taxonomic group may increase the confidence levels further, because it is parsimonious to assume that extinction events would not have affected distantly related taxa in an identical way. Differences in dispersal potential between taxa, however, need careful consideration, because such differences can strongly influence a hypothesis (see for example Myers 1993)

THE SPECTRE OF EXTINCTION

A taxon having a limited geographical range attributable to recency of origin (because theoretically there has been insufficient time for it to expand its range) has been termed a neoendemic. A taxon with a limited geographical range even though it has a considerable evolutionary age, i.e. a relict having undergone extensive extinctions, has been termed a palaeoendemic (Engler 1882). Paleoendemics should, in theory, provide a signal of ancient biogeography provided that it is possible to distinguish real absences from extinctions. In practice, distinguishing endemics as either new or old may not be particularly informative in a biogeographic analysis. The limited distribution of neoendemics is assumed to be due to the fact that they have not yet had time to expand their ranges. This may not hold true for jump dispersers, which on entering a "new" area in which they have had no recent evolutionary history find vacant niches or poorly competitive residents (see Sax & Brown 2000). There is also, a spatial component (independent of the temporal component) of range expansion, i.e. the presence of biogeographic barriers, which cannot be ignored. Organisms trapped on an island (either a true island or a continental island) may be archaic (by definition palaeoendemics), but if they have had no opportunity during their evolutionary history to expand their range, they will give the same biogeographic signal as neoendemics. If, they have undergone *in situ* phylogenesis then the result will be a flock of taxa of variable ages. The age of a taxon is not critical; of importance is whether it once had a much wider range since modified by extinctions. Most species will have undergone some population extinctions in their evolutionary history, but it is necessary in most types of biogeographic analysis to be able to discern those species which have modified their distributions significantly through prior extinctions. Clearly the biogeographic interpretation of endemism depends upon the spatio-temporal scale of the analysis and the level in the taxonomic hierarchy. In the early Tertiary, adapid lemurs are known as fos-

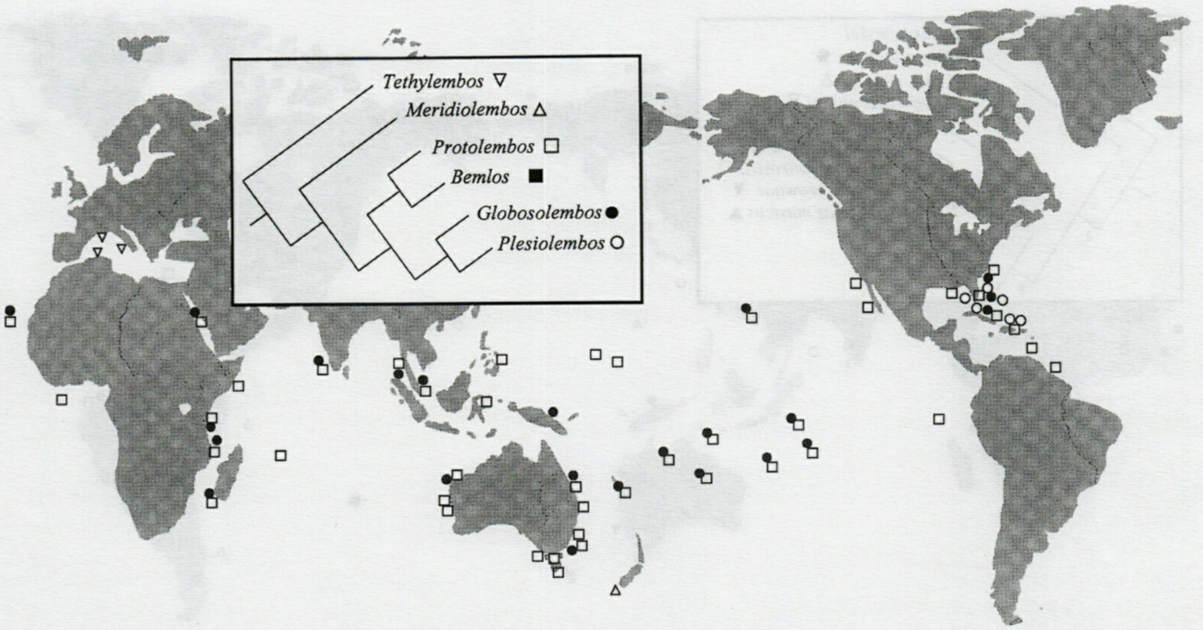

Fig. 5. – The distribution and phylogeny of the *Bemlos* clade (Amphipoda: Aorinae) (phylogeny from Myers 1988).

sils from America (Notharctinae) and Europe (Adapinae) (Hill 1953). At some stage Adapinae reached Madagascar where they have since undergone explosive phylogenesis, producing a high diversity of *in situ* endemic taxa. The Malgache lemurs can therefore be defined either as relict paleoendemics (the adapid clade) or as *in situ* neoendemics (the species of Lemuridae, Indridae and Daubentoniidae). Either definition is correct for a given context.

It would be particularly valuable to be able to distinguish between distributions mediated by extensive extinction, here referred to as cryptoendemics and those whose distributions have not been significantly altered by prior extinctions, here referred to as euendemics (see Table I). Indeed, without this knowledge, we may not be able to interpret areas of endemicity effectively. In general, disjunct species are likely to be euendemics. If they had been isolated for considerable periods of time they would almost certainly have changed from their ancestors through anagenetic processes (selection or genetic drift). Endemic sister taxa and higher taxa represent *in situ* evolution (phylogenesis) from a common ancestor and may be euendemics or cryptoendemics. The higher in the taxonomic hierarchy the older the ancestral geographic relationship.

UNDERSTANDING ENDEMIC PATTERNS

If endemism is to be used as a primary database for any biogeographic analysis, it is necessary to be certain that the areas under study are not paraphyletic. If endemic taxa in the areas under study were at one time distributed extrinsically and have only since become restricted to the areas under study (by extinctions in the extrinsic area), then the areas analysed are in fact paraphyletic. Any assumptions about biogeographic relationship would, in such a scenario, be fundamentally flawed. Even if the taxa concerned have never had an extrinsic distribution, they may once have been more widely distributed within the area (thus confounding the signal of area relationships) or may even have been cosmopolitan within the area (symplesiomorphic) so confounding any inferences of relationship.

It is clearly not possible to determine the real distribution of any taxon through its history, even with the existence of a fossil record. Phylogenetic analyses, however, provide insights that enable parsimonious decisions to be made between the claims of competing hypotheses.

Frequently some members of a taxon are stenoendemics whilst others are euryendemics. In such cases, a clade in which an ancestral taxon is widespread and the derived taxa have a restricted distribution will suggest a different history from a clade in which one or more of the derived taxa are widespread. The genus *Discias* Rathbun (Caridea, Disciadidae), for example, is widespread across all world oceans (Fig. 4). Two species, *D. atlanticus* Gurney and *D. exul* Kemp are euryendemics, the former in all oceans, the latter in the Indo-west Pacific. Two species *D. serratirostris* Lebour and *D. serrifer* Rathbun are rhoendemics, the former in the western Atlantic, the other in the Eastern Pacific and four *D. pascuensis* Fransen, *D. vernbergi* Boothe & Heard, *D. musicus* Holthuis, and *D. brownae* Kensley are stenoendemics. A phylogenetic analysis (Fig. 4) reveals that *D. atlanticus*, the widespread taxon, is ancestral whilst *D. pascuensis* for example – a species known only from Easter Island – is a more recently derived taxon. With these data, it is parsimonious to hypothesise that *D. pascuensis* is a stenoendemic whose ancestor arrived at some time in Easter Island and has not undergone significant extinction events elsewhere on a global scale. A similar scenario could be applied to the other stenoendemics, *D. serratirostris, D. serrifer* and *D. vernbergi*. The euryendemic *D. exul*, has spread widely in the Indo-west Pacific but has been unable to cross the ocean gap to the east Pacific, suggesting that the range expansion occurred after the development of that gap in the late Mesozoic (see Myers 1991). It is also reasonable to hypothesise that the extant distribution of *D. atlanticus* represents a distribution derived at a time in the past when the world was topographically different and colonisation of all the major oceans was still a possibility. A competing hypothesis could be that the ancestral *D. atlanticus* maintained a limited distribution over most of its evolutionary history and only recently spread rapidly to attain its present range. Such a jump-dispersal scenario is, however, less parsimonious since it requires two assumptions:

1. that the taxon had a restricted range through most of its evolutionary history and
2. that it underwent more recent jump-dispersal into all the major oceans.

The vicariant hypothesis requires only one assumption, that it became widespread during a period in history when barriers to its dispersal were not significant.

An alternative pattern is illustrated by a phylogeny of the *Bemlos* clade of aorid amphipods (Fig. 5). Two genera, *Bemlos* Shoemaker and *Globosolembos* Myers are euryendemics, occurring throughout the tropical oceans of the world and extending into the warm temperate of Australia. Ancestral taxa *Meridiolembos* Myers and *Tethylembos* Myers are stenoendemics restricted to the Mediterranean and New Zealand respectively. The most parsimonious hypothesis is that *Tethylembos* and *Meridiolembos* are antitropical relicts of an ancient flock of taxa most of which were driven to extinction within the tropics by competition with derived taxa now represented by the widespread tropical genera *Bemlos* and *Globosolembos*. The sister taxon of *Bemlos (Protolembos* Myers) and of *Globosolembos (Plesiolembos* Myers) are stenoendemics. They may be either ancestral or derived with respect to their euryendemic sister taxon.

If a taxon is composed of several narrow rhoendemics, these may be either vicariants, or relicts of a once more widely distributed clade. Again, a phylogenetic analysis can help to illuminate the spatial parameters of the ancestral clade.

The genus *Parisia* Holthuis consists of six species, four in Madagascar and two in Australia. The two Australian species share a number of character states and appear to be more closely related to each other than either is to the Malagasy species (Williams 1964). No cladistic analysis has yet been performed on this genus but if the above relationships are confirmed, there is an orderly relationship between phylogeny and distribution. Under these circumstances there is no reason to hypothesise other than that each clade evolved *in situ*, after a vicariant event had first divided the ancestral taxon. An alternative to this pattern would be realised if a phylogenetic analysis revealed that the closest sister of a taxon was not its nearest geographic neighbour. The barnacle genus *Chthamalus* Ranzani may be an example of this. The two species *Chthamalus montagui* Southward and *C. stellatus* (Poli), sympatric along north-east Atlantic shores are apparently not sister taxa (Dando & Southward 1980). *C. stellatus* is thought to be more closely related to two species from the west Atlantic, viz. C. *angustitergum* Pilsbry and *C. bisinuatus* Pilsbry, whilst *C. montagui* is thought to be more closely related to Pacific species such as *C. challengeri* Hoek and *C. dalli* Pilsbry. Unfortunately no cladistic analysis has been carried out on *Chthamalus* to support the relationships suggested by morphological and electrophoretic studies within the genus. Three possible explanations, other than a falsified phylogeny, exist for such a phylogenetic relationship:

1) They may have been euryendemics which subsequently underwent extensive extinction to leave a geographically unordered pattern of relicts in widely separated localities.

2) Tectonic activity may have altered the earth's geography to such an extent that the extant distributions can only be understood by plotting them onto a map of ancient topography

3) Jump dispersal may have occurred.

CONCLUDING COMMENTS

Higher taxa above the genus level generally have little biogeographic information content. In the main, families are cosmopolitan, although this may hold less for plants. Genera tend to be more narrowly endemic and species are frequently stenoendemic. Endemism originates in three different ways:

1) by extinction of populations in part of their range.

2) by range restriction through biogeographic barriers (after anagenesis or phylogenesis)

3) by jump dispersal followed by anagenesis or phylogenesis.

Whilst no known technique can distinguish absolutely between these different routes to endemicity, phylogenetic cladistics provides the best method on which to erect a parsimonious hypothesis.

With an awareness of the importance of preserving the Earth's biodiversity comes the need not only to determine which areas contain large numbers of species unique to them, but also how such areas of endemicity originate.

An appreciation of the complexity of origins of endemics and of the alternative routes to narrow endemicity may improve our understanding of how areas of endemicity have come about.

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APPENDIX

Characters and character states analysed

1. Rostral tip acute (0) or rounded (1).
2. Lateral margin of rostrum entire (0) or serrate (1).
3. Dorsal ridge on rostrum present (0) or absent (1).
4. Rostrum triangular shaped (0) or broad (1).
5. Supra-orbital spine present (0) or absent (1).
6. Branchiostegal spine present (0) or absent (1).
7. Mid-dorsal spine on posterior margin of second abdominal segment present (0) or absent (1).
8. Distolateral tooth of antennal scale present (0) or absent (1).
9. Three (0), four (1) or more than four (2) pairs of posterior telson spines.
10. Mandibular incisor toothed (0) or entire (1).
11. Mandibular palp with none (0), one (1) or more (2) than one segment.
12. Dactyli of third to fifth pereiopods serrate (0) or entire (1).
13. Exopods on fourth and fifth pereiopods present (0) or absent (1).
14. Lateral margin of uropodal exopod serrate (0) or entire (1).

Data matrix

D. atlanticus Gurney, 1939	1 0 0 1 1 1 0 0 0 0 ? 1 0 1
D. brownae Kensley, 1983	0 1 1 1 1 1 0 1 0 0 2 1 0 1
D. exul Kemp, 1920	0 1 0 1 1 1 0 1 1 0 2 1 0 1
D. musicus Holthuis, 1981	0 0 0 1 1 1 0 1 0 0 0 1 0 1
D. pascuensis Fransen, 1987	0 1 0 1 1 1 0 1 0 0 1 1 0 1
D. serratirostris Lebour, 1949	0 1 1 1 1 1 0 1 0 0 1 1 0 1
D. serrifer Rathbun, 1902	0 1 1 1 1 1 0 1 1 0 2 1 0 0
D. vernbergi Boothe & Heard, 1987	0 1 0 1 1 1 1 1 2 0 2 1 0 0
T. transkei Kensley, 1983	0 0 1 0 0 0 1 0 2 1 2 0 1 1

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EVOLUTION AND ECOLOGY OF BIRDS ON ISLANDS: TRENDS AND PROSPECTS

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INSULAR SYNDROME
ISLAND BIOGEOGRAPHY
SPECIATION
TAXON CYCLE
EXTINCTION VORTEX
CONSERVATION
BLUE TIT

ABSTRACT. - This paper reviews ecological and evolutionary processes that operate among and within insular communities, species and populations. Being basically non-evolutionary the MacArthur and Wilson's paradigm of island biogeography holds well in explaining processes that operate on the short ecological time, and proved to be helpful in explaining such issues as colonisation-extinction processes, species richness at equilibrium and species turnover. But several limitations make it insufficient as a modern tool for explaining evolutionary changes on islands. Colonising an island necessarily entails rapid evolutionary changes as a response to both non-selective and selective evolution. This results in a cascade of changes of life history traits, the so-called insular syndrome. Components of this syndrome include changes in morphology (size and shape), demography (age-specific fecundity, survival, dispersal) and behaviour. Shifts in behaviour are among the most spectacular features in insular vertebrates. Surprisingly few systematic and broad-scale analyses of demographic changes on islands have been designed to document the classical tenet of evolutionary shifts from high reproductive rates and short life span towards the opposite combination of life history traits as a result of high intraspecific competition in crowded insular populations. Examples of shifts in life history traits are given from a detailed case study on the biology of Blue tits in the island of Corsica, and most of these changes fit the predictions of an insular syndrome. An interesting trend resulting from shift from dispersal to sedentariness and habitat fidelity in islands is the potential for population differentiation at much smaller spatial scales than on mainland regions. This results in enhancing within-species diversity which counterbalances the species impoverishment of insular biotas. Although ecological adjustments and evolutionary changes make insular communities self-regulating assemblages of species that are resistant face to the risks of spontaneous extinction and invasion, insular communities are among the most vulnerable biota on Earth. The most important threats to island birds are discussed and some directions are given for promoting studies that could contribute to fill the most important gaps in our knowledge on evolution on islands and contribute to conservation issues.

SYNDROME D'INSULARITÉ
BIOGÉOGRAPHIE INSULAIRE
SPÉCIATION
CYCLE DE TAXONS
VORTEX D'EXTINCTION
CONSERVATION
MÉSANGE BLEUE

RÉSUMÉ. - Cet article fait un bilan résumé de nos connaissances sur les processus écologiques et évolutifs qui caractérisent les communautés, espèces et populations d'Oiseaux en milieu insulaire. Le paradigme de biogéographie insulaire de MacArthur et Wilson s'est montré fort utile pour expliquer les processus qui opèrent à l'échelle relativement courte du temps écologique, notamment les processus de colonisation, d'extinction, de renouvellement d'espèces, ainsi que certains changements tels que l'élargissement des niches et différentes modalités de partage des ressources, de sélection de l'habitat et de densité de population. Mais il ne se prononce pas sur les processus évolutifs, ce qui en limite la portée. Lorsqu'une propagule réussit à s'implanter sur une île, des processus évolutifs de type non-sélectif (dérive, mutations) et sélectif (nouveaux régimes de sélection) entraînent de profondes modifications dans les traits d'histoire de vie, ces modifications caractérisant ce qu'on appelle le syndrome d'insularité. Les composantes de ce syndrome sont d'ordre morphologique (taille et forme), démographique (fécondité, survie, dispersion) et comportemental. Les modifications du comportement sont généralement spectaculaires chez les vertébrés insulaires. Peu de travaux se sont attachés à tester l'hypothèse classique selon laquelle les populations insulaires de vertébrés présentent un glissement démographique tendant à réduire la fécondité et augmenter la survie. Un exemple bien documenté de modifications de traits d'histoire de vie, celui de la Mésange bleue en Corse, révèle que la plupart des changements observés vérifient les prédictions du syndrome d'insularité. La tendance à la sédentarité et à la fidélité de l'habitat, qui est un trait régulier en milieu insulaire, se traduit par une différenciation des populations à des échelles d'espace bien moindres que sur le continent. Cela favorise une diversité intra-spécifique élevée qui, d'un point de vue adaptatif, compense en partie le fait que les communautés insulaires soient appauvries en espèces. Bien que les ajustement écologiques et changements évolutifs qui caractérisent les communautés insulaires les rendent résistantes aux perturbations et invasions spontanées, ces communautés sont pourtant parmi les plus menacées de la planète. Les menaces les plus sérieuses sont examinées et quelques pistes de recherche sont données qui permettraient de combler certaines lacunes dans nos connaissances et favoriser la mise en œuvre de stratégies efficaces de conservation.

INTRODUCTION

The question why organisms are so diverse has been addressed by evolutionary biologists for more than a century and a half. This is especially true for bird diversity on islands which has been the object of a particular focus for two reasons. First, being conspicuous, mostly diurnal and popular as study models, birds are well known and suitable for observation, field studies and sometimes experiments. Second, being discrete small areas, islands have many advantages over larger mainland regions where shifts in distribution, geographical variation of populations and species, and problems of spatial scales complicate attempts to reconstruct evolutionary history and patterns of diversity. It is a commonplace since Darwin and Wallace to say that islands are natural laboratories for the study of evolution and it is true that whatever we learn about avian evolution on islands can be used as a basis for constructing explanations for diversification at larger spatial scales. By diversification, I not only mean taxonomic differentiation and speciation but also any evolutionary changes that occur at the level of populations and modify life history attributes in morphology, demography, physiology and behaviour.

Diversification on islands at the species level will not be considered further here (see Grant 1998). Suffice is to say that the main ideas inherited from the nineteenth century (e.g. Darwin 1859, Wallace 1871) have not been dethroned. Basically, speciation in birds is an allopatric process whereby natural selection causes divergence of geographically isolated populations. The most genetically similar populations are most often allopatric populations, not sympatric congeners (Grant 1998), which confirms the long-standing tenet that phenotypic resemblance reflects phylogenetic relatedness (Mayr 1942). These patterns are inconsistent with the theory of sympatric speciation which, on ecological and behavioural grounds, is unlikely in birds (Grant & Grant 1989). This is not to say that a deeper understanding of the mechanisms of species diversification did not occur during the twentieth century. Since the Perkins' (1903, 1913) pre-genetical theory of insular differentiation applied to the radiation of the 36 forms of Drepanid honeycreepers on the Hawaiian archipelago, much insight has been given on the tempo and mode of species divergence. Recently, biochemical techniques such as electrophoresis (Hubby & Lewontin 1966) and then molecular data used to reconstruct phylogenies (Fitch & Margoliash 1967) made the new systematics shift from the mostly morphological (phenotypic) systematics of the first half of the century (Huxley 1942, Mayr 1942) to molecular systematics (Mindell 1997). Molecular data have the advantage to provide information on the temporal context of speciation as well as on the degree of genetic relatedness among the different taxa of a clade.

In this paper I will mostly focus on biogeographical, ecological and microevolutionary processes that operate among and within insular communities, species and populations. I shall try to show that combining the provinces of ecology and evolution in the field of evolutionary ecology is a prerequisite to answer fundamental questions on differentiation and adaptive radiation. Books on island biology are generally concerned with either evolution (e.g. Grant 1998) or ecology (e.g. Gorman 1979, Vitousek *et al.* 1995) but few encompass both ecological and evolutionary concerns (one exception is Williamson 1981). Islands are land masses isolated from others by water, but islands and mainland differ only arbitrarily in scale in relation to organisms: what is an island for birds may be a large mainland for ants so that investigating insular patterns involves to scale study areas to the dispersal range of organisms.

COLONISING AN ISLAND NECESSARILY RESULTS IN EVOLUTIONARY CHANGES

When a propagule, say a few individuals of a species, succeeds in colonising an island, both selective evolution resulting from new selection regimes in a new environment and non-selective evolution (founder effect and genetic drift because a propagule is necessarily a genetic bottleneck) inevitably lead the new population to evolve rapidly and diverge from its mainland mother population. Molecular studies have confirmed that the founding of a new population by a few individuals involves a loss of genetic diversity (Mundy *et al.* 1997, Tarr *et al.* 1998), in an inverse proportion to the size of the founder group (Merilä *et al.* 1996) and that larger populations contain more genetic variation (Avise 1994). Since mutations inevitably arise and are subject to drift as well as selection, local environments do not have to differ for genetic divergence to occur in isolated populations (Grant 1998). The substitution at genetic loci of certain alleles for others from random drift is conducive to phenotypic change irrespective of any changes in selection regimes. However, selection regimes in the new insular environment of a colonising population inevitably differ from those on the source mainland because of differences in both abiotic (climate) and biotic (resources, competitors, predators, parasites) factors. Many comparisons of bird populations between islands and adjacent mainland regions or among islands within archipelagos have been used to infer differences in regimes of natural selection in different environments (Mayr 1940, Grant 1965a, Keast 1970, Alatalo & Gustafsson 1988, Roff 1994, Fitzpatrick 1998).

Divergence may eventually lead to speciation and insular endemism if differentiation conducive to reproductive isolation of a first colonising propagule is attained before a second colonisation event by the same mother population occurs. This is the case of double invasion of pairs or more rarely triplets of species on several islands around the world (Grant 1968). A common feature of these sister species is a large difference in both ecological characters and morphology. On the Canary Islands, the Blue chaffinch *Fringilla teydea* evolved from a first colonisation event by the European chaffinch *F. coelebs*, and much later, the islands have been colonised again by the European chaffinch. In the meantime *F. teydea* achieved reproductive isolation, hence a full species status, so that the two species occur sympatrically without hybridising. This scenario, which had been proposed a long time ago from resemblance between the two species and common-sense, has been recently confirmed from molecular data (Marshall & Baker 1998). Whether species-specific adaptations to different habitats by the two species permits their coexistence or competitive interactions produced the divergence is difficult to assess (Grant 1998). Most non-oceanic islands are too close to the mainland, however, for differentiation having a chance to occur between two colonisation events, which explains why few species evolved as endemics in islands that are close to the mainland. For example very few birds evolved as endemic species in the Mediterranean archipelago because of the closeness of all islands to the mainland.

BIRD ASSEMBLAGES ON ISLANDS: A CASCADE OF ECOLOGICAL SHIFTS

Summarising the evidence from a great many studies on insular biology, Rosenzweig (1995) came to the conclusion that, in spite of much debate, controversies and shortcomings (see e.g. Blondel 1991), the MacArthur & Wilson's (1963, 1967) theory of island biogeography holds up well in explaining species diversity, immigration rates, extinction rates and turnover rates on islands. However, being basically non-evolutionary the theory captures only two of the three fundamental processes that determine biogeographic patterns, namely immigration, extinction and evolution although taken in a broader context the theory is not silent on evolutionary processes within the basic assumption of equilibrium (Whittaker 1998, 2000). Therefore the MacArthur & Wilson's paradigm has mostly been designed to explain processes that operate on the short ecological time and at relatively small-scale circumstances, which implies several over-simplistic assumptions (Heaney 2000, Lomolino 2000a).

What determines species richness on islands ?

Contrary to what is too often written, even in the best international journals, species impoverishment on islands is not an issue of the MacArthur & Wilson's model. The realisation that islands are depauperate in species in comparison with areas of similar size on the nearby mainland dates back to biogeographers of the nineteenth century (e.g. Wallace 1880) who noticed that the size of an island is the most important determinant of the size of the pool of species that coexist on it. The key point of MacArthur & Wilson is not species richness *per se*, but the existence of a turnover of species on islands as a result of an equilibrium between colonisation and extinction events in communities that are assumed to be more or less saturated in species. The role of island characteristics in shaping insular communities has received much attention from both theoretical and empirical studies (Hamilton & Armstrong 1965, Haila *et al.* 1980, Williamson 1981, Blondel 1991, Wiggins & Møller 1997). A positive relationship between island area and species richness has been so widely demonstrated that it became an universal law (Ricklefs & Lovette 1999 and references herein). However, disentangling direct from indirect effects of area on species richness has proven quite difficult. At least three factors interplay in determining species numbers on islands (see also Fox & Fox 2000). First, as the size of an island increases, so does the size of species' populations. Thus, the probability of extinction decreases as the island area increases. Second, as the size of an island increases, so does its probability of encompassing a wider range of habitats that will be suitable for colonisation by a wider range of species. Watson (1964) on the Aegean islands, Greece, Haila *et al.* (1983) on the Aland archipelago, Finland, Martin *et al.* (1995) in the Queen Charlotte Islands, Canada, and Ricklefs & Lovette (1999) in the Lesser Antilles gave good illustrations that species-area curves are primarily determined by the diversity of habitats. Analysing 30 studies of bird species-area relationships that included some measure of habitat diversity, Ricklefs & Lovette (1999) reported that 22 studies found a significant area effect, 21 found a significant habitat-diversity effect, and 10 found both effects. Third, distance to the mainland source often explains a significant amount of the variance, especially in remote oceanic islands as first demonstrated by Diamond (1974) in a series of islands off New Guinea. For example, Reed (1987) found a significant relationship between the residuals of a regression that fitted island area to bird diversity and log distance to mainland for birds of the Bahama islands.

Insular communities are not a random sample of the source mainland pool of species

Besides the mere number of species, a point of major interest is whether or not the species present on an island are a random subset of the pool of species of the nearby source mainland, i.e. have all species of the mainland pool the same chance to successfully colonise the island as assumed in the MacArthur & Wilson's model ? Answering this question requires comparative studies on species-specific attributes in relation to colonising abilities. Species differ in their rates of immigration, dispersal abilities and aptitude to construct viable populations, which explains why islands include a non-representative sample of species from the mainland. Some species, the so-called tramps and supertramps (Diamond 1974), arrive at higher rates whereas others immigrate at imperceptible rates. Thus, the most successful colonists will on average be those species that arrive first on an island since rates of extinction are a function of the number of species already present. Successful island colonists are often small generalist species that are common, widespread and very mobile on the mainland, so to say flexible in habitat selection and in utilising resources. The smaller the island the more likely it will be colonised by a low number of small species that are common everywhere in the nearby mainland (Blondel 1991, 1995).

Another sorting process in colonisation probabilities is body size. For similar population sizes, large organisms need on average more space than small organisms. Hence a lower proportion of the larger species on islands in most taxonomic groups. This explains that predators are under-represented in most island biota. Predator populations being necessarily smaller than those of their victims, they are likely to become accidentally extinct with a much higher probability than their victims. Thus, island communities are 'disharmonic', a term which refers to changes in the relative proportions of different taxa or trophic levels on islands as compared with those on the nearby mainland. As a result, species richness alone is a poor characteristic of insular communities because the relation between species number and area is indirect. This relation is mediated by a chain of interrelated factors that include habitat structure, habitat size, and species-specific attributes (Haila *et al.* 1983).

In series of islands of different sizes not far from a mainland source, species assemblages are usually nested, which means that communities of lower species numbers (smaller islands) are non-random subsets of more diverse assemblages (larger islands). Each subset of species does not include species that are already absent from the next richer assemblage (Patterson & Atmar 1986, Simberloff & Martin 1991). In perfectly nested subsets one or several species are lost as species richness declines as a result of reduction of the size of the island, and none of the species lost from the richer communities reappears in any of the lower-rank communities once it has been lost. True biological nestedness requires that communities share a common biogeographic history, live in similar environments and have hierarchical niche relationships (Patterson & Brown 1991). Such situations are likely to occur in habitat islands resulting from forest fragmentation or in archipelagos not far from a same mainland source (Cutler 1991). Oceanic islands that were colonised from different mainland pools at different time intervals are much less likely to exhibit nested species assemblages (Patterson & Atmar 1986, Wright *et al.* 1998). Note that one approach to analyse sets of separate communities that are not independent, e.g. nested insular communities, is spatial autocorrelation (Koenig 1999).

Community structure and dynamics

What are the consequences of species impoverishment and disharmony on community dynamics and resource sharing ? Detailed bird censuses conducted at different scales of space in islands as compared to areas of similar size on the mainland frequently show that species impoverishment differ depending on scales and that impoverishment at the scale of the whole island does not necessarily translate at lower levels of the hierarchy, i.e. landscapes and habitats. For example 109 species of breeding birds occur in the whole island of

Corsica, as compared to 170 to 173 species in three mainland areas of similar size, a 37 % impoverishment, whereas there is hardly any impoverishment at the scale of a landscape including six habitat types ranging from a grassland to a mature forest (42 *versus* 43 species) (Blondel 1991). At the habitat level (the so-called alpha diversity), some habitats, especially old forests, are heavily impoverished on the island whereas other habitats, such as shrublands, have many more species than their mainland counterparts. Thus, there are on average higher alpha diversities on the island than on the mainland and lower beta diversities for a similar overall richness (gamma diversity) at the scale of a series of habitats combined. This results in a slow-down in turnover (beta diversity) among habitats on the island as compared to the mainland. This is because many species expand their habitat-niche and spill-over from their preferred habitat into other habitats (Blondel *et al.* 1988). In other words, species on an island recognise fewer habitats than on the nearby mainland. I will come back later on this process of 'niche expansion', first described by Lack (1969), which is a regular feature in island biota and results in a much looser structure of bird assemblages along habitat gradients.

MICROEVOLUTIONARY CHANGES

Ecological characters of insular species cannot be dissociated from evolutionary changes to which they are intimately related. These changes are both idiosyncratic, that is specific to each particular organism or island, and general and widespread (Grant 1998). Similar characters in a group of organisms living in the same environment may be due to common inheritance and/or shared environmental pressures whereas similar trends among different unrelated organisms occupying different islands are more likely to reveal general evolutionary forces. One challenge is to disentangle which factors are responsible for the similarity of characters or trends.

The new environment of a colonising population is characterised by many changes including species impoverishment, new interspecific interactions, new genetic background, all resulting in a cascade of changes in the ecology and life history of that population. Many of them presumably evolved as mechanisms against extinction risks. They include higher population densities which reduce vulnerability to stochastic extinctions (Pimm *et al.* 1988, Tracy & George 1992), changes in body size and shape (van Valen 1973, Case 1978), broadening of several components of the niche (habitats, diet, foraging sites), modifications of fitness-related traits such as fecundity, survival, dispersal (Blondel 1991), and changes in social behaviour (Stamps & Buechner 1985). All these characters are parts of a so-called insular syndrome (MacArthur *et al.* 1972a, Williamson 1981, Crowell 1983, Stamps & Buechner 1985, Blondel 1991, 1995). I will comment some of them.

Reduced dispersal

A common and repeated response of both plants and animals to new selective pressures in insular environments is a reduction in traits that allow them to disperse over long distances (Carlquist 1974). Hence is the paradox that the best long-distance immigrants are organisms with powerful dispersal abilities whereas the most efficient colonists are poor dispersers within the island. The response may be ecological, evolutionary, or both. At the level of ecology, bird communities in continental islands quite often include a disproportionate proportion of sedentary species, or species that become sedentary, which is repeatedly the case in remote oceanic islands (Blondel 1991). At the evolutionary level, a repeated trend is the reduction of morphological traits such as powerful wings in animals. Flightlessness is common in island populations of birds and insects because the advantages of sedentariness increase as the advantages of dispersal decrease (Darlington 1943, Carlquist 1974), including for winged organisms to be accidentally blown off islands by strong winds which often occur on islands. Flightlessness is also an energy saving mechanism in birds whenever a permanent habitat with a local year-round food supply and the absence of predation favour strong habitat fidelity (McNab 1994). Rails for example have evolved flightlessness many times (McNab 1994, Steadman 1995). Long-distance dispersal to find suitable habitats allowed this group of birds to colonise a large number of small islands sometimes quite remote as in the Pacific Ocean. Then walking while exploiting the habitats in the manner of large herbivores such as Dodos, Moas of Elephant-birds led to the progressive atrophy of wings which became useless because of the small distance to cover in the predator-free insular environments.

Size changes

A general trend on islands is changes in body size and shape which repeatedly evolved in most groups of plants and animals (Van Valen 1973, Carlquist 1974, Grant 1998). Plants usually evolved greater size and stature with herbs becoming shrubs and trees. In vertebrates, explanations for size trends are difficult because they involve interactions between many factors such as food resources, competition and predation (Case 1978, Heaney 1978, Lomolino 1985). Generalisation is probably impossible because different size trends depend on species, islands and factors involved. In the absence of predators and competitors there is however a trend for mammals evolving large individual size in rodents (Foster 1964, Williamson 1981) and small individual size in carnivores which are supposedly food-limited (Klein 1968, Heaney 1978, Lomolino 1985, McNab 1994). In birds both gigantism in the case of large herbivorous species (Moas, Dodos, Elephant birds, *Sylviornis*), and dwarfism in many passerines are found on islands. However, the mechanisms that lead to either gigantism or dwarfism remain largely unknown and there are so many exceptions to this "rule" (e.g. Kikkawa 1976) that any generalisation would be premature. Ecological release from competitive and predatory constraints is often inferred from the measurement of ecologically significant morphological traits as a mechanism of changes in body size and/or shape. For example, island birds from a variety of taxonomic groups tend to have large beaks and long tarsi (Murphy 1938, Grant 1965b), and that independently of body size which does not necessarily follow the same trend.

High population sizes and niche expansion

The reduced species richness of island bird communities is often associated with higher population densities of species as compared to those in similar mainland habitats (Crowell 1962, MacArthur *et al.* 1972a, Yeaton 1974, George 1987, Blondel 1991, Ricklefs & Lovette 1999). Kikkawa (1976) reported on densities of the silvereye *Zosterops lateralis chlorocephaha* reaching an astonishing figure of 125 pairs per ten ha on Heron Island in the Great Barrier Reef, Australia. Such a density is higher that the highest recorded density of all land birds in a mainland rain forest of Australia ! In addition to higher population sizes, many island vertebrates (lizards, mammals, birds) expand the range of habitats occupied or dimensions of their feeding niche (MacArthur *et al.* 1972a, Williams 1972, Blondel 1991, Roughgarden 1995, Kikkawa 1976). A classical explanation of these patterns is a relaxation of interspecific competition for resources and different patterns of resource partitioning in species-poor islands. The rationale which follows from the niche theory and the dynamic equilibrium theory is that island habitats are saturated with fewer species than mainland ones with the result that extra-resources become available for more conspecifics. Several other hypotheses have been proposed to explain larger population densities, including reduced predation (Higuchi 1976, Abbott 1980, Nilsson *et al.* 1985, Williamson 1981), and reduced dispersal, the so-called "fence effect" (MacArthur *et al.* 1972b, Tamarin 1977). Reduced predation may also result in a release in habitat selection because camouflage is less important in the absence of predators, favouring niche expansion in suboptimal habitats. Unfortunately, very few rigorous attempts have been made to test these hypotheses (Abbott 1980, George 1987), including the hypothesis of a causal relationship between species richness and population density. One exception has been provided by George (1987) who experimentally demonstrated that higher densities of small land birds on the Coronados islands, Mexico, resulted from lower predation rates than on the nearby mainland.

Responses of niche breadth and population density on islands are often called competitive release and density compensation respectively (MacArthur *et al.* 1972a). They have long been interpreted as a deterministic output of competitive processes in the framework of the assembly rules proposed by Diamond (1975). These rules assume the improbability of finding on the same depauperate island certain combinations of species, mostly species that overlap greatly in their ecological needs. Unfortunately they have rarely been tested and confronted to null hypotheses but one exception has been provided by Moulton & Pimm (1987) who elegantly demonstrated the likelihood of the role of competition in shaping insular bird assemblages. These authors showed that native species of the Hawaiian islands that were the most likely to be competitively wiped out by introduced species were those species that were morphologically and ecologically the most similar to the introduced ones.

However, changes in population sizes and niche breadth may also arise from other factors such as restricted dispersal or intraspecific spill-over, a neutral term to mean that increased niche breadth may be due to mechanisms other than competitive release. For this reason, the terms density inflation (Crowell 1983) has been proposed instead of density compensation because it does not imply any causal mechanism. In addition, comparing niche width of an insular population with that of a single mainland population may be misleading. A sound comparison should involve comparing insular niche width with the mainland niche width at the scale of the whole range of niches and habitats occupied by the species on the mainland, which is, of course, very hard to do.

Broadening of the niche and ecological generalisation on islands seem to contradict the tenet of a sharp specialisation of local endemics which is so characteristic of remote oceanic islands. The reason why niche broadening and ecological generalisation appear to be insular features is that there are many more small islands than large ones including clusters of small islands in large and well-isolated archipelagos. Populations on small islands are maintained in initial stages of evolutionary changes presumably because of limited ecological opportu-

Table 1. – Components of an insular syndrome in Corsican blue tits. Yes means that the trend fits the prediction of the insular syndrome. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Trait	Insular syndrome	Island/mainland
Ecology		
Body size	Yes	15% smaller ***
Population density	Yes	2.5 pairs *vs* 1 pair.ha^{-1}***
Habitat niche ($e^{H'}$)	Yes	2.92 *vs* 1.0 ***
Feeding niche (H')	Yes	4.18 *vs* 3.72 ***
Breeding		
Laying date	Yes	11 May *vs* 15 April ***
Clutch size	Yes	6.6 eggs *vs* 8.6 ***
Breeding success	No	0.56 *vs* 0.57 ns
Nb. Fledglings/pair	Yes	3.5 *vs* 5.1 ***
Fled. Mass/ad. mass	Yes	1.14 *vs* 0.98 **
Nestling period	Yes	22 days *vs* 18.5 days *
Adult survival	No	0.56 *vs* 0.58 ns
Yearling survival	Yes	0.64 *vs* 0.48 **
Behaviour		
Territory size	Yes	0.94 ha *vs* 2.08 ha ***
Territory overlap	Yes	Circumstantial evidence
Aggressiveness	Yes	Much lower on Corsica

nities, and also possibly frequent extinctions (Mayr 1965). On large oceanic islands and archipelagos, ecological generalisation is far from being a necessary outcome of evolutionary trajectories. In fact the opposite is likely to be true whenever speciation can produce several efficient specialists from an original generalist. This happened for examples for Darwin's finches in the Galapagos (Lack 1947) and honeycreepers in the Hawaiian archipelago (Perkins 1913). The ultimate fate of such specialists is expected to be extinction from competition when a new generalist species colonises the island, which results in the end of a taxon cycle and the initiation of a new cycle of differentiation and specialisation (Wilson 1961, Ricklefs & Cox 1972).

Life histories

The large changes in community structure and species-specific attributes observed in insular biota result in large changes in life histories of species. One example of these changes has been provided by studies of insular and mainland populations of blue tits *Parus caeruleus* in the French Mediterranean region. As compared to their mainland counterparts, blue tits on Corsica strikingly differ in morphology, ecology, breeding patterns and behaviour. Most of the changes fit the predictions of an insular syndrome and are summarised in Table I (see also Higuchi 1976 for a study of insular populations of the varied tit *Parus varius*). In interpreting these changes, one problem arises: could the differences between island and mainland features be simply different phenotypic expressions of the same genotypes raised under different environmental conditions ? Very few studies investigated whether differences between island and mainland populations have a genetic basis. Alatalo & Gustafsson (1988) demonstrated from cross-fostering experiments that the larger size of the Coal tit *Parus ater* on the island of Gotland is due to genetic factors, and Blondel *et al.* (1990) and Lambrechts *et al.* (1997) showed from common garden experiments that the large differences in laying date between a Corsican and a mainland population of blue tits were also genetically based.

Changes in fitness-related traits, i.e. breeding patterns and social structures, have often been interpreted as trade-offs among life history traits in response to high population densities in insular environments, especially between clutch-size and survival (Cody 1966, 1971, Ricklefs 1980). High population densities in insular environments were expected to result in high intraspecific competition, high adult survival, and hence low clutch-size. Reduction of clutch size in islands as compared to mainland has been reported in several species (Crowell & Rothstein 1981, Blondel 1991) including Darwin's finches (Grant & Grant 1989) and an extreme case is that of the predator- and competitor-free Seychelles warbler (*Acrocephalus sechellensis*) whose clutch size is only one egg while adult survival is as high as 83 % and life expectancy at the age of one year 3.9 years, which is extremely high for a small passerine (Komdeur 1994). However, a systematic and broad-scale analysis of reduced birth rates on islands controlling for latitudinal effects on clutch size has not yet been performed (Grant 1998) and George (1987) found no difference in clutch size between conspecific island and mainland populations of three land birds on Coronados islands. If the trend of low birth rates combined with high adult survivorship is confirmed, it may reflect an evolutionary shift away from high reproductive rates and short life span towards the opposite combination of life history traits as a result of high intraspecific competition in crowded insular populations, that is an evolutionary shift from *r*-selection to *K*-selection (MacArthur & Wilson 1967, Boyce 1984).

Behavioural shifts

Shifts in behaviour are among the most spectacular features in insular vertebrates and many descriptions have been given of the tameness and apparent fearlessness of islands birds. Stamps & Buechner (1985) emphasised that the social behaviour of a variety of insular vertebrates (reptiles, mammals and birds) reveals a remarkable convergence in behavioural traits such as 1) reduced territory size, 2) increased territory overlap, 3) acceptance of subordinates, 4) reduced situation-specific aggressiveness, and 5) abandonment of territorial defence. A much lower aggressiveness of Corsican blue tits as compared to their mainland counterparts has been shown by Perret & Blondel (1993) to be associated with differences, probably genetically determined, in the ratio of sexual hormones. The higher the oestrogenous/androgenous ratio, the lower the level of aggressiveness because it has been demonstrated that both singing activity and aggressiveness depend on testosterone levels. Several hypotheses for explaining these shifts in behaviour have been proposed among which the "defence hypothesis" which predicts that a release in aggressiveness should be selected for if defence costs become exaggerated in crowded populations where encounters between territory contenders are frequent. Saving time and energy by reducing defence costs and decreasing territory size is expected to improve fitness payoffs per territory owners and result in the production of more competitive offspring. Breeding traits of Corsican blue tits and of an insular population of varied tits in Japan (Higuchi & Momose 1981) include higher ratio of fledging mass/adult mass, longer nestling period, prolonged infantile behaviour, higher survivorship of fledglings relative to adults, small territory size and large territory overlap. All these trends are consistent with the defence hypothesis. Kikkawa (1976) reported, however, that the insular silvereye of Heron Island, Australia, is more aggressive than its mainland counterpart, but interestingly, he noticed that the breeding success of dominant birds may not be as high as that of submissive birds in some years, which runs in the line of predictions from the defence hypothesis. Behavioural shifts on islands could have important consequences on genetic mating systems of socially monogamous birds, with lower levels of extra-pair paternity in insular populations than in their mainland counterparts (Griffith 2000, Petrie & Kempenaers 1998).

POPULATION DIFFERENTIATION ON ISLANDS

An evolutionary trend resulting from shift from dispersal to sedentariness is the differentiation from a single generalist species first colonising an island or archipelago to several locally adapted specialist species as a result of local adaptation. Radiation of such groups as Darwin's finches in the Galapagos or honeycreepers in the Hawaii islands are examples of such mechanisms which may eventually result in a taxon cycle of evolution leading to extinction of specialist species and their replacement by a new generalist species, which makes the cycle begin again (Wilson 1961, Ricklefs & Cox 1972, Pregill & Olson 1981, Grant 1998).

A consequence of low dispersal, sedentariness, high site fidelity and strong philopatry of insular birds is the potential for differentiation at smaller spatial scales than on mainland regions, even at a smaller scale than the dispersal range of organisms. This may seem surprising because in such highly mobile organisms as birds, the homogenizing effects of gene flow are supposed to preclude adaptive differentiation at spatial scales that are smaller than the dispersal range of individuals. However, theory predicts that such a differentiation can potentially occur if divergent selection pressures are strong enough.

Examples of large interpopulation differentiation at a small geographical scale are that of the white-eyes (*Zosterops* spp.) in the Mascarene islands (Cheke 1987), and, even more convincingly, the spectacular variation of bill size of Darwin's finches on the Galapagos islands in relation to the size and hardness of their seed food resources (Schluter 1996, Grant 1999). Food supply of the Darwin's finches has been found to differ on different islands in a way that is consistent with differences in the bill size of the birds, thus supporting the hypothesis that morphological differences result from different selection pressures acting on genetic variation (Schluter & Grant 1984). Evolutionary responses to oscillating natural selection on heritable variation in bill shape have been demonstrated when food supply changed after an El Niño event (Grant & Grant 1989, 1995).

One example of local differentiation of populations within an island as a result of resource-based divergent selection is that of the blue tit (*Parus caeruleus*) in Corsica. Two populations only 25 km-apart are highly specialised to their local habitats and differ so much in demographic and morphometric traits that they are apparently reproductively isolated (Blondel *et al.* 1999). These two populations responded to contrasting local selection regimes involving large differences in the timing and abundance of food resources, which resulted in divergent adaptive response of suites of life-history traits. Such a local adaptation to local environments at small spatial scales is a demonstration that selection can cause divergence, presumably in the face of substantial gene flow, giving support to the divergence-with-gene-flow model of speciation (Rice & Hostert 1993). Differentiation at such a small scale is really an insular feature because in a similar configuration of habitats on the mainland, much higher dispersal rates and gene swamping prevented local adaptation and resulted in local maladaptation (Dias *et al.* 1996, Dias & Blondel 1996). Thus strong habitat fidelity and reduced dispersal which are components of an insular syndrome (Diamond 1983, Blondel 1995, Grant 1998) explain that population differentiation of birds can occur at much smaller spatial scales on islands than on mainland. A somewhat similar case of incipient parapatric speciation has been suggested for *Neospiza* buntings on Inaccessible Island in the Tristan da Cunha archipelago (Ryan *et al.* 1994). Interestingly, the lower inter-species diversity which is so characteristic of island biota is to some extent counterbalanced by a higher intra-species diversity. These examples open the door to direct studies of observable evolution in natural populations which are surprisingly rare despite their interest to understand and interpret the rather static analysis of evolution in the past, and to predict evolutionary changes as responses to man-induced environmental changes.

STRENGTH AND VULNERABILITY OF ISLAND BIOTA

Resistance of insular species to natural disturbance

The insular syndrome involves ecological adjustments as well as evolutionary changes that make insular communities self-regulating assemblages of species that are resistant face to the risks of extinction and invasion. The mechanisms whereby insular communities are highly integrated and resistant biological constructs remain obscure, and the vague concept of diffuse competition proposed by MacArthur (1972) to explain the resistance opposed by insular communities to potential colonists is not very helpful because it is impossible to test experimentally. The systems that control island diversity work by the principle of feedbacks. Low diversity causes diversity to grow and high diversity causes diversity to fall (Rosenzweig 1995). Although species turnover on islands is the keystone of the theory of island biogeography, there are few well documented case studies of turnover on islands and some classical examples are controversial because it is questionable whether observed changes in species composition between two census intervals are due to competition-mediated immigration-extinction mechanisms or to idiosyncratic habitat changes as a result of human action (Diamond & May 1977). Turnover can operate at long scales of time, thus remaining unnoticed, especially in remote oceanic islands where, on very long time scales, it turns to result in species replacement as exemplified by the taxon cycle (Ricklefs & Cox 1972). Indeed, even though islands are subject to natural disasters including drought, fire, severe storms and hurricanes which can devastate entire populations on smaller islands (Wiley & Wunderle 1994), to date the fossil record has revealed no major loss of species from natural causes (Steadman 1995). Even in some Galapagos islands where severe droughts such as those produced by El Niño events, may reduce population sizes to very few individuals, no extinction events seem to have occurred in the recent past in Darwin's finches (Grant 1986, Grant & Grant 1989). On the small six-ha Mandarte Island, British Columbia, Canada, heavy storms can reduce the population size of the Song sparrow (*Melospiza melodia*) to just a few individuals but no extinction of this small isolated population has been reported so far (Smith *et al.* 1991).

Yet, the lack of connection with larger areas with which populations could exchange propagules makes small insular populations potentially vulnerable to environmental, demographic and genetic stochasticity which together can precipitate them in an 'extinction vortex'. Stochastic fluctuations of life history traits may be conducive to demographic thresholds below which rare events may lead to extinction (Lande 1987).

There are critical factors of population size and structure below which inbreeding and loss of selectable variation could lead a population to extinction (Frankel & Soulé 1981, Soulé 1987). The "Allee effect" is a basic assumption underlying the so-called extinction vortex, stating that populations that become too small will inevitably be doomed to extinction as a result of the combined effects of demographic and genetic processes. Therefore, loss of genetic variability and reduced viability and fecundity due to inbreeding depression are probably a threat in small isolated populations. The relative impact of inbreeding on the viability of natural populations has been questioned, however, because there is little evidence of deleterious effects of inbreeding depression in animal populations. Van Noordwijk & Scharloo (1981) demonstrated clear effects of inbreeding in a population of Great tit (*Parus major*) on the island of Vlieland, The Netherlands. Reduced hatching success has been shown in inbred zygotes and in clutches of inbred females. Both the average number of not hatching eggs (7.5 % for every 10 % increase in inbreeding coefficient) and the proportion of clutches in which any eggs fail to hatch increased with the degree of inbreeding. However, there were no indication of smaller clutch size or a reduced fertility in inbred adults. Moreover, the effects of inbreeding in early stages of the life cycle were compensated in later stages because successful young have been shown to have higher survival rates and higher recruitment rates (twice as many as expected). In fact continuous inbreeding probably exerts a strong selection against lethals. Purging of deleterious recessive alleles from the genome has been put forward as a potential effect resulting from periods of intense inbreeding following bottlenecks. In the small population of song sparrow on the Mandarte island that experienced a severe population bottleneck as a result of demographic crashes, those individuals that survived the crash were not a random subset of the pre-crash population in respect to inbreeding (Keller *et al*. 1994). After two crashes (1980 and 1989) the mean inbreeding coefficient in the breeding population was actually lower in the season after the crash than in the previous season. Natural selection clearly favoured outbred individuals which does not mean, however, that inbreeding does not affect survival in the wild. When there is a succession of crashes, serial bottlenecks cannot entirely purge the genetic load sufficiently to alleviate the negative effects of inbreeding. Thus environmental and genetic effects on survival may interact in such a way that their effects on individuals and populations should not be considered independently.

The holocaust of island birds

Islands are among the most threatened biota on Earth with more than two thirds of extinct avian species being insular endemics. Why are they so vulnerable in spite of them having evolved life history traits that successfully allow them to persist as explained above ? The answer is that insular biota became evolutionarily resistant to most natural disturbance events but they are ecologically sensitive to human-induced disruption. This explains that suddenly insularizing an area may have dramatic consequences on species which do not have the time to evolve the suite of life-history traits which would allow them to withstand new constraints of the recently isolated environment. An example is that of Barro Colorado Island (BCI). This artificial island has been created in 1914 when the canal of Panama has been built. Within some decades, as many as 60 species of birds became extinct. Extinction has been attributed to several causes including predation and a differential loss of species of undergrowth (Wilson & Willis 1975, Karr 1982). Interestingly, Karr *et al*. (1990) provided evidence that the species that were the most likely to disappear from the island were those that had the lowest survival rates. Among the 25 mainland species they analysed, survival rates of 8 species that vanished on BCI have been estimated as 0.50 ± 0.05 as compared to 0.59 ± 0.02 for the 17 species still present. Although the absolute difference may appear small, its demographic consequences are considerable.

Perhaps the most important threat to island birds is the disruption of interspecific interactions such as competition, predation and parasitism. As many as 49 different species of birds have been introduced in the Hawaiian islands between 1869 and 1963. In the meantime, a large proportion of the 36 endemic species of Hawaiian honeycreepers went extinct. From computer simulations on the morphological space of introduced and extinct species, Moulton & Pimm (1987) showed that competition must have happened among them at the expense of native species because extinct species were significantly closer to the introduced species in the morphological space than are the still existing native and introduced species among them. This strongly suggests that introduced species have been the direct cause of extinction for most of the native species. Additional causes of extinction of Hawaiian honeycreepers have been the disease from malaria (*Plasmodium*) which has been introduced with non-native bird species (Van Riper *et al*. 1986).

Release from predation pressure is one of the most conspicuous features of island communities. In communities that are naturally poor in predators, birds did not evolve defence mechanisms and are naïve and particularly tame and easy to approach and catch. At the time of European invasion of many islands, an incredible tameness of mammals and birds was reported in a number of so far uninhabited oceanic islands. Resident land birds on most oceanic islands are still remarkably tame, as illustrated for example by a photograph showing a Galapagos hawk sitting on the hat of Peter Grant (Grant 1998). In the Cousin island, the Seychelles warbler lacks natural predators and can be approached just a few metres (Komdeur 1994). New predators had catastrophic effects in such communities where introduced mice, cats and dogs become as harmful for defenceless prey as are weasels, lynxes and wolves, respectively, in mainland communities. The combination of tameness and flightlessness resulted in an unprecedented holocaust of thousands of species, especially in remote oceanic islands, as soon as man invaded them (Olson & James 1984, Steadman 1995). In the Hawaiian islands which are renowned for the radiation of Hawaiian honeycreepers, flightless ducks, geese and ibises, at least 60 endemic species of land birds have become extinct since human arrival at about 1500-2000 yr BP. Combining seabirds and land birds, Steadman (1995) conservatively estimated that an average of 10 species or populations in most families of Pacific island birds (rails, pigeons, doves, parrots, passerines) have been lost on each of the 800 major islands of the Pacific, yielding a total loss of 8000 species ! Most extinct species were flightless forest dwellers endemic to a single island. Flightless rails alone, with an estimate of one to four species per island, may account for 2000 species that have been doomed to extinction. In nearly all islands in the large archipelagos of the Pacific Ocean (Melanesia, Micronesia, Polynesia) birds have been decimated as soon as man reached them as early as 30,000 yr BP in Melanesia and much later, about 3500 yr BP in West Polynesia and Micronesia. Once people occupied an island, human predation, habitat loss, and introduced predators, competitors, or pathogens were responsible for mass extinction of native species within a very short period of time.

PERSPECTIVES FOR FUTURE STUDIES

Despite an impressive body of knowledge accumulated on island biology since the time of Darwin and Wallace, there are still much ignorance and controversies about both ecological and evolutionary matters in island biota, including the very first step of describing their biological diversity. The equilibrium theory of island biogeography has undoubtedly been very useful to revitalise and rejuvenate insular studies by providing a novel and unifying theory that stimulated hundreds of studies for nearly 35 years. However, several limitations and new insights in the biology of isolates make the theory insufficient as a modern tool to explain patterns that span over a broad range of spatial, temporal and ecological scales, including habitat islands resulting from habitat fragmentation (Fox & Fox 2000, see also the special issue of *Global Ecol Biogeogr* 6, January 2000). Time is ripe to replace the long-standing MacArthur and Wilson's paradigm by a more comprehensive theory taking into consideration scale effects as advocated in the spatial and temporal continuum proposed by Haila (1990). A new model, the general conceptual framework of which has been offered by Lomolino (2000b), should incorporate those features not included in the MacArthur & Wilson's theory but which have been shown to be important in determining insular communities: 1) the fact that basic biogeographic processes are not only immigration and extinction, but also evolution, 2) the importance of island-specific characteristics (physiography, climate, stochastic abiotic events) in basic biogeographic processes, 3) the role of feedbacks among components of insular systems, including both processes and species, and 4) the species-specific variation of life-history attributes which affects microevolutionary processes and explains the non-random variation among species on islands (Lomolino 1999, 2000b).

In this context evolutionary issues should be considered at both scales of phylogenetic diversification, i.e. speciation, and microevolutionary changes within populations and species which operate on the same time-scale as colonisation and extinction. Processes of phylogenesis can generate patterns of species richness almost independently of colonisation and extinction with not only endemic species, but also entire endemic clades including many species as in the Galapagos and Hawaiian islands (Heaney 2000). Many microevolutionary questions remained to be answered before broad generalisations can be made. Each island is a singular system with its own history, environmental characteristics and living communities so that processes that have a significant impact on one species or set of species on an island may be unimportant for others on another island. Evolutionary changes on islands that are assumed to be components of an insular syndrome too often received *ad hoc*, "panglossian" (Gould & Lewontin 1979) and circular interpretations. Such explanations cannot be accepted until they rely on measured selective forces producing adaptations and until it has been demonstrated that similar trends evolved among different organisms living in the same or different islands. Interpretations of evolution on islands are strongest whenever a trend is statistically demonstrable and/or known from phylogenetic analyses to have arisen independently and several times in unrelated taxa, and are repeated in geographically distant areas (Grant 1998). Such conditions are rarely met but could be so thanks to recent improvements in the comparative method (e.g. Felsenstein 1985, Harvey & Pagel 1991).

Given the present state of the art of our knowledge on bird evolution on islands, several points should deserve investigations in the future. I shall limit myself to mention only a few of them. For example no generalisation should be made on the balance between birth rates and death rates until much further insight is given on the overall demography and trade-offs between traits from long-term population studies. The link between loss of genetic variation due to founder effect and evolutionary change, which is assumed from conventional wisdom, remains to be determined because not all insular populations, including small populations, are genetically depauperate (Merilä *et al.* 1996, Tarr *et al.* 1998). Addressing the challenge of what determines genetic variation on islands requires an answer on the time period over which evolutionary changes occurred, and hence how much the island's environmental history needs to be known. Modern molecular techniques using mtDNA or microsatellites for constructing phylogenies at the intraspecific level combined with quantitative genetics on fitness-related traits, that respond within a few generations to strong directional selective pressures, should give an insight on the response of populations to environmental changes. Coupling historical data on islands' environments with genetic data on extant populations should help interpret the microevolutionary history of island populations and predict their responses to man-induced environmental changes including the forthcoming changes due to global warming. Reconstructing past environments to interpret evolutionary changes is a great challenge, however. If geophysical history is not too complicated to reconstruct and should give cues to understand adaptive radiations in archipelagos at the species level, as shown for example by Carson & Clague (1995) for the Hawaiian honeycreepers, or by Grant & Grant (1996) for the Darwin's finches in the Galapagos, the ecological history of islands on time scales that are consistent with microevolutionary changes is a much more difficult task which requires a multidisciplinary approach involving disciplines of both earth and life sciences. Molecular approaches are quite promising to track the history of species. For example, the expectation of Ricklefs & Cox (1972) that the relative ages of island populations could be inferred from the degree of taxonomic differentiation among island populations has been confirmed by analyses of DNA sequence divergence among West Indian birds (Ricklefs & Bermingham 1999).

Finally the alarming number of bird species that have become endangered or extinct in recent years (Diamond 1989), especially endemic forms on islands (Collar *et al.* 1994), is much more than a mere impoverishment in biological diversity. Among the many arguments to be made for conserving our biological heritage (Reaka-Kudla *et al.* 1996), one of them is that missing species make it difficult to interpret both ecological processes and evolutionary pathways. Missing species from ecological communities or from evolutionary clades are like missing pages in a book. When too many pages are lost, the message becomes obscure, and finally unintelligible. This makes urgent a thorough assessment of the causes of species declines and an insight in the relative impact on the demography of species of various threats such as habitat loss and fragmentation, pollution, the introduction of exotic predators, competitors and disease, human impact, unexpected catastrophes and human-induced climate changes. This can be achieved through population viability analysis (PVA) which has been developed to assess extinction risks and to compare alternative management options (Brook & Kikkawa 1998). PVA computer simulations based on demographic, environmental and genetic parameters (Gilpin & Soulé 1986, Boyce 1992) are currently widely applied to conservation biology thanks to recent improvements in the parameterisation of the models. Current technical sophistication makes the PVA recognised by the World Conservation Union (UICN) as one of the five internationally accepted criteria for risk categorisation and development of management decisions (Clark *et al.* 1991), especially because PVA simulations allows to rank the relative severity of risks and develop potential management strategies accordingly.

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PARASITE BIOGEOGRAPHY: A REVIEW OF THE ORIGINS AND IDEAS WITH SPECIFIC EXAMPLES FROM HOLARCTIC FISHES

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HOST-PARASITE BIOGEOGRAPHY
HOLARCTIC
HISTORICAL ECOLOGY
FISH PARASITES

ABSTRACT. – The origins and major ideas underpinning parasite biogeography started in western Europe and North America with von Ihering who used parasites to study host distributions. A similar approach was used by Metcalf, Johnston, Harrison and Manter whereas Dogiel and coworkers used parasites of fish to recognize different biogeographic zones. More recently, Brooks advanced the field by introducing phylogenetic systematics as a method to investigate parasite biogeography and historical ecology. Although infrequently combined to date, two complementary approaches to parasite biogeography are historical and ecological. Historical biogeography considers questions relating to the origins of parasite distributions and host associations while ecological biogeography is concerned with contemporary factors that contribute to present distributions and abundances. Data from Holarctic fishes are used to outline ideas relevant to parasite ecological biogeography at the scale of continental distributions. These data support the hypothesis that most of the parasites have continental distributions even though the hosts have intercontinental distributions. While hosts contribute to the distribution of parasites, many parasites of Holarctic fishes show stronger affinities to geography than to the host. This suggests that parasite distributions, although ultimately dependant on a host, are influenced by factors in addition to host factors. Strict host-specificity does not confirm coevolutionary roots for predictable host-parasite associations. However, predictable associations exist at higher taxonomic levels and these may or may not have coevolutionary origins. Widespread parasite distributions can be a consequence of having numerous hosts across taxa. Historical ecological associations and sympatric hosts sharing food items that transmit parasites, ensures homogenization of the parasitofauna. Predictable associations at higher host taxonomic levels, combined with widespread Holarctic distributions at higher parasite taxonomic levels, suggests an ancient origin for many of these parasite species. These observations are true for parasites of Holarctic fish species and may also be true for fish parasites in the north-south axis of the major continents. The combination of widespread distribution of parasite species with numerous fish hosts, and endemic parasite species with restricted geographic and host associations, makes parasites fruitful models for comprehensive biogeographic studies.

BIOGÉOGRAPHIE DES PARASITES
ET DES HÔTES
HOLARCTIQUE
ÉCOLOGIE HISTORIQUE
PARASITES DE POISSONS

RÉSUMÉ. – les origines et notions fondamentales de la biogéographie des parasites remontent aux travaux de von ihering qui se servit de parasites afin d'étudier la répartition des hôtes dans la partie ouest de l'Europe et en Amérique du Nord. Metcalf, Johnston, Harrison et Manter utilisèrent une approche similaire, tandis que Dogiel et ses collaborateurs se servirent de parasites de Poissons pour reconnaître les différentes zones biogéographiques. Plus récemment, des progrès dans le domaine ont été réalisés par Brooks qui s'est servi de la systématique phylogénétique comme méthode d'étude de la biogéographie des parasites et de l'écologie historique. Bien qu'étant rarement associées, l'histoire et l'écologie sont deux approches complémentaires de la biogéographie des parasites. La biogéographie historique tient compte des questions relatives aux origines des associations d'hôtes et de la répartition des parasites, tandis que la biogéographie écologique se rapporte aux facteurs contemporains qui contribuent aux répartitions et aux abondances présentes. Les données brutes sur les Poissons Holarctiques servent à mettre en valeur les idées pertinentes de la biogéographie écologique des parasites à l'échelle continentale de la distribution. Ces données confirment l'hypothèse selon laquelle la plupart des parasites se répartissent en fonction des continents même si les hôtes se répartissent sur plusieurs continents. Alors que les hôtes contribuent à la répartition des parasites, de nombreux parasites de Poissons Holarctiques dépendent plus de la géographie que de leurs hôtes. Cela sous-entend que même si la répartition des parasites dépend finalement d'un hôte, les facteurs qui influencent cette répartition ne proviennent pas uniquement de cet hôte. La stricte spécificité des hôtes ne confirme pas les causes co-évolutives des associations prévisibles parasites-hôtes. Cependant, on peut prévoir des associations à des niveaux de taxonomie plus élevés, que ces associations aient ou non des origines co-évolutives. Les répartitions très répandues de parasites peuvent être une des conséquences du nombre important d'hôtes parmi les nombreux groupes taxonomiques. Les associations écologiques à travers le temps et les hôtes découverts au même endroit et qui ont partagé la même nourriture transmettant les parasites, assurent une homogénéisation de l'ensemble des parasites. A des niveaux taxonomiques plus élevés, des associations prévisibles d'hôtes combinées à la répartition Holarctique de parasites très répandue, suggèrent que la plupart de ces espèces de parasites ont eu une toute autre forme de vie dans le passé. Ces observations sont vraies en ce qui concerne les parasites de l'espèce des Poissons Holarctiques et il se peut qu'il en soit de même en ce qui concerne les parasites de Poissons de l'axe nord-sud des continents majeurs. Des espèces de parasites à vaste répartition combinées avec de nombreux Poissons-hôtes, et des espèces endémiques de parasites confrontées à une géographie restreinte et des associations d'hôtes, font des parasites des modèles fructueux pour de vastes études biogéographiques.

INTRODUCTION

Biogeography is defined as the science that studies geographic distribution and abundance of organisms (Darlington 1957, Brown & Gibson 1983). These studies may incorporate data from geology, palaeontology, systematics, evolution, behaviour and ecology. Unlike free-living organisms, parasite biogeography is not limited to explaining geographical distribution and abundance patterns, as the distribution and abundance of parasites in their hosts also can be investigated. Such studies can range in scale from explaining differences in the distribution and abundance of parasites in host individuals to how parasites distribute and associate with host taxa. Host related attributes such as behaviour, feeding, age, size, immunological status and host distributions, as well as abiotic factors that are frequently water related contribute to the distribution and abundance of parasites in hosts. There are two general and complementary approaches to parasite biogeography: historical and ecological. Historical parasite biogeography is interested in the evolutionary origins for parasite geographic distributions and host associations and depends on estimates for the phylogeny of the taxa, both parasite and host. These phylogenies form the basis for determining geographic patterns among monophyletic taxa and congruence in these patterns is taken as evidence for common cause for the distribution of these organisms. Ecological parasite biogeography describes present zoogeographic distributions, abundances, and host associations of parasites, and how these distributions and associations are maintained. Explanations are found in parasite and host ecology, behaviour and physiology. Historical and ecological approaches are mutually reinforcing but are rarely studied in concert. Although these ecological and historical biogeographic approaches are not exclusive, only recently are there studies directly reporting both (Choudhury & Dick in review, Carney & Dick in review).

The purpose of this review is to summarize briefly some of the significant historical contributions of parasite biogeography, consider methods to investigate parasite biogeography, and outline some current contributions from parasitology to the study of historical biogeography and ecological biogeography. Data from Holarctic fishes will be used as examples to illustrate ecological aspects. These data will show that, although parasites by definition require a host, their distributions show geographic affinities ranging in scale from watersheds to continents that may not correspond exactly with host distribution. As a consequence parasites are a good model to study biogeography.

CONCEPTS

The effect of scale is important when studying parasite distributions and abundance as parasites and their communities occur hierarchically. This allows studies at the scale of the individual host (infrapopulation or infracommunity [Bush & Holmes 1986]), within the population of a single host species (component community [Holmes & Price 1986]) within all hosts in a given geographic location (compound community) and how they distribute with different hosts across continental scales. Approaches to questions at one scale may be inappropriate for questions at another scale. For example, host attributes such as age, feeding behaviour, or immunological competence may affect the distribution of a parasite species among individual hosts. On the other hand, these attributes may not answer questions at larger scales such as why a parasite species is absent in an area where the host is present, or, how the parasite and host originally came to be associated.

Parasites are not randomly distributed among all available host species and this reflects differences in host-specificity. Host-specificity is recognized by parasite species occurring only in phylogenetically related hosts. However, all hosts are phylogenetically related at some level and this imprecise definition has resulted in host-specificity being recognized at the taxonomic level of host species, genus and even family. In fact, all parasites have predictable associations to hosts at some taxonomic level. It is well documented that parasites have predictable associations at higher host taxonomic levels. We believe that these predictable associations occur as a continuum across host taxonomic ranks, and that for many fish parasites the important association may be at the level of host family. For example, a given parasite species may be associated with many, or all, of the species in a host family, and will be found rarely, if at all, in host species outside of that host family. We define a host-specific parasite as one that reaches reproductive maturity in a single host species, with reproductive maturity being recognized by the presence of sexually mature and/or gravid adults. This strict definition is consistent with that used by parasitologists studying monogenean parasites on the gills of fishes.

The capacity for a parasite to diversify among hosts is constrained by strict host-specificity. Because a host-specific parasite is unable to colonize new hosts then not only is its distribution among host species limited, but the opportunity for the parasite to enter new geographic areas is limited by the dispersal abilities of the associated host species. This suggests that parasites with larger numbers of potential hosts i.e., broader associations, should have greater geographic distributions. Furthermore, while the geographic distributions of strict host-specific parasites is limited by the distribution of the host, parasites with broader host associations may have their geographic distributions limited by factors unrelated to host distributions (e.g. Lawler & Scott 1954).

HISTORICAL BACKGROUND

There is a long and productive history in the study of biogeography derived from the discipline of parasitology. Early efforts utilized parasites to explain the geographical distributions of hosts and/or using parasites as biological data to discuss geological history and frequently invoked assumptions of host-parasite coevolution (see Klassen, 1992a for historical review). Ihering (1891), anticipating Wegener's theory of continental drift, argued for an ancient land connection between South America and Australia, including as evidence the presence of the commensal *Temnocephalus chiliensis* with closely related freshwater crustaceans found in New Zealand and South America. Ihering (1902) reinforced this belief in an ancient New Zealand/South America connection with interpretations of the distribution and association of Acanthocephala with fish, birds and mammals. This contention of an affinity between Australia and South America was buttressed by Metcalf (1929, 1940) who reported the presence of opalinid protozoans in leptodactylid frogs from South America and Australia. Metcalf (1920, 1923, 1929) proposed that parasites could be used to explain the geographical distribution and migration routes of animals and plants. Other researchers also used parasites to investigate the biogeography of hosts (Johnston 1913, 1914, Harrison 1926, 1928) and Manter (1940, 1955, 1963, 1966) extended it to include the Atlantic and Pacific distributions of marine fishes and their digenean parasites. Manter (1955) did not suggest continental drift to explain biotic similarities between New Zealand and the northern hemisphere suggesting instead that dispersal was assisted by oceanic currents.

Weaknesses in the early use of parasites to infer host evolution and biogeography was the assumption of coevolution and the non-independence of methods used to construct host and parasite phylogenies and distributions (Klassen 1992a). Furthermore, because the emphasis was on the host, parasite geographic distribution was rarely studied. Exceptions include parasites causing disease in humans where interest centered on delimiting zones of infection rather than biogeography of the parasite and studies of Dogiel and coworkers (Dogiel *et al.* 1958) who conducted large scale and wide spread parasite surveys of fishes. A result of these efforts by Dogiel *et al.* (1958) was the recognition of different biogeographic regions based solely on parasite distributions (Shulman 1958). A major advance in parasite biogeography came when Brooks (1977) applied the phylogenetic methodology of Hennig (1966) to develop phylogenetic hypotheses for parasites and compare these to host phylogenies to interpret coevolutionary and biogeographic relationships for both. This pioneering work resulted in investigations relating to the origins of parasite-host associations and parasite geographic distributions (Brooks & McLennan 1991, 1993, Hoberg 1992, Choudhury & Dick in review, Carney & Dick in review).

Parasite data have also been used to test existing biogeographical theories. For example, Dritschilo *et al.* (1975) substituted hosts for islands in applying the concepts of island biogeography (MacArthur & Wilson 1967) to study mites of North American cricetid rodents. Dritschilo *et al.* (1975)

concluded that hosts with greater geographic distribution had more parasites and this was consistent with the predictions of island biogeography theory. The substitution of hosts for islands and their conclusions were criticized by Kuris & Blaustein (1977). Other applications of this theory to hosts and parasites reached inconsistent and conflicting interpretations. For example, Kennedy (1978) found that island populations of Arctic charr (*Salvelinus alpinus*) had more parasites than mainland populations. By contrast, Coneely & McCarthy (1984) and Marcogliese & Cone (1991) reported that hosts on islands had fewer parasites than those hosts on the nearest mainland. As Marcogliese (1992) has pointed out, this reduction in parasite species may reflect an inability of the colonizing host to carry its parasites with it, and have less to do with island biogeographic theory as it relates to parasites. Price & Clancy (1983) found that increased host range was significantly correlated with increased numbers of parasite species for fishes in the British Isles, a pattern also noted by Gregory (1990) for parasites of waterfowl. However, Guégan & Kennedy (1993) reanalyzed the data used by Price & Clancy (1983) and found that increased parasite richness was correlated with the amount of time the host species had been in the area. Host size has also been used as a predictor of parasite community richness (e.g. Guégan *et al.* 1992) but Poulin (1995) has demonstrated that when host phylogeny is taken into account the correlation can disappear.

PRESENT CONTRIBUTIONS

The two areas of research in parasite biogeography are 1) historical biogeography which seeks explanations for the evolutionary origins for parasite geographic distributions and host associations based on vicariance, dispersal, coevolution and host-switching as mechansims to explain patterns and 2) ecological biogeography which seeks explanations for how parasite geographic distributions and host associations are maintained based on contemporary biotic and abiotic influences.

Parasite historical biogeography requires the development of hypotheses of phylogeny for the taxa of interest based in phylogenetic systematics (Hennig 1966, Wiley 1981). Generally, the major approaches used in parasite biogeography include comparison of parasite and host clades and comparison of clades with regions (e.g. Hoberg 1986, Hoberg & Adams 1992, Carney & Dick in review). Methods include Brooks Parsimony Analysis or BPA (e.g. Brooks 1981, 1990, Wiley 1988), component compatibility (e.g. Page 1988, 1989, 1990, 1994a, b) and panbiogeography of Croizat (1958) (e.g. Brooks 1977, 1979, Choudhury & Dick in review). These methods differ in their underlying assumptions and the way in which rare and widespread taxa are treated. Clearly, the choice of methods is far from settled (Morrone & Carpenter 1994, Morrone & Crisci 1995).

One of the key pioneering studies dealing with parasite biogeography is by Brooks *et al.* (1981). The stingray family Potamotrygonidae is entirely freshwater and is present only in the major Atlantic drainages of South America. Brooks *et al.* (1981) developed hypotheses of phylogeny for several parasite taxa inhabiting these stingray hosts to infer the origins of Potamotrygonidae, consistent with the previous history of using parasites to infer host biology (Metcalf 1920, 1929, Manter 1966). These parasite phylogenetic hypotheses were the basis for the hypothesis that the freshwater stingrays of South America were derived from Pacific Ocean ancestors. This conclusion has been criticised on both empirical grounds and for the use of parasites to infer host ancestry (Straney 1982, Caira 1990, 1994, Lovejoy 1997). Nevertheless, the research initiated by Brooks *et al.* (1981), (and subsequent studies [Brooks & McLennan 1991, 1993 and references therein]) into the parasites of South American freshwater stingrays is important as it contributed significantly to the development and refinement of methodologies for biogeographic analysis (Brooks 1981, 1992, Wiley 1988) and stimulated further studies on the evolution and biogeography of stingrays (Lovejoy 1996). Interestingly, Brooks, who has long argued that the evolution of parasites can be and should be studied independent of the host (Brooks & McLennan 1991, 1993) has made studying the evolution of the stingray host dependent on the parasites.

Parasite historical biogeography also has generated interesting zoogeographic hypotheses such as in the studies of Hoberg (1986, 1992) and Hoberg & Adams (1992). The Arctic usually is considered to be a region of extinction, particularly in association with Pleistocene glaciation (Pielou 1979, Vrba 1985) but this idea was questioned by Hoberg (1986, 1992) and Hoberg & Adams (1992) who examined the historical biogeography of cestode parasites of seabirds and pinnipeds in the Arctic. Hoberg (1986, 1992) and Hoberg & Adams (1992) incorporated hypotheses of phylogeny for 2 different groups of cestode parasites with existing host phylogenies and contemporary distributions, and knowledge of past geologic events, to arrive at a novel marine refugium hypothesis. During periods of maximum glaciation host ranges contracted resulting in vicariant isolation of host and parasite populations leading to parasite speciation and host-specificity. During interstadials, host ranges expanded and the intermingling of host species with shared feeding habits made colonization of new hosts possible, depending on the degree of host-specificity attained by the parasites during stadials. These investigations indicate that the Arctic was an area of biological diversification, at least for some species. Some other studies incorporating a historical approach to parasite biogeography include Adamson & Richardson (1989), Brooks & O'Grady (1989), Brooks & McLennan (1991, 1993 and references therein), Platt (1992) and Choudhury & Dick (1996, 1998). Because parasite historical biogeography requires the incorporation of host data, results from these studies give new insights into the evolution of biotic associations and provide novel hypotheses explaining the origins for animal distributions.

Ecological parasite biogeography deals with what affects and maintains present day distributions and abundances and searches for patterns in abundance and distribution of parasites both geographically and among host taxa. Abiotic factors such as temperature and aquatic characteristics influence parasite distributions. For example, Lawler & Scott (1954) showed that the southern limit of tapeworms in the genus *Triaenophorus* correlates with temperature and not with the potential hosts that are more widely distributed. Chubb (1970) and Esch (1971) concluded that lake trophic status was significant in determining the distribution of parasite species, a conclusion not supported by Carney & Dick (2000). Biotic factors such as host type, physiology, ecology and behaviour have also been used to explain patterns of parasite distribution and abundance (Kennedy *et al.* 1986, Aho & Bush 1993, Carney & Dick 2000). Some other studies incorporating a distributional or ecological approach to parasite biogeography include Khalil (1971), Rohde (1978, 1982, 1986), Price & Clancy (1983), Cone & Wiles (1985), Bailey & Margolis (1987), Gregory (1990), Guégan & Lambert (1990), Byrnes & Rohde (1992), Klassen (1992b), Marcogliese (1992, 1995), Esch & Fernandez (1993 and references therein), Kennedy (1993) and Marcogliese & Cone (1993).

Only recently have studies combined ecological and historical approaches to explain the present distributions of parasites among hosts and across geography. Choudhury & Dick (in review) studying historical and ecological associations between sturgeons and their parasites demonstrated that sturgeon parasites had predictable associations (considered by Choudhury & Dick to be host-specific but at different taxonomic levels) some of which could be explained by coevolution. However, there was a substantial group of parasite species that were characterized by host switching and affinities to geographic regions distinct from the geographic distributions of the sturgeon hosts. Similarly, Carney & Dick (1999, 2000 in review) investigated the parasites of perch using both ecological and historical approaches. Carney & Dick (1999) demonstrated that, in spite of extensive parasite lists with essentially no specific parasites, there were very few parasite species shared between the North American yellow perch (*Perca flavescens*) and its sister species the Eurasian perch (*Perca fluviatilis*). Carney & Dick (in review) demonstrated that the historical basis for the association between yellow perch and its parasites was a consequence of extensive host switching from other sympatric hosts (e.g. Centrarchidae, Ictaluridae). The basis of this host switching was postulated to be ecological overlap, in particular shared feeding habits (Carney & Dick 2000 in review). Studies of Choudhury & Dick (2000, in review) and Carney & Dick (2000 in review) were able to propose time frames for some of the associations based on the geological record.

ECOLOGICAL BIOGEOGRAPHY OF HOLARCTIC FISHES

Parasites of Holarctic fishes, especially freshwater fishes, provide a useful model system to study ecological parasite biogeography that can subsequently be used to frame questions relating to the historical biogeography of these organisms. There are many monophyletic groups of fishes in this region that are endemic to their continents, are widespread among continents, and have strict host-specific parasites, predictable associations and non host-specific parasites. Furthermore, the geological history of the Holarctic region is well known and involves episodes of continental connection and fragmentation and has comparatively recent periods of glaciation.

Carney & Dick (1999) investigated the association of parasite species with *Perca flavescens* in North America and *Perca fluviatilis* in Eurasia and demonstrated the parasite communities of each host were comprised of taxonomically distinct but ecologically similar parasites. These hosts are sister taxa but are found on different continents. Despite the close phylogenetic relationship of these hosts they share few parasites species and those that are shared were uncommon. The majority of parasites common to perch hosts in North America and Eurasia are those that either mature in birds (e.g. *Diplostomum* spp.), or in other hosts (e.g. *Triaenophorus nodulosus* matures in pike; *Diphyllobothrium* spp. matures in mammals). For these parasites, the percid fish host is not the final host within which the parasite matures. Enteric parasites that mature in the percid host show a more general pattern of association with the continent instead of the host. Enteric parasites with Holarctic distributions with many host taxa are not strictly host-specific, but may have predictable associations at higher host taxonomic ranks. For example, *Crepidostomum farionis* is reported from many Holarctic host species but is predictably associated

Table I. – Parasites recorded from species of *Stizostedion* from North America and Eurasia.

Parasite Species	*Stizostedion vitreum* North America	*Stizostedion canadense* North America	*Stizostedion lucioperca* Eurasia	*Stizostedion volgensis* Eurasia
ECTOPARASITES				
MONOGENEA				
Ancyrocephalus paradoxus			x	x
Cleidodiscus sp.	x			
Dactylogyrus extensus	x			
Gyrodactylus longiradix			x	
Gyrodactylus luciopercae			x	
Gyrodactylus mizellei	x	x		
Gyrodactylus schmidti	x			
Tetraonchus sp.	x			
Urocleidus aculeatus	x	x		
CRUSTACEA				
Ancyrocephalus paradoxus				
Achtheres percarum			x	x
Argulus appendiculosus	x	x		
Argulus biramosus	x	x		
Argulus canadensis	x			
Argulus coregoni			x	
Argulus foliaceus			x	
Argulus stizostethii	x	x		
Argulus versicolor	x			
Caligus lacustris			x	
Ergasilus caeruleus	x	x		
Ergasilus centrarchidarum	x	x		
Ergasilus confusus	x			
Ergasilus luciopercarum	x	x		
Ergasilus sieboldi			x	x
Ergasilus versicolor	x			
Lernaea cruciata		x		
Lernaea cyprinacea	x			
Lernaea esocina			x	
Lernaea variabilis		x		
Lernaeocera sp.		x		
ENTERIC PARASITES				
DIGENEA				
Allocreadium lobatum	x			
Aponurus tschugunovi			x	
Azygia acuminata	x			
Azygia angusticauda	x			
Azygia bulbosa	x			
Azygia longa	x			
Azygia lucii			x	x
Brachyphallus crenatus (marine)			x	
Bucephaloides ozakii	x			
Bucephalus markewitschi			x	
Bucephalus polymorphus			x	
Bucephalus pusilla		x		
Bunocotyle cingulata			x	
Bunodera luciopercae	x		x	x
Bunodera sacculata	x			
Centrovarium lobotes	x	x		
Crepidostomum cooperi	x			
Crowcrocaecum skrjabini			x	
Phyllodistomum angulatum			x	x
Phyllodistomum folium			x	
Phyllodistomum pseudofolium			x	
Phyllodistomum superbum	x	x		
Prosorhynchoides pusilla	x	x		
Ptychogonimus fontanus	x			
Rhipidocotyle illense			x	
Rhipidocotyle papillosa	x			
Sanguinicola occidentalis	x			

Parasite Species	*Stizostedion vitreum* North America	*Stizostedion canadense* North America	*Stizostedion lucioperca* Eurasia	*Stizostedion volgensis* Eurasia
CESTODA				
Biacetabulum macrocephalum	x			
Bothriocephalus claviceps	x	x		
Bothriocephalus cuspidatus	x	x		
Bothriocephalus scorpii (marine)			x	
Caryophyllaeus laticeps			x	
Cyathocephalus truncatus			x	
Eubothrium sp.	x			
Proteocephalus cernuae			x	x
Proteocephalus fluviatilis	x			
Proteocephalus luciopercae	x	x		
Proteocephalus macrocephalus	x			
Proteocephalus pearsei	x			
Proteocephalus percae			x	x
Proteocephalus pinguis	x			
Proteocephalus stizostethi	x	x		
Proteocephalus torulosus			x	
Triaenophorus stizostedionis	x			
NEMATODA				
Camallanus ancylodirus	x			
Camallanus lacustris	x		x	x
Camallanus oxycephalus	x	x		
Camallanus truncatus			x	x
Capillaria catenata	x			
Coitocaecum skrjabini			x	
Contracaecum bidentatum			x	
Contracaecum spiculigerum	x			
Contracaecum squalii			x	
Cucullanus cirratus			x	
Cystidicola lepisostei	x			
Dichelyne cotylophora	x			
Hysterothylacium brachyurum	x	x		
Philometra abdominalis			x	
Philometra cylindracea	x			
Raphidascaris acus	x			
Rhabdochona canadensis	x			
Spinitectus carolini	x			
Spinitectus gracilis	x			
ACANTHOCEPHALA				
Acanthocephalus anguillae			x	
Acanthocephalus lucii			x	x
Echinorhynchus salmonis	x	x	x	
Leptorhynchoides thecatus	x			
Neoechinorhynchus crassus	x			
Neoechinorhynchus cylindratus	x	x		
Neoechinorhynchus rutilii	x		x	
Neoechinorhynchus strigosus	x			
Neoechinorhynchus tenellus	x	x		
Pomphorhynchus bulbocolli	x			
Pomphorhynchus laevis			x	
Pseudoechinorhynchus clavula			x	x
LARVAL PARASITES				
DIGENEA				
Apophallus americanus	x			
Apophallus muhlingi			x	
Apophallus venustus	x			
Ascocotyle coleostoma			x	
Bucephalus polymorphus	x		x	x
Bunocotyle cingulata			x	
Centrovarium lobotes	x	x		
Clinostomum complanatum	x	x	x	
Crassiphiala bulboglossa	x			

Parasite Species	*Stizostedion vitreum* North America	*Stizostedion canadense* North America	*Stizostedion lucioperca* Eurasia	*Stizostedion volgensis* Eurasia
Diplostomum sp.	x	x	x	
Diplostomum clavatum			x	
Diplostomum scheuringi	x			
Diplostomum spathaceum	x		x	x
Hysteromorpha trilobata			x	x
Ichthyocotylurus communis	x	x		
Ichthyocotylurus pileatus	x		x	x
Ichthyocotylurus platycephalus			x	
Metagonimus yokogawai			x	x
Neascus sp.	x	x		
Ornithodiplostomum ptychocheilus	x			
Paracoenogonimus ovatus			x	
Posthodiplostomum angulatum			x	
Posthodiplostomum minimum	x			
Ptychogonimus fontanus	x			
Rhipidocotyle illense			x	
Rossicotrema donicum			x	x
Tetracotyle communis	x	x		
Tetracotyle diminuta	x			
Tetracotyle percae-fluviatilis			x	
Tetracotyle variegatus			x	
Tylodelphys clavata			x	
Uvulifer ambloplitis	x			
CESTODA				
Diphyllobothrium latum	x	x	x	
Ligula intestinalis			x	
Proteocephalus ambloplitis	x	x		
Triaenophorus crassus	x			
Triaenophorus nodulosus	x	x	x	
NEMATODA				
Agamospirura sp.			x	
Anisakis sp. (marine)			x	
Contracaecum spiculigerum	x			
Contracaecum squalii			x	
Desmidocercella sp.			x	
Eustrongylides sp.	x	x		
Eustrongylides excisus			x	x
Eustrongylides mergorum				x
Eustrongylides tubifex	x			
Gnathostoma sp.			x	
Hysterothylacium brachyurum	x	x		
Philometra cylindracea	x			
Philometra obturans			x	
Porrocaecum reticulatum			x	
Raphidascaris acus	x		x	
ACANTHOCEPHALA				
Corynosoma semerme (marine)			x	
Corynosoma strumosum (marine)			x	
Leptorhynchoides thecatus	x			
Pomphorhynchus bulbocolli	x			

Sources: Barysheva & Bauer 1957, Bykhovskaya-Pavlovskaya *et al.* 1962, Craig 1987, Dontsov & Markov 1981, Hoffman 1999, Margolis & Arthur 1979, McDonald & Margolis 1995, Molnar 1980, Ozcelik & Deufel 1989, Pojmanska *et al.* 1980, Rokicki 1975, Scholz & Hanzelova 1998, Waluga & Wlasow 1988.

Table II. – Number of shared parasites recorded from species of *Stizostedion* from North America and Eurasia. # of species indicates how many parasite species have been reported from these hosts.

	S. vitreum	*S. canadense*	*S. lucioperca*	*S. volgensis*
	North America	North America	Eurasia	Eurasia
# species	95	35	74	20
S. vitreum North America	X	32	12	5
S. canadense North America		X	3	0
S. lucioperca Eurasia			X	18
S. volgensis Eurasia				X

with Salmoniformes. Similarly, *Bunodera luciopercae* is reported from percids, and other hosts, throughout the Holarctic. The nematode *Camallanus oxycephalus* and the cestodes *Bothriocephalus claviceps* and *Cyathocephalus truncatus* are reported from *Stizostedion* and *Perca* on both continents. There are 2 different Acanthocephala species, *Echinorhynchus salmonis* and *Neoechinorhynchus rutili*, reported from *Perca* hosts on both continents and neither show predictable associations to any hosts other than freshwater fish. These observations confirm that an absence of strict host-specificity contributes to an increased geographic distribution of a parasite species.

In a subsequent investigation Carney & Dick (2000) emphasized the importance of ecology reporting that distributions and abundance of parasites in yellow perch (*Perca flavescens*) were based in the feeding habits of the host, enhanced by the presence of other hosts, particularly birds, and constrained by the local biotic conditions. Carney & Dick (in review) then examined the historical ecology of the parasites of yellow perch in North America and found that they were best characterized by host-switching from other endemic North American fish species with shared feeding habits. This is consistent with the basis for host switching postulated by Hoberg (1986, 1992) and Hoberg & Adams (1992) for arctic seabirds and pinnipeds and suggests that ecological factors are dominant in colonization of new host species.

Some might argue that the results of Carney & Dick (1999, 2000) from parasites of yellow perch will not hold at higher taxonomic levels. For this reason, we considered the parasites from fish species in the family Percidae that often associate with the genus *Perca* given that taxa within this group are closely related and widely distributed in North America and Eurasia. Parasites associated with species of *Stizostedion*, also in the family Percidae (Table I), show a similar pattern to perch with their parasites having greater affinity with the continent rather than with congeners across continents (Table II). For example, *Stizostedion canadense* in North America shares only 4 parasite species with *Stizostedion luciopercae* and no parasite species with *Stizostedion volgensis*, both European species. By contrast, the 2 North American species, *S. vitreum* and *S. canadense*, share 33 parasite species and the 2 European *Stizostedion* species have 17 parasite species in common (Table II). The parasites shared by *Stizostedion* spp. in Eurasia and North America are not strictly host-specific (e.g. *Camallanus lacustris*, *E. salmonis*, and *N. rutili*) or are larval species that have fish-eating birds as final hosts and use a wide variety of fish species as intermediate host. These three species are an example of parasites with transcontinental distributions which have no predictable host association except for freshwater fish in the northern hemisphere.

Even though parasites of percids revealed that their parasitofauna was more affected by continent and ecology than by host phylogenetic association it was not clear if this pattern was present for other Holarctic species of fish. Interestingly, when we compared several additional fish groups from North America and Eurasia a similar pattern emerges. For example, the parasites of *Esox lucius* in North America and Eurasia shared comparatively few parasite species from the different continents (Dick & Choudhury, 1996). Those that are shared included 2 parasites predictably associated with *Esox* spp. (*Triaenophorus* spp. and *Raphidascaris acus*), larval forms that mature in fish-eating birds (e.g. Diplostomum spp.), and those with no evidence of host predictability (*E. salmonis*, *N. rutili*). In the case of the pike parasites there are predictable associations at the generic level that play a role in shaping the parasite communites on both continents.

Comparisons of parasites from species of *Coregonus* in North America and Eurasia show similar patterns to those reported for the percids (Table III). The Arctic cisco, *Coregonus autumnalis*, oc-

Table III. – Helminth and arthropod parasites recorded from *Coregonus* and *Thymallus* species from North America and Eurasia.

Parasite Species	*Coregonus autumnalis* Eurasia	*Coregonus autumnalis* North Amerca	*Coregonus nasus* Eurasia	*Coregonus nasus* North Amerca	*Coregonus sardinella* Eurasia	*Coregonus sardinella* North Amerca	*Thymallus arcticus* Eurasia	*Thymallus arcticus* North Amerca
ECTOPARASITES								
MONOGENEA								
Discocotyle sagittata			x	x	x			x
Tetraonchus alaskensis	x						x	x
Tetraonchus borealis							x	x
Tetraonchus grumosus	x	x						
Tetraonchus rauschi							x	x
Tetraonchus sp.				x				
CRUSTACEA								
Achtheres coregonorum	x				x			
Achtheres extensus	x		x		x			
Achtheres strigatus					x			
Argulus coregoni								x
Argulus foliaceus					x			
Coregonicola orientalis	x		x					
Coregonicola producta					x			
Ergasilus nerkae								x
Ergasilus sieboldi					x			
Salmincola carpionis							x	
Salmincola corpulentis	x		x	x				
Salmincola edwardsi								x
Salmincola extensus				x				
Salmincola thymalli							x	x
ENTERIC PARASITES								
DIGENEA								
Allocreadium isoporum								x
Ariella baikalensis								x
Azygia lucii							x	
Brachyphallus crenatus				x				
Clinostomum complanatum								x
Crepidostomum farionis	x		x	x	x	x	x	x
Crepidostomum isostomum								x
Crepidostomum metoecus								x
Derogenes varicus (marine)							x	
Lecithaster sp. (marine)	x				x			
Phyllodistomum conostomum	x		x		x			
Phyllodistomum folium							x	
Phyllodistomum megalorchis							x	
Phyllodistomum simile							x	
Sphaerostoma bramae							x	
CESTODA								
Bothrimonas sturionis (marine)	x	x			x			
Cyathocephalus truncatus	x		x	x	x	x	x	
Eubothrium crassum	x				x			
Eubothrium salvelini								x
Proteocephalus arcticus						x		
Proteocephalus exiguus	x		x		x	x		
Proteocephalus longicollis	x						x	
Proteocephalus thymalli							x	
Proteocephalus tumidocollis								x
NEMATODA								
Ascarophis skrjabini (marine)							x	
Ascarophis sp. (marine)				x				
Camallanus lacustris	x		x					
Coregonema sibirica	x		x		x		x	
Cystidicola farionis	x			x			x	x
Hysterothylacium aduncum (marine)						x		
Philometra ovata					x			
Rhabdochona cascadilla								x
Rhabdochona denudata							x	
Sterliadochona ephemeridarum								x
Truttaedacnitis truttae							x	

ACANTHOCEPHALA								
Acanthocephalus anguillae							x	
Echinorhynchus clavula							x	
Echinorhynchus gadi					x	x		
Echinorhynchus leidyi		x				x		
Echinorhynchus salmonis		x	x	x	x	x	x	x
Neoechinorhynchus rutili					x	x	x	x
Neoechinorhynchus tumidus		x	x	x	x			
Neoechinorhynchus venustus				x				
Neoechinorhynchus sp.				x				
Pomphorhynchus laevis							x	
LARVAL PARASITES								
DIGENEA								
Clinostomum complanatum								x
Diplostomum baeri						x		
Diplostomum scheuringi								x
Diplostomum spathaceum			x		x			x
Diplostomum sp.				x				
Ichthyocotylurus erraticus			x		x			x
Tetracotyle intermedia			x		x			
CESTODA								
Diphyllobothrium dendriticum		x				x	x	
Diphyllobothrium ditremum						x		
Diphyllobothrium latum		x					x	
Diphyllobothrium minus	x				x			
Diphyllobothrium norvegicum							x	
Diphyllobothrium strictum	x		x		x			x
Diphyllobothrium sp.				x				
Proteocephalus sp.				x				
Triaenophorus crassus	x		x	x	x	x		x
Triaenophorus nodulosus								x
NEMATODA								
Raphidascaris acus			x	x				

Sources: Bykhovskaya-Pavlovskaya *et al.* 1962, Choudhury & Dick 1977, Hoffman 1999, Margolis & Arthur 1979, McDonald & Margolis 1995, Pronin *et al.* 1979, Pugachev 1984, Scholz and Hanzelova 1998, Shostak *et al.* 1986, Valtonen 1980, van Maren 1979.

curs in North America and Eurasia. One of two parasite species that occurs in this host species from both North America and Eurasia (Table IV) is *Bothrimonus sturionis*. It is a marine parasite and it is acquired by this anadromous host species on both continents likely as a consequence of ecological overlap while in the marine environment. By contrast, *Coregonus autmunalis* shares 11 parasite species with *C. nasus* and 12 species with *C. sardinella* if only Eurasian populations are considered (Table IV). Similarly, *C. sardinella* from Eurasia also shares more parasites with Eurasian congeners than with *Coregonus sardinella* from North America. Parasites with little evidence of strict host-specificity and wide distribution include the cestode *Cyathocephalus truncatus* and the acanthocephalans *Echinorhynchus salmonis* and *Neoechinorhynchus rutili* and *N. tumidus*.

Larval parasites seem to be less important in contributing to intercontinental similarity in the parasite fauna of *Coregonus* hosts, unlike the *Stizostedion* example. *Triaenophorus* spp. predictably are shared among coregonid hosts from Eurasia and North America and are occasionally reported from lake trout. These parasites mature in pike, a host that is widespread in the Holarctic reagion. This is a good example of the importance of past and current ecological associations on parasite distributions.

The digenean *Crepidostomum farionis* also is commonly reported from *Coregonus* host species and provides an example of the distinction between strict host-specificity and predictable associations at higher host taxonomic ranks. *Crepidostomum farionis* is a parasite associated with hosts belonging in the Salmoniformes and it is at this taxonomic level that the association is predictable. Given that Salmoniforme species have a natural Holarctic distribution, and that *C. farionis* is associated with Salmoniformes, it should not be surprising that this parasite has a Holarctic distribution.

Coregonus nasus is an exception to this pattern of hosts sharing more parasites with congeners from the same continent than with conspecifics from another continent. *Coregonus nasus* from North America shares more parasites with *C. nasus* from Eurasia than with other *Coregonus* species from North America. By contrast, *C. nasus* from Eurasia shares more parasites with Eurasian *C. sardinella* than with *C. nasus* from North America. There is a paucity of reports on parasites from *C. nasus* throughout its distribution, particularly from

Table IV. – Number of shared parasites recorded from species of *Coregonus* and *Thymallus* from North America and Eurasia.
# of species indicates how many parasite species have been reported from these hosts.

	Coregonus autumnalis Eurasia	*Coregonus autumnalis* North Amerca	*Coregonus nasus* Eurasia	*Coregonus nasus* North Amerca	*Coregonus sardinella* Eurasia	*Coregonus sardinella* North Amerca	*Thymallus arcticus* Eurasia	*Thymallus arcticus* North Amerca
# species	20	7	18	18	26	13	28	30
Coregonus autumnalis Eurasia	X	2	11	4	13	4	6	4
Coregonus autumnalis North Amerca		X	2	2	3	3	3	2
Coregonus nasus Eurasia			X	8	14	5	4	9
Coregonus nasus North Amerca				X	6	4	4	7
Coregonus sardinella Eurasia					X	7	5	9
Coregonus sardinella North Amerca						X	5	4
Thymallus arcticus Eurasia							X	8
Thymallus arcticus North Amerca								X

North America, and more information may reveal greater similarity of the parasitofauna with different host species from the same continent than with the same host species from different continents.

The grayling, *Thymallus arcticus*, presents an interesting case as it appears to share more parasites with Eurasian species of *Coregonus* than with either North American species of *Coregonus* or Eurasian *Thymallus arcticus*. By contrast, Eurasian *Thymallus arcticus* share fewer species with any of the above hosts and have more shared parasites with *Thymallus arcticus* from North America (Table IV). If parasite data really do provide insights into host origins then these data would support the testable hypothesis that *Thymallus arcticus* has a North American origin.

Even if anadromous species of *Oncorhynchus* are compared there is a greater similarity among the parasites shared among congeneric hosts from the same continent than conspecific hosts from different continents (Table V, VI). For example, Asian *O. gorbuscha* shares more parasite species with other Eurasian *Oncorhynchus* species than with *Oncorhynchus gorbuscha* from North America (Table VI). When the parasites reported from other species of *Oncorhynchus* are compared, it is clearly seen that these hosts share more parasites with different host species from the same continent than they do with the same host species from a different continent. Similarly, sticklebacks of different genera on the same continent share more parasites than do hosts of the same species from different continents (Tables VII, VIII). This pattern is not unique to a single host family (Percidae, Esocidae, Salmonidae, Coregonidae, Gasterosteidae), nor is it unique to strictly freshwater (Percidae, Esocidae) or anadromous (Salmonidae, Coregonidae) fish hosts.

If the distribution of parasite species among host species is host-driven, as is often believed, then hosts of the same species should share more parasites despite being on different continents, than with different hosts on the same continent. Our data do not support this contention, at least for Holarctic freshwater fish hosts. Parasites of these hosts have a greater affinity for the continent than with the host species. This indicates that the parasites have a unique evolutionary history that, although inevitably tied to a host, is based more on geography than on the host's identity, at least at the level of species. The degree of predictability of the association between a parasite and its host(s) is relevant to this assertion. It may be that the relevant association between parasite and host in these examples is not at the level of host species, but at a higher taxonomic level. For example, parasite genera may associate with host genera or family. As a consequence, parasite species belonging in widespread genera may then have continental affinities that may not track the intercontinental distributions of the individual host species, but would track intercontinental distributions of a host family (e.g. Choudhury & Dick, in review). This would produce the pattern of the same host species on different continents having different parasite species. Furthermore, it suggests that for these systems, parasites are speciating as a consequence of geological vicariance despite the apparent lack of host speciation, and that sharing of parasites among hosts species is based on ecological considerations and enhances the geographic distribution of the parasite. Byrnes & Rohde (1992) reported a similar pattern for ectoparasites of marine fishes in Australian waters. The monogenean parasites had a wider geographic distribution than any of the individual host species, and the distribution of the parasites

Table V. – Helminth and arthropod parasites recorded from 5 species of *Oncorhynchus* from North America and Eurasia.

Parasite Species	*O. gorbuscha* Eurasia	*O. gorbuscha* North America	*O. keta* Eurasia	*O. keta* North America	*O. kisutch* Eurasia	*O. kisutch* North America	*O. nerka* Eurasia	*O. nerka* North America	*O. tshawytscha* Eurasia	*O. tshawytscha* North America
ECTOPARASITES										
MONOGENEA										
Gyrodactyloides strelkovi							x	x		
Gyrodactylus nerkae	x						x			
Gyrodactylus salmonis						x				
Laminiscus strelkovi						x				
Octomacrum lanceatum										x
Tetraonchus alaskensis					x	x	x			
ARTHROPODA										
Argulus coregoni	x		x							
Argulus pugettensis (marine)						x				
Bomolochus cuneatus (marine)		x								
Bomolochus sp. (marine)										x
Caligus clemensi (marine)		x		x		x		x		x
Elthusa vulgaris (marine)										x
Ergasilus briani			x							
Ergasilus nerkae						x		x		x
Ergasilus turgidus (marine)								x		
Lepeophtheirus salmonis (marine)	x		x	x		x		x		x
Lernaeopoda fulculata								x		
Rocinela maculata (marine)						x				
Salmincola beani										x
Salmincola californiensis		x		x		x		x		x
Salmincola carpionis								x		
Salmincola edwardsi								x		
Salmincola falculata	x						x	x	x	x
Salmincola lata			x							
Salmincola salmonea			x							
DIGENEA										
Brachyphallus crenatus (marine)	x	x	x	x	x	x	x	x	x	x
Copiastes katuwo (marine)						x		x		x
Copiastes filiferum (marine)		x						x		
Crepidostomum farionis	x			x		x		x		x
Derogenes aspina (marine)						x				
Derogenes varicus (marine)	x						x			x
Genolinea anura (marine)	x									
Genolinea laticauda (marine)								x		
Genolinea oncorhynchi (marine)		x								x
Hemiurus appendiculatus (marine)	x									
Hemiurus levinseni (marine)	x	x		x		x		x		
Isoparorchis hypselobagri			x							
Lampritrema miescheri (marine)										
Lampritrema nipponicum (marine)		x						x		
Lecithaster gibbosus (marine)	x	x	x	x	x	x	x	x		x
Lecithaster salmonis (marine)								x		
Lecithaster stellatus (marine)	x		x							
Lecithophyllum botryophorum (marine)		x		x				x		
Parahemiurus merus (marine)	x	x				x		x		
Phyllodistomum umblae								x		
Plagioporus shawi						x		x		x
Podocotyle shawi (marine)								x		
Pronoprymna petrowi (marine)		x								
Pronoprymna umblae (marine)								x		
Prosorhynchoides gracilescens (marine)	x		x			x				x
Prosorhynchoides basargini (marine)		x						x		
Tubulovesicula lindberghi (marine)	x	x	x	x		x		x		

Parasite Species	O. gorbuscha Eurasia	O. gorbuscha North America	O. keta Eurasia	O. keta North America	O. kisutch Eurasia	O. kisutch North America	O. nerka Eurasia	O. nerka North America	O. tshawytscha Eurasia	O. tshawytscha North America
CESTODA										
Bothriocephalus sp.						x				x
Bothriomonas sturionis (marine)		x						x		
Cyathocephalus truncatus					x	x	x	x		
Diplocotyle olrikii		x						x		
Eubothrium crassum	x		x		x	x	x		x	x
Eubothrium salvelini		x		x		x		x		x
Nybelinia lingualis (marine)	x		x							
Nybelinia surmincola (marine)	x	x	x		x			x	x	
Pelichnibothrium speciosum (marine)	x		x	x	x		x	x	x	
Phyllobothrium ketae (marine)				x						
Phyllobothrium salmonis (marine)										x
Proteocephalus ambloplitis						x				
Proteocephalus arcticus						x		x		
Proteocephalus exiguus			x	x				x		
Proteocephalus laruei								x		
Proteocephalus parallacticus		x				x				x
Proteocephalus salmonidicola						x		x		
NEMATODA										
Ascarophis sebastodis (marine)						x		x		
Ascarophis skrjabini (marine)	x									
Ascarophis sp. (marine)		x								
Capillaria bakeri						x				
Contracaecum spiculigerum								x		x
Cucullanus laevis	x									
Cystidicola farionis					x			x		
Cystidicola tenuissima		x								
Hysterothylacium aduncum (marine)	x	x		x	x	x	x	x	x	
Philonema agubernaculum								x		
Philonema oncorhynchi			x	x		x	x	x		x
Pseudocapillaria salvelini						x				
Rhabdochona canadense		x				x				
Rhabdochona kisutchi						x		x		
Rhabdochona sp.										x
Salvelinema salmonicola						x		x		
Salvilinema walkeri						x				x
Spinitectus gracilis		x				x				x
Truttaedacnitis truttae								x		
ACANTHOCEPHALA										
Acanthocephalus aculeatus								x		
Acanthocephalus opsariichthydis							x			
Echinorhynchus gadi (marine)	x	x	x	x	x	x	x	x		x
Neoechinorhynchus rutili				x	x	x	x	x		
Neoechinorhynchus salmonis						x		x		x
Neoechinorhynchus tumidus		x				x				x
Neoechinorhynchus sp.				x						
Paracanthocephalus tenuirostrus	x									
Rhadinorhynchus trachuri (marine)		x				x		x		x
LARVAL PARASITES										
DIGENEA										
Apophallus donicus						x				
Diplostomum baeri								x		x
Diplostomum spathaceum								x		x
Galactosomum phalacrocoracis (marine)		x		x						
Isoparorchis hypselobagri			x							
Nanophyetus salmincola				x		x				x
Neascus sp.				x		x				x
Tetracotyle intermedia								x		
Tetracotyle sp.				x				x		

Parasite Species	*O. gorbuscha* Eurasia	*O. gorbuscha* North America	*O. keta* Eurasia	*O. keta* North America	*O. kisutch* Eurasia	*O. kisutch* North America	*O. nerka* Eurasia	*O. nerka* North America	*O. tshawytscha* Eurasia	*O. tshawytscha* North America
CESTODA										
Diphyllobothrium sp.		x						x		x
Diphyllobothrium dendriticum						x		x		
Diphyllobothrium ditremum						x		x		x
Diphyllobothrium latum								x		
Diphyllobothrium sp.		x		x						
Diplocotyle olrikii		x						x		
Gilquinia squali (marine)										x
Hepatoxylon trichiuri (marine)			x							
Nybelinia lingualis (marine)	x		x							
Nybelinia surminicola (marine)	x	x	x		x			x	x	
Paradilepis simoni (marine)								x		
Pelichnibothrium speciosum (marine)	x		x	x	x		x	x	x	
Phyllobothrium caudatum (marine)		x		x		x		x		
Phyllobothrium salmonis (marine)										x
Scolex pleuronectis (marine)	x	x	x	x	x		x	x		
Triaenophorus crassus				x				x		
NEMATODA										
Anisakis simplex (marine)	x		x							
Anisakis sp. (marine)		x		x		x		x		
Contracaecum spiculigerum								x		x
Contracaecum sp.				x						
Cucullanus laevis	x									
Eustrongylides sp.						x				
Hysterothylacium aduncum	x				x	x	x		x	
Truttaedacnitis truttae								x		x
ACANTHOCEPHALA										
Bolbosoma caenoforme (marine)	x	x	x				x	x		
Corynosoma semerme (marine)								x		
Corynosoma strumosum (marine)		x						x		
Corynosoma villosum (marine)		x	x					x		

Sources: Bailey *et al.* 1989, Bakke & Bailey 1987, Bykhovskaya-Pavlovskaya *et al.* 1962, Hoffman 1999, Margolis & Arthur 1979, McDonald & Margolis 1995, Nagasawa *et al.* 1983, Scholz & Hanzelova 1998, Whitaker 1985.

did not conform to biogeographic regions that were recognized based on free-living organisms. It may be that the parasites have unique biogeographical patterns that are distinct from those of individual host species, despite the requirement of a host for the survival of the parasite. Phylogenetic analyses of the parasites and hosts would contribute to resolving these possible hypotheses. Alternatively, the association may be dependent on the host ecology. Hosts belonging to the same genera or family may have similar ecologies, in particular with regard to feeding. If this is the case, then the distribution of parasites in Holarctic freshwater fishes may be driven by ecological factors and less by historical phylogenetic factors. This is consistent with the observations of Carney & Dick (in review) for parasites of yellow perch (*Perca flavescens*) in North America. Carney & Dick (in review) demonstrated that the origin of the association of several parasite species with the perch host was host-switching with other host species due to ecological overlap among the relevant host taxa. This overlap was either sympatry, shared feeding habits, or both. There was little evidence for a phylogenetic basis for the associations between parasite species and *Perca flavescens*, even for the host-specific monogenean *Urocleidus adspectus*. Regardless, historical considerations need to be investigated to demonstrate the ecological basis for these observations.

Many studies of parasite biogeography using a historical phylogenetic approach examine hosts with many apparently strictly host-specific parasites (e.g. Brooks, 1992). This may bias estimates of coevolution (but see Hoberg 1992) as a source of zoogeographic pattern. Carney & Dick (1999, 2000, in review) have demonstrated there are recoverable patterns across geographic and taxonomic scale for parasite-host assemblages that are not characterized by strict host-specificity. Furthermore, the data reported here for other species of

Table VI. – Number of shared parasites recorded from species of *Oncorhynchus* from North America and Eurasia. # of species indicates how many parasite species have been reported from these hosts.

	O. gorbuscha Eurasia	*O. gorbuscha* North America	*O. keta* Eurasia	*O. keta* North America	*O. kisutch* Eurasia	*O. kisutch* North America	*O. nerka* Eurasia	*O. nerka* North America	*O. tshawytscha* Eurasia	*O. tshawytscha* North America
# species	32	38	27	29	15	51	19	73	9	45
O. gorbuscha Eurasia	x	11	18	11	11	12	13	16	9	10
O. gorbuscha North America		x	9	14	7	16	6	26	4	12
O. keta Eurasia			x	10	9	8	8	14	6	8
O. keta North America				x	8	17	9	22	4	12
O. kisutch Eurasia					x	9	12	12	8	4
O. kisutch North America						x	10	28	4	26
O. nerka Eurasia							x	13	7	7
O. nerka North America								x	7	24
O. tshawytscha Eurasia									x	3
O. tshawytscha North America										x

percids in North America and Eurasia, indicates that parasites of these hosts seem to originate with their geographic location rather than the percid hosts. This observation is supported by Carney & Dick (in review) who demonstrated that 3 of the parasites species predictably associated with yellow perch had their evolutionary origins in North America and the extant association with yellow perch resulted from host switching. The idea of geographic affinity rather than host affinity for parasites of North American freshwater fishes is supported by Amin (1985, 1986) who considered the biogeography of 3 species of North American *Acanthocephalus* by combining a cladistic analysis of the parasites with geologic information and data regarding contemporary parasite geographic distributions. Amin (1985, 1986) proposed that these parasites were derived from an ancestor associated with the Mississippi basin prior to Wisconsinian glaciation. Retreat of the glaciers permitted widespread dispersal of one species, *Acanthocephalus dirus*, producing 3 extant parasite populations with a large number of suitable hosts. The other 2 species have restricted geographic distributions, and a small number of suitable hosts. One species, *Acanthocephalus tahlequahensis*, is postulated to have its geographic distribution limited by the distribution of its host (Amin, 1985). The other species, *A. alabamensis*, may be a consequence of vicariance associated with the Mobile River basin. The large number of suitable hosts and wide geographic distribution for *Acanthocephalus dirus*, and few suitable hosts and narrow geographic distribution for *A. tahlequahensis* and *A. alabamensis* are consistent with our earlier observation that strict host-specificity may constrain parasite geographic distribution (Price 1980).

In summary, parasite biogeography is historically rich and has contributed to our understanding of biogeographic patterns. Data from Holarctic fish and parasite communities are providing the basis for some interesting insights into factors past and present which have and will continue to shape fish and parasite communities. Undoubtedly strict host-specificity and predictable associations at higher taxonomic levels contribute to defining and predicting biogeographic patterns. However, in future studies we must clearly define at what level of parasite-host association we are working i.e., individual species, genus, etc. The predictable associations of the parasites and hosts we have discussed at the highest taxonomic levels are undoubtedly ancient given their widespread Holarctic distributions. It is apparent that we can not fully explain host-parasite associations, at whatever level, only on the basis of cospeciation or phylogenies of the parasites and/or of the hosts, but that ecological associations and sympatric hosts with shared feeding patterns are also important. Moreover the paucity of shared parasite species across continents by closely related fish hosts for several major fish groups is additional support for strong ecological and geographical influences. The application of these ideas is evidence of the important contributions that host parasite systems make to the study of biogeography.

Table VII. – Helminth and arthropod parasites recorded from *Gasterosteus aculeatus* and *Pungitius pungitius* from North America and Eurasia.

Parasite Species	*Gasterosteus aculeatus* Eurasia	*Gasterosteus aculeatus* North America	*Pungitius pungitius* Eurasia	*Pungitius pungitius* North America
ECTOPARASITES				
MONOGENEA				
Diplozoon paradoxum		x		
Gyrodactylus aculeati		x		
Gyrodactylus alexandri		x		
Gyrodactylus arcuatus	x	x		
Gyrodactylus armatus			x	
Gyrodactylus avalonia		x		x
Gyrodactylus bychowskyi	x		x	
Gyrodactylus canadensis		x		x
Gyrodactylus elegans	x	x	x	
Gyrodactylus eucaliae				x
Gyrodactylus lairdi		x		
Gyrodactylus memorialis		x		
Gyrodactylus rarus	x	x	x	
Gyrodactylus pungitii	x		x	
Gyrodactylus stephanus				x
Gyrodactylus terranovae		x		
CRUSTACEA				
Argulus alosae (marine)		x		
Argulus foliaceus	x		x	
Argulus funduli				x
Argulus stizostethi		x		
Bomolochus cuneatus (marine)		x		
Caligus clemensi (marine)		x		
Caligus lacustris (marine)	x	x		
Elthusa californica (marine)		x		
Ergasilus auritus	x	x		x
Ergasilus manicatus		x		
Ergasilus turgidus		x		
Holobomolochus sp. (marine)		x		
Lepeophtheirus sp. (marine)		x		
Lernaea cyprinacea	x			
Thersitina gasterostei (brackish)	x	x	x	x
ENTERIC PARASITES				
DIGENEA				
Azygia lucii			x	
Brachyphallus crenatus	x	x		x
Bunodera eucaliae		x		
Bunodera luciopercae	x	x	x	x
Bunodera mediovitellata		x		x
Crepidostomum cooperi		x		
Crepidostomum farionis		x		
Derogenes varicus (marine)		x		x
Hemiurus appendiculatus (marine)				x
Hemiurus communis (marine)	x			
Lecithaster gibbosus (marine)	x			
Lecithaster salmonis (marine)		x		
Parahemiurus merus (marine)		x		
Peracreadium gasterostei (marine)	x			
Phyllodistomum folium	x	x		
Phyllodistomum pungitii			x	
Phyllodistomum sp.			x	
Podocotyle atomon (marine)	x	x		x
Podocotyle reflexa (marine)	x			
Sphaerostoma bramae			x	

Parasite Species	*Gasterosteus aculeatus* Eurasia	*Gasterosteus aculeatus* North America	*Pungitius pungitius* Eurasia	*Pungitius pungitius* North America
CESTODA				
Bothriocephalus claviceps	x	x		
Bothriocephalus scorpii (marine)	x		x	
Cyathocephalus truncatus		x		
Eubothrium crassum	x			
Eubothrium salvelini				x
Proteocephalus ambiguus			x	
Proteocephalus cernuae	x	x		
Proteocephalus exiguus				x
Proteocephalus filicollis	x	x	x	x
Proteocephalus longicollis	x			
Proteocephalus percae	x		x	
Proteocephalus pugetensis		x		
NEMATODA				
Ascarophis morrhuae (marine)		x		
Camallanus lacustris	x		x	
Camallanus truncatus	x			
Cystidicola farionis	x	x		
Hysterothylacium aduncum (marine)	x			
Philonema agubernaculum		x		
ACANTHOCEPHALA				
Acanthocephalus clavula	x			
Acanthocephalus dirus				x
Acanthocephalus lucii	x		x	
Echinorhynchus clavula	x		x	
Echinorhynchus lateralis		x		x
Echinorhynchus salmonis	x	x	x	x
Leptorhynchoides thecatus				x
Neoechinorhynchus cristatus			x	x
Neoechinorhynchus pungitius				x
Neoechinorhynchus rutili	x	x	x	x
Paracanthocephalus curtus			x	
Pomphorhynchus bulbocolli		x		x
Pomphorhynchus laevis	x			x
LARVAL PARASITES				
DIGENEA				
Apatemon gracilis		x		x
Apophallus brevis		x		
Bucephalus polymorphus		x	x	
Cotylurus pileatus	x		x	
Cryptocotyle concavum	x			
Diplostomum gasterostei	x	x		
Diplostomum pungitii		x		
Diplostomum spathaceum	x	x	x	x
Hemiurus appendiculatus (marine)				x
Holostephanus lukei	x			
Ichthyocotylurus erraticus				x
Nanophyetus salmincola		x		
Neascus sp.		x		
Posthodiplostomum cuticola	x		x	
Posthodiplostomum minimum		x		
Pygidiopsis ardea	x			
Tetracotyle sp.		x		x
Tylodelphys clavata	x		x	

Parasite Species	*Gasterosteus aculeatus* Eurasia	*Gasterosteus aculeatus* North America	*Pungitius pungitius* Eurasia	*Pungitius pungitius* North America
CESTODA				
Diphyllobothrium dendriticum	x	x	x	x
Diphyllobothrium ditremum		x		x
Diphyllobothrium norvegicum	x		x	
Diphyllobothrium sp.		x		x
Ligula intestinalis				
Schistocephalus gasterostei	x		x	
Schistocephalus pungitii	x		x	x
Schistocephalus solidus	x	x	x	x
Triaenophorus nodulosus	x		x	x
NEMATODA				
Anisakis sp. (marine)		x		
Contracaecum sp.		x		x
Cosmocephalus obvelatus		x		x
Eustrongylides sp.		x		x
Hysterothylacium aduncum (marine)	x			
Paracuaria adunca		x		x
Pseudoterranova decipiens (marine)		x		x
Raphidascaris acus	x	x	x	x
ACANTHOCEPHALA				
Corynosoma semerme (marine)	x			
Corynosoma strumosum (marine)	x		x	

Sources: Barysheva & Bauer 1957, Bykhovskaya-Pavlovskaya *et al.* 1962, Chubb 1970, Dartnall & Wackey 1979, Donoghue 1988, Harris 1998, Hoffman 1999, Kennedy 1974, Koie 1992, 1995, Marcogliese 1992, 1995, Margolis & Arthur 1979, McDonald & Margolis 1995, Orlovskaya *et al.* 1995, Rokicki 1975, Scholz & Hanzelova 1998, Soleng & Bakke 1998, Sysoev *et al.* 1992, Wootten 1973.

Table VIII. – Number of shared parasites recorded from *Gasterosteus aculeatus* and *Pungitius pungitius* from North America and Eurasia.
# of species indicates how many parasite species have been reported from these hosts.

	Gasterosteus aculeatus Eurasia	*Gasterosteus aculeatus* North America	*Pungitius pungitius* Eurasia	*Pungitius pungitius* North America
# parasite species	53	67	35	43
Gasterosteus aculeatus Eurasia	X	21	25	15
Gasterosteus aculeatus North America		X	12	27
Pungitius pungitius Eurasia			X	12
Pungitius pungitius North America				X

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MOLECULAR PHYLOGENETIC ANALYSIS OF 28S rDNA SUPPORTS A GONDWANAN ORIGIN FOR AUSTRALASIAN HYRIIDAE (MOLLUSCA: BIVALVIA: UNIONOIDA)

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GONDWANALAND
NEW ZEALAND
HYRIIDAE
28S rDNA
MOLECULAR PHYLOGENETICS
VICARIANCE
BIOGEOGRAPHY

ABSTRACT. – The Hyriidae (Mollusca: Bivalvia: Unionoida) have a disjunct distribution, occurring on South America, Australia, and New Zealand. Most previous macroevolutionary studies of the Hyriidae pre-dated widespread acceptance of both continental drift and phylogenetic systematics. For this study, we applied molecular phylogenetic techniques to test the hypothesis that the observed disjunction of Australasian hyriids across the Tasman Sea is due to the disintegration of Gondwanaland (>80 million years ago). We sequenced a fragment of 28S rDNA for representative hyriid Velesunionini (Australia), Hyridellini (Australia and New Zealand), and Hyriinae (South America) and for outgroups belonging to the unionoid families Margaritiferidae and Unionidae. The topology of the single 28S tree [i.e., (Margaritiferidae, Unionidae, (Velesunionini, (Hyridellini, Hyriinae)))] recovered by both maximum parsimony and maximum likelihood did not support a monophyletic Australasian clade, and the branch lengths were consistent with Mesozoic vicariance. We also acquired COI sequences for the Australian subset of mussels to corroborate the 28S branch lengths. Our results suggest that (1) the Hyriidae pre-date the break up of Gondwanaland and (2) the New Zealand Hyridellini are relics rather than colonizers. Alternative long-distance dispersal hypotheses are discussed in the context of our results, historical geology, and mussel life history.

GONDWANA
NOUVELLE ZÉLANDE
HYRIIDAE
28S rADN
PHYLOGÉNIE MOLÉCULAIRE
VICARIANCE
BIOGÉOGRAPHIE

RÉSUMÉ.– Les Hyriidae (Mollusca: Bivalvia: Unionoida) ont une répartition disjointe en Amérique du Sud, en Australie et en Nouvelle Zélande. La plupart des études passées sur la macroévolution datent d'avant l'acceptation générale de la dérive des continents et de la systématique phylogénétique. Dans cette étude nous avons appliqué des techniques de phylogénie moléculaire pour tester l'hypothèse selon laquelle la répartition disjointe des Hyriidés d'Australie et de Nouvelle-Zélande séparés par la mer tasmanienne est due à la désintégration du Gondwana il y a environ 80 millions d'années. Nous avons séquencé un fragment du 28 S rADN de représentants des Hyriidés Velesunionini (Australie), Hyridellini (Australie et Nouvelle Zélande) et des Hyriinae (Amérique du Sud), et pour les outgroups, des Unionoidés Margaritiferidae et Unionidae. La topologie du seul arbre 28 S [(Margaritiferidae, Unionidae, (Velesunionini, (Hyridellini, Hyriinae)))] obtenue par la parcimonie du maximum de vraisemblance et de « Maximum Likelihood » ne conforte pas la monophylie du clade australasien, et la longueur des branches est en faveur d'une vicariance datant du Mésozoïque. Nous avons également traité les séquences COI pour le sous-ensemble des Moules d'Australie afin de corroborer les longueurs du branchement 28S. Nos résultats suggèrent (1) que les Hyriidae existaient avant la désintégration du Gondwana et (2) que les Hyridellini de Nouvelle Zélande sont des relictes plutôt que des colonisateurs. Les hypothèses alternatives de dispersion à grande distance sont discutées dans le contexte de nos résultats, de la géologie historique et des traits d'histoire de vie des Moules.

INTRODUCTION

Freshwater mussels (Unionoida) are a globally distributed, ancient group of strictly continental bivalves. Their diversity and unique parasitic larvae have attracted a great deal of ecological study, especially from a conservation perspective [see Kat (1984) and Watters (1994) and references cited

Table I. - Taxonomy and Distribution of the Hyriidae. The nomenclature of the Hyriidae has been updated to standardize the views of Iredale (1934), McMichael & Hiscock (1958), Parodiz & Bonetto (1963), and Graf (2000): the Australian family and subfamilies have been demoted to a subfamily with four tribes. † Indicates presence on Tasmania. Distribution data references: [1]McMichael & Hiscock (1958), [2]Walker *et al.* (2000), [3]McMichael (1956), [4]McMichael (1958), [5]Parodiz &Bonetto (1963).

Taxon	New Guinea[1,2,3]	Australia[1,2]	New Zealand[1,2,4]	South America[5]
Hyridellinae				
Hyridellini	X	X†	X	
Cucumerunionini	X	X	X	
Velesunionini	X	X†		
Lortiellini		X		
Hyriinae				
Hyriini [= Prisodontini]				X
Diplodontini				X
Castaliini				X

therein]. Much of that research was focused on the Nearctic mussel assemblage and, until very recently, has lacked a modern evolutionary context (Graf & Ó Foighil 2000). This is surprising given that the age, distribution, and diversity of the Unionoida provide ample pattern with which to test hypotheses of macroevolutionary processes such as character evolution and biogeography.

Of special interest is the zoogeography of the freshwater mussel families confined to the Southern Hemisphere: Etheriidae, Iridinidae, and Hyriidae (Etherioidea). These mussels are presently restricted to the southern continents, although there is paleontological data suggesting their Mesozoic inhabitance of North America (Henderson 1935, Morris & Williamson 1988). The modern distribution of the Etherioidea led Graf (2000) to speculate about the influence of the disintegration of Gondwanaland on the evolution of those mussels. His morphological cladistic study principally tested the relationships of the Hyriidae, a family found in both South American and Australasian fresh waters. However, it did little to clarify the relationships within the Hyriidae. The object of this paper is to address the evolution and biogeography of Australasian hyriid clades, especially the problem of disjunction of New Zealand freshwater mussels across the Tasman Sea.

Based upon their morphology, there seems little doubt that the Hyriidae is monophyletic (Graf 2000). If this is true, however, their present distribution presents a dramatic disjunction: the Neotropical Hyriinae and the Australasian Hyridellinae (Table I). Unfortunately, nearly all discussion of these families pre-dated both (1) the widespread acceptance of phylogenetic systematics as a scientific means to discover organismal relationships and (2) the recognition of continental drift as a potential mechanism for vicariance. Thus, the narrative of hyriid macroevolution has yet to be formally purged of problematic hypotheses involving waif dispersal or migration of hypothetical "ancestral stocks" across post-Mesozoic "land bridges" (e.g., Ortmann 1921, Modell 1942, McMichael & Hiscock 1958, McMichael & Iredale 1959, Parodiz & Bonetto 1963).

While the Hyriinae is limited to South America, the Hyridellinae presents its own disjunction. The Australian Hyriidae occur on Australia, Tasmania, New Guinea, and the Solomons on the western and northern sides of the Tasman Sea, and New Zealand on the eastern side. Two of the eight genera that inhabit the region occur on New Zealand: *Hyridella menziesi, H. aucklandica,* and *Cucumerunio websteri* (McMichael 1958). The consensus has been that the observed disjunction among the Hyridellinae is due to late Tertiary long-distance dispersal via phoresy upon migratory birds (McMichael 1954, 1958, McMichael & Hiscock 1958) or host fish (Walker *et al.* 2000) from Australia.

Until the relatively recent realization of continental drift (Wegener 1966), trans-oceanic dispersal or migration across "land bridges" would have been the only options available to explain the disjunctions of the Hyriidae (e.g., Darlington 1957). Modern biogeographic theory suggests an alternative. The Hyriidae may have been distributed widely on Mesozoic Gondwanaland, the southern supercontinent composed of what are now South America, Africa, Madagascar, India, Antarctica, Australia, and New Zealand. When that landmass rifted apart, the respective hyriid faunas of South America, Australia, and New Zealand were isolated and have persisted into modern times. A review and chronology of the disintegration of Gondwanaland can be found in Storey (1995: Fig. 1) and Brown & Lomolino (1998: Fig. 6.17). In summary, rifting and sea floor spreading around 160 million years ago (Mya) (Jurassic) split South America and Africa from the rest of Gondwanaland. However, southern South America remained in close proximity to Antarctica into the Tertiary. On the other side of Antarctica around 100 Mya (Cretaceous), Australia began to separate from Antarctica. New Zealand remained locked to both Australia and Antarctica until roughly 90 Mya. Since 80 Mya, New Zealand has been isolated from Australia; and since 60 Mya, the two have been separated by a minimum distance of over 1000 km (Cooper *et al.* 1993). Vicariance hypotheses to explain the distributions of southern continent freshwater mussels have received almost no attention and have gone largely untested (McMichael 1967, Graf 2000, Walker *et al.* 2000).

For this study, we attempted to falsify vicariance as the biogeographic mechanism of hyriid disjunction across the Tasman Sea. From the alternative biogeographic process hypotheses (i.e., dispersal vs. vicariance), we derived predictions of molecular phylogenetic pattern. If the vicariance hypothesis is true, the origin of the genus *Hyridella* must predate the barrier. We predicted that if the New Zealand hyriids achieved their present distribution by vicariance 80 Mya (i.e., the rifting of New Zealand from Australia and Antarctica), then the branch lengths separating New Zealand *Hyridella* spp. from their Australian congeners should be long relative to the internal branch supporting the clade. We presumed that the length of these terminal branches should be of the same order (or longer) than the branch lengths presented by other late Mesozoic freshwater mussel splits. This assumes a reasonably constant rate of molecular evolution, allowing branch length to serve as a loose proxy for time (i.e., long branch . long time, and vice versa). Strictly speaking, clades containing both New Zealand and Australian species should be "leafy" (Salisbury 1999). Short terminal branch lengths for New Zealand hyriids or a"stemmy" topology would reject a vicariance hypothesis and support more recent dispersal.

Several studies have demonstrated the value of nucleic acid characters in recovering the family-level phylogeny of freshwater mussels (Rosenberg *et al.* 1994, 1997, Lydeard *et al.* 1996, Hoeh *et al.* 1998, Graf & Ó Foighil 2000). To test the vicariance hypothesis, we sequenced domain 2 of 28S rDNA from South American, Australian, and New Zealand hyriids, as well as representative northern continent unionoids to serve as outgroups and for branch length comparisons. That gene fragment has been successfully employed to recover late Mesozoic phylogenetic branching patterns among the Bivalvia (Park & Ó Foighil 2000). In our preliminary work, we discovered some hyriids exhibit unexpectedly high levels of intraspecific 28S rDNA variation. As an independent test of branch lengths among the Hyridellinae, we also sequenced a stretch of cytochrome oxidase subunit I (COI) for our Australian and New Zealand species. Our results allow us to reevaluate the story of the evolution of the Hyriidae from a modern biogeographic perspective.

METHODS AND MATERIALS

Acquisition of Nucleotide Sequences: Domain 2 of 28S rDNA sequences were obtained from 11 species of freshwater mussels, including five outgroups (Table II). PCR and cycle-sequencing primers for 28S were D23F and D4RB (Park & Ó Foighil 2000 for PCR and sequencing protocol). We also harvested partial COI sequences from the Australasian Hyridellini and Velesunionini (Table II) using the Folmer *et al.* (1994) primers LCO1490 and HCO2198 as described in Graf & Ó Foighil (2000). All sequences are available through GENBANK (National Center for Biotechnology Information, National Institutes of Health; http://www.ncbi.nlm.nih.gov). Multisequence alignments were compiled and manipulated using Sequence Monkey 2.8.0 (available from http://www.members.tripod.com/sequence_monkey) and Clustal_X (Thompson *et al.* 1994, 1997; available from http://ncbi.nlm.nih.gov) and refined manually where necessary. The matrices (in NEXUS file format) are available from the corresponding author.

Phylogenetic Analysis: Phylogenetic analyses were carried out using PAUP* 4.0b3 (Swofford 1998). Maximum Parsimony (MP) and Maximum Likelihood (ML) optimality criteria were both applied to recover the phylogeny of the Hyriidae. MP searches ran as branch-and-bound with gaps in the alignment treated as missing data. ML searches (heuristic searches, 5 random sequence additions) were performed under the HKY model (Hasegawa *et al.* 1985) with rate heterogeneity. The transition: transversion ratio, proportion of invariable sites, and gamma shape parameter were estimated by maximum likelihood. Analogous searches were performed for both 28S and COI. However, the COI matrix was composed only of the hyridellid taxa from Australia and New Zealand and was intended only as an independent test of the branch lengths obtained from the 28S phylogeny.

To gauge the "robustness" of the topology recovered from the 28S MP analysis, Jackknife resampling analysis (50% character deletion each replication; 1000 replications, heuristic searches, 10 random additions each) was run using PAUP*. Also, Bremer-Decay Index (BDI) values were calculated using TreeRot (available from http://mightyduck.bu.edu/TreeRot), which creates a

Table II. - Taxa from which sequences were acquired. See text for explanation of protocol and references.

		GENBANK Accession #	
Taxon	Locality	28S	COI
Velesunionini			
Velesunio ambigua (n = 2)	New South Wales, Australia	AF305378	AF305371
		AF305379	AF305372
Hyridellini			
Hyridella australis (n = 2)	New South Wales, Australia	AF305373	AF305367
		AF305374	
H. depressa (n = 3)	New South Wales, Australia	AF305375	AF156496
		AF305368	
H. menziesi (n = 2)	North Island, New Zealand	AF305376	AF305369
	South Island, New Zealand	AF305377	AF305370
Diplodontini			
Diplodon chilensis	Chile, South America	AF305380	
Castaliini			
Castalia sp.	Paraguay, South America	AF305381	
outgroups			
Cumberlandia monodonta	Minnesota, USA	AF305382	
Unio pictorum	Austria	AF305383	
Pyganodon grandis	Michigan, USA	AF305384	
Amblema plicata	Michigan, USA	AF305385	
Lampsilis cardium	Michigan, USA	AF305386	

constraint file for PAUP*. For each node, BDI indicates the difference in length of the next shortest tree without that node. The larger the BDI, the better the support (Bremer 1995).

Alternative topologies were constructed using MacClade 3.07 (Maddison & Maddison 1997). These were scored with PAUP* under both parsimony and the likelihood model derived from the ML search. Kishino & Hasegawa (1989) tests were used to gauge the significance of alternative topologies. The likelihood of the optimal 28S phylogeny was also analyzed both with and without a molecular clock enforced, and a Likelihood Ratio Test (LRT) was applied to test the significance between the two models. The molecular clock analysis was rooted between the Hyriidae and (*Cumberlandia*, Unionidae) based on Graf 2000, Graf & Ó Foighil 2000.

Stemminess of the *Hyridella* clade was calculated similar to the methods of Salisbury (1999), where stemminess equals the average internal to terminal branch length ratio. Terminal branch length is the distance from each terminal taxon to the node in question. Stemminess was estimated from the branch lengths assigned by PAUP* (ACCTRAN character-state optimization) on the 28S phylogeny for both MP and ML. Stemminess values greater than 1.0 indicate a "stemmy" topology with short terminals relative to the internal branch; less than 1.0 indicates a "leafy" topology with long terminal branches.

RESULTS

Fourteen partial 28S rDNA sequences acquired from 11 species were aligned into a matrix of 446 characters. On average, outgroup sequences were slightly longer than those of the ingroup. Whereas the five outgroup sequences averaged 430.2±2.2 nucleotides (nt) in length, the median ingroup sequence length was 412 nt, with only *Diplodon* (413 nt), *Castalia* sp. (387), and one of the *Hyridella menziesi* (307) deviating. In the case of *Castalia*, the missing nt were from the ends of the gene fragment; we truncated these due to a high number of ambiguous bases. The *H. menziesi* from the North Island of New Zealand, on the other hand, had a deletion extending from positions 234 to 349 in the

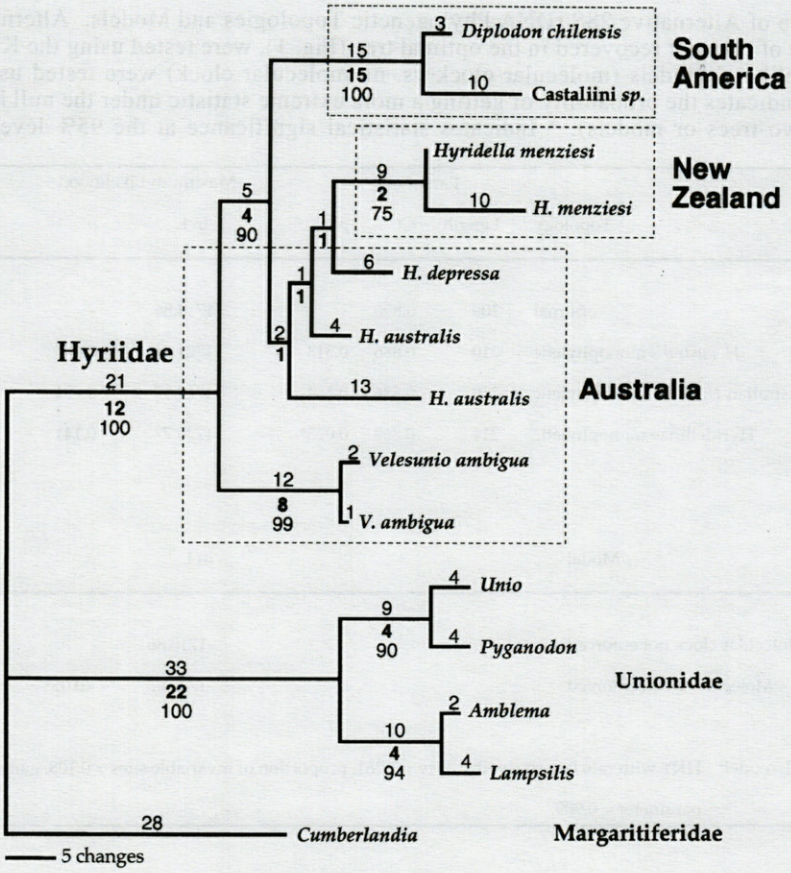

Fig. 1. - 28S rDNA Domain 2 Phylogeny of the Hyriidae. Numbers above the branches are MP branch lengths; those below are BDI (boldface) and Jackknife resampling values also from the MP analysis. The ML analysis recovered the same branching order.

aligned matrix. In addition to sequence length variation, we also uncovered unexpected intraspecific sequence divergence among the Australasian hyriids: *H. australis* (4.4%), *H. menziesi* (3.3%), and *Velesunio ambigua* (0.7%). All three *H. depressa* individuals we studied exhibited the same 28S rDNA sequence.

MP and ML analysis of the 28S data set recovered a single phylogeny (Fig. 1). The *Hyriidae* were recovered as monophyletic. However, contrary to Graf's (2000: Fig. 1) phylogeny, the Australasian "hyridellinae" were paraphyletic relative to the Hyriinae. In addition, *H. australis* was recovered as paraphyletic. Analysis of an alternate topology with a monophyletic *H. australis* was found to be insignificantly different from the optimal tree under both MP and ML, while a monophyletic Hyridellinae was significantly different from the optimal topology only under MP (Table III). The ML model is provided in Table III. The 28S terminal branch lengths among *Hyridella* spp. are long relative to the internal branch supporting that clade (Fig. 1). The Stemminess value for *Hyridella* is decidedly "leafy" regardless of whether it is calculated from MP (0.22) or ML (0.17) branch lengths (Table V). These 28S data are not consistent with a perfect molecular clock (Table III).

Seven COI sequences were obtained from nine individuals representing four species of Australian and New Zealand hyriids (Table II). We aligned these into a matrix of 638 nt that contained no insertion-deletions. Mitochondrial DNA, as we had suspected *a priori*, proved of little value in recovering the phylogeny of the Australian region Hyridellinae, as evidenced by the insignificantly different topologies favored by the two optimality criteria. Results of phylogenetic analyses of COI are presented in Table IV and Fig. 2. However, COI served to put the observed 28S rDNA variation into perspective. For example, whereas the 28S sequences of the two *H. australis* differed by > 4%, the COI haplotypes of these two individual mussels were identical. In addition, the mean uncorrected, interspecific, pairwise distance among the COI haplotypes was 14.0 ± 1.0%. This corresponds to the average divergence between the Pleurobemini and Lampsilini (Graf & Ó Foighil, unpublished), a suspected Cretaceous split (Haas 1969, Lydeard *et al.* 1996).

Table III. - Examination of Alternative 28S rDNA Phylogenetic Topologies and Models. Alternative topologies, constraining the monophyly of taxa not recovered in the optimal tree (Fig. 1), were tested using the Kishino-Hasegawa Test, and the alternative likelihood models (molecular clock vs. no molecular clock) were tested using an LRT. CI is the Consistency Index; *p* indicates the probability of getting a more extreme statistic under the null hypothesis (*i.e.*, no difference between the two trees or models). * Indicates statistical significance at the 95% level.

	Parsimony			Maximum Likelihood	
Topology	Length	CI	*p*	-ln L	*p*
optimal	209	0.890	-	1718.86	-
H. australis monophyletic	210	0.886	0.318	1721.06	0.465
Australian *Hyridella* monophyletic	210	0.886	0.564	1719.57	0.884
Hyridellinae monophyletic	214	0.869	0.025*	1726.77	0.141

Model	ln L	*p*
Molecular clock not enforced	-1718.86	-
Molecular clock enforced	-1736.07	<0.05*

ML model: HKY with rate heterogeneity, ti/tv = 1.261, proportion of invariable sites = 0.108, gamma parameter = 0.909.

Table IV. - Examination of Alternate COI Phylogenetic Topologies. Abbreviations and statistics are as in ML model: HKY with rate heterogeneity, ti/tv = 3,91, proportion of invariable sites = 0.69, gamma parameter = ∞(set to maximum allowable value: 300).

Alternative topologies

MP tree: (*Velesunio*, (*Hyridella menziesi*, (*H. australis*, *H. depressa*)))

ML tree: (*Velesunio*, (*Hyridella australis*, (*H. depressa*, *H. menziesi*)))

	Parsimony			Maximum Likelihood	
Topology	Length	CI	*p*	ln L	*p*
MP	206	0.903	-	-1772.38	0.64
ML	210	0.886	0.37	-1771.40	-

DISCUSSION

The patterns recovered by our phylogenetic analyses cast a new light on the evolution of the Hyriidae (Fig. 1). This is relevant not only to the limited biogeographic problem among *Hyridella* spp. in Australasia, but also to the evolution of the Hyriidae on the southern continents. Our results are consistent with ancient vicariance caused by the rifting of New Zealand from Australia and Antarctica as the mechanism behind the disjunction of freshwater mussels across the Tasman Sea. We find this result incompatible with late Tertiary dispersal as suggested by McMichael 1958, McMichael & Hiscock 1958. Other available evi-

Table V. - MP and ML Stemminess Values for *Hyridella* 28S rDNA. IBL is the internal branch length; TBL is the terminal branch length. See text for an explanation of the stemminess calculation.

	Parsimony			Maximum Likelihood		
species	IBL	TBL	Stemminess	IBL	TBL	Stemminess
(1) *H. menziesi*	2	21	0.10	4.2×10^{-3}	6.5×10^{-2}	0.06
(2) *H. menziesi*	2	11	0.18	4.2×10^{-3}	2.9×10^{-2}	0.15
H. depressa	2	8	0.25	4.2×10^{-3}	2.1×10^{-2}	0.20
(1) *H. australis*	2	13	0.15	4.2×10^{-3}	3.5×10^{-2}	0.12
(2) *H. australis*	2	5	0.40	4.2×10^{-3}	$1.3\mathrm{X}10^{-2}$	0.32
Mean			**0.22±0.12**			**0.17±0.10**

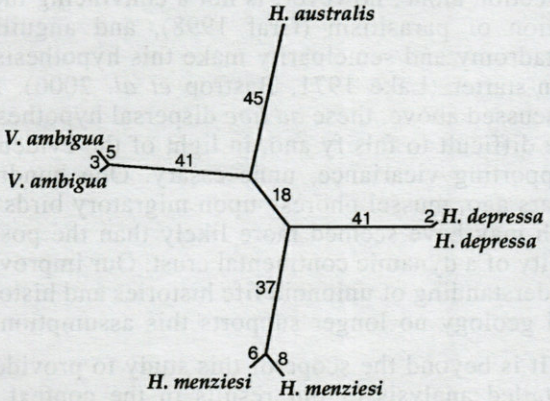

Fig. 2. - COI MP phylogeny of the representative Hyridellinae. Numbers associated with the branches are MP branch lengths. The ML phylogeny has a different topology (Table IV), but the terminal branch lengths are of a similar magnitude relative to the internal branch.

dence, inconsistent with the dispersal model, is reviewed below.

Most systematists of the Hyriidae have considered the Hyridellinae of Australasia to be a "well-defined unit" (McMichael & Hiscock 1958: 496). An ancestral hyriid invaded the region from southeastern Asia (Iredale 1934, McMichael & Hiscock 1958) or South America via Antarctica (Parodiz & Bonetto 1963), and the present endemic diversity resulted from speciation on the isolated continent. This model predicts that the Hyridellinae are monophyletic and that the ancestor of the clade was limited to Australasia. This was supported by Graf's (2000) morphological analysis of the Etherioidea.

However, the results of our molecular phylogenetic analyses lead us to reject this model. Fig. 1 shows that the Australasian "hyridellinae" are paraphyletic relative to the South American Hyriinae and that this result is robust. From a vicariance perspective, this topology suggests that hyriids pre-date the disintegration of Gondwanaland and that they were widespread on that supercontinent. The present endemism of the two Australasian tribes represented in our analysis, Velesunionini and Hyridellini, is due to persistence rather than cladogenesis on an isolated continent. Ortmann's (1921), also Modell (1942) "land bridge" scenario is also consistent with our phylogenetic results: the Hyriidae arose on Australia and spread via Antarctica to South America.

McMichael (1954, 1958), McMichael & Hiscock (1958) and McMichael & Hiredale (1959) argued for freshwater mussel phoresy upon migratory birds as the mechanism of dispersal to New Zealand from Australia. Based on the conchological similarity of the New Zealand mussel species to those of modern Australia, he (1958: 430) argued for "fairly recent" dispersal, but did not elaborate on the timing beyond Tertiary. More recently, Walker *et al.* (2000) have also allowed for trans-oceanic dispersal of hyriids upon their host fish. Our results, however, are not consistent with these models, at least as far as *H. menziesi* is concerned.

The 28S phylogeny in Fig. 1 shows a "leafy" *Hyridella* clade. Although this result is complicated by unexpected rapid intraspecific evolution in *H. menziesi* and *H. australis* and by the unconvincing branching order within *Hyridella* (Table III), our COI results corroborate the long 28S branches (Fig. 2). Intraspecific variation in nuclear rDNA is not uncommon but is peculiar under the current paradigm of paralogous sequence homogenization by "concerted evolution" (Hillis & Dixon 1991, Park & Ó Foighil 2000). Our results suggest that perhaps 28S rDNA sequence evolution is mediated by another mechanism in the Hyriidae.

Any correlation between sequence divergence and time would have extremely wide confidence limits (Hillis *et al.* 1996). But with that in mind, it is interesting to note that the observed 28S and COI branch lengths between *H. menziesi* and its Australian congeners generally match or exceed those between mussel taxa suspected of late Mesozoic divergence [*(Unio, Pyganodon)* and *(Amblema, Lampsilis)* in Fig. 1; Graf & Ó Foighil, unpublished]. This is consistent with vicariance due to the break up of Gondwanaland as an explanation for the disjunction of *Hyridella* across the Tasman Sea. In the same vein, these data also suggest that the split between *H. depressa* and *H. australis* dates to a similarly ancient time.

Based upon our results, we reject the hypotheses of late-Tertiary/Quaternary dispersal of freshwater mussels by birds or fish across the Tasman Sea – at least for *Hyridella menziesi*. The philosophical hurdle that must be addressed when applying dispersal hypotheses to problems of disjunction is that dispersal, as a biogeographical mechanism, is generally not testable (Croizat *et al.* 1974, Ball 1976). Succinctly put, for each realized falsifiable prediction supporting a vicariance hypothesis, a consistent *ad hoc* dispersalist scenario can also be concocted. This is not to say that individual dispersal hypotheses can not be rejected. Fortunately, vicariance hypotheses are generally falsifiable. They differ fundamentally from dispersal hypotheses in that they describe a temporally and spatially discrete vicariance event: the formation of a barrier. Dispersal, on the other hand, refers to an essentially infinite series of improbable events spanning the entire history of the barrier. Our molecular phylogenetic results alone are not inconsistent with ancient transoceanic dispersal, but post-Gondwana migration is in conflict with other lines of evidence, namely the fossil record, unionoid life history, and the distributions of other southern continent taxa.

While the reality of continental drift had not yet taken hold by the late 1950s, the theory of past connection between the southern continents, especially based on their shared floras (*e.g.* Hooker 1867), enjoyed wide recognition (Brown & Lomolino 1998). McMichael (1958; McMichael & Hiscock 1958) was correct to predict that, for a vicariance (*i.e.*, land bridge) hypothesis, the common ancestor of the New Zealand and Australian hyridellids must have (1) pre-dated the formation of the Tasman Sea (Cretaceous) and (2) been found on both sides of that barrier (Platnick & Nelson 1978). He was, however, incorrect in his assessment of the available fossil evidence. The terrestrial paleontological record for New Zealand is far from complete (Cooper *et al.* 1993, Daugherty *et al.* 1993), and McMichael's (1958) rejection of continuous mussel occupation of New Zealand since the Mesozoic based on the lack of an uninterrupted transitional series seems unfounded. Ideally, the nearest common ancestor of Australian and New Zealand Hyridella would be identified from the fossil record. In practice, that is unlikely. The bottom line is that there are Mesozoic fossil hyriids on New Zealand, including at least one tantalizingly hyridelline specimen (McMichael 1957). While inconclusive, this is still consistent with the vicariance hypothesis.

Among the most damning evidence against long-distance avian dispersal of freshwater mussels is that it has never been observed, it is purely hypothetical. Contrary to historical anecdotes (*e.g.*, Cotton 1934), all available evidence suggests that freshwater mussels are dispersed only via their host fish (Johnson 1970, Graf 1997, 1998). It has been suggested by Walker *et al.* (2000) that *H. menziesi* might have reached New Zealand via *Anguilla*, which the mussel is known to infect (Hine 1978). Infection alone, however, is not a convincing indication of parasitism (Graf 1998), and anguillid catadromy and semelparity make this hypothesis a non-starter (Lake 1971, Bastrop *et al.* 2000). As discussed above, these *ad hoc* dispersal hypotheses are difficult to falsify and, in light of the evidence supporting vicariance, unnecessary. One hundred years ago, mussel phoresy upon migratory birds or fish may have seemed more likely than the possibility of a dynamic continental crust. Our improved understanding of unionoid life histories and historical geology no longer supports this assumption.

It is beyond the scope of this study to provide a detailed analysis of our results in the context of vicariant distributions among other New Zealand taxa (*e.g.*, Platnick & Nelson 1978, Rosen 1978, Craw 1985). Suffice it to say that New Zealand is home to more than a few Gondwanan "relics" – taxa incapable of trans-oceanic dispersal like frogs *(Leiopelma)*, tuataras *(Sphenodon)*, onycophorans *(Peripatus)*, beeches *(Nothofagus)*, *etc.* [reviewed in Cooper *et al.* (1993), Daugherty *et al.* (1993), and Humphries & Parenti (1986)]. *Hyridella* should be added to that list.

Based on our molecular phylogenetic analyses, we failed to reject the hypothesis that vicariance due to the break up of Gondwanaland was the biogeographic mechanism of hyriid disjunction across the Tasman Sea. Taken together, the results of our molecular phylogenetic analyses and our review of the data for and against long-distance dispersal provide a compelling case for vicariance, and, at the same time, demonstrate that there really is no data in favor of the long-distance dispersal model. However, our study was based on only a single clade: *Hyridella menziesi* on New Zealand and a limited sample of its congeners on Australia. Further testing is necessary, especially with regard to the generality of our conclusions to the other two New Zealand freshwater mussels, *H. aucklandica* and *Cucumerunio websteri*.

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REVERSALS AS BRANCH SUPPORT IN BIOGEOGRAPHICAL PARSIMONY ANALYSIS

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HISTORICAL BIOGEOGRAPHY
PARSIMONY
REVERSALS
BROOKS PARSIMONY ANALYSIS
PARSIMONY ANALYSIS OF ENDEMICITY
MATRIX REPRESENTATION

ABSTRACT. – When Brooks Parsimony Analysis (BPA) or Parsimony Analysis of Endemicity (PAE) is performed under Wagner Parsimony, some branches in the resulting resolved area cladogram(s), may be supported by reversals, interpreted as extinctions. Such support is meaningless, so one may perform the analysis with irreversible characters. This, in turn, will increase the number of independent forward character changes on the resolved area cladogram(s) which can also be problematical in BPA, but not in PAE.

BIOGÉOGRAPHIE HISTORIQUE
PARCIMONIE
RÉVERSIONS
ANALYSE DE PARCIMONIE DE BROOKS
ANALYSE DE PARCIMONIE DE L'ENDÉMICITÉ
MATRICE

RÉSUMÉ. – La méthode de "Brooks Parsimony Analysis (BPA") ou celle de "Parsimony Analysis of Endemicity (PAE)", avec la parcimonie de Wagner, peuvent aboutir à des branches de cladogramme(s) résolu(s) des aires résultantes, dues à des réversions qui sont interprétées comme des extinctions. Ce type de détermination est sans signification, et il vaut mieux réaliser l'analyse avec des caractères irréversibles. Cependant, cette dernière procédure peut augmenter le nombre des changements indépendants des caractères sur le(s) cladogramme(s) résolu(s) des aires, ce qui peut être un problème dans l'analyse de BPA, mais pas dans l'analyse de PAE.

INTRODUCTION

Derivation of area cladograms from distributional and phylogenetic data on taxa of living or fossil organisms has become a major objective of historical biogeography. Among the methods for translating one (or more) taxon-area cladogram(s)/**TAC**(s) into one (or more) resolved area cladogram(s)/**RAC**(s) which have been proposed (for reviews, see Morrone & Carpenter 1994, Morrone & Crisci 1995, Humphries & Parenti 1999), some include parsimony analysis of matrices. Brooks Parsimony Analysis, or BPA (Wiley 1988, Brooks 1990) uses area x (taxa+ancestors) matrices. Parsimony Analysis of Endemicity, or PAE (Rosen 1988, 1992) uses area x taxa matrices without considering phylogeny. In both methods, relationships between areas are deduced from shared "apomorphies" as indicated by the parsimony analysis: areas which come out as "sister groups" in the resulting RAC(s) are supposed to share a history not shared by the other areas in the analysis.

The methods of three-area statements (TAS: Nelson & Ladiges 1991) and paralogy-free subtrees (Nelson & Ladiges 1996) also work by parsimony analysis of matrices, but the matrices are of a more derived nature than simple area x taxa or area x (taxa+ancestors) ones. The present paper is about BPA and PAE exclusively.

In BPA, the TAC is transformed into a matrix in which the areas take the role of taxa, and the taxa and their hypothetical ancestors take the role of characters. Each taxon, and each ancestor (node) is coded as a character for the areas involved; presence is coded as 1, absence as 0. BPA proceeds under "Assumption 0" according to which widespread taxa (i.e., taxa present in more than one of the areas of distribution under consideration) are regarded as valid evidence of area relationships (see discussion in Enghoff 1996). When more than one TAC are involved (in which case the outcome of the analysis is not only one or more RAC(s) but at the same time **(a) general area cladogram(s)** (Morrone & Carpenter 1994, Morrone & Crisci 1995), areas missing from some of the TACs are coded with question marks (Wiley 1988). Under the BPA protocol, the TAC in Fig. 1 transforms into the matrix in Table I. The informative characters in Table I are provided by the widespread taxa and those ancestors which are not scored as present in all areas. It is possible to eliminate the evidence from widespread taxa either by adding the distribution of the sister-group of a widespread taxon to its own distribution (*cf.* Zandee & Roos 1987) or by deleting the

Table I. – Character matrix from the TAC in Fig. 1. Character numbers correspond to taxa 1-5 and hypothetical ancestors 6-9 in Fig. 1. An all-zero outgroup has been added.

Char. no.	12345 6789
OUT	00000 0000
AREA	10000 1001
BREA	10100 1011
CREA	10011 1111
DREA	01001 1111
EREA	00001 0111

Table II. – Occurrence of taxa 1-9 in areas AREA-EREA.

area/taxon	1	2	3	4	5	6	7	8	9
AREA	+	-	-	-	-	+	-	-	+
BREA	+	-	+	-	-	+	-	+	+
CREA	+	-	-	+	+	+	+	+	+
DREA	-	+	-	-	+	+	+	+	+
EREA	-	-	-	-	+	-	+	+	+

character provided by the widespread taxon (*cf.* Kluge 1988). BPA has been used by many biogeographers (e.g., Crisci *et al.* 1991, Pollock 1995, Härlin 1996, van Soest & Hajdu 1997, de Jong 1998, Hugot & Cosson 2000). The last-mentioned authors called their method "Constructing general area cladograms by matrix representation with parsimony" but as applied by Hugot and Cosson (2000), this method is identical to BPA. Andersson (1996) recommended BPA although it has been criticized by proponents of alternative methods for RAC construction (see references in Morrone & Crisci 1995).

PAE can be seen as an extreme Assumption 0 approach, because with this method *only* the widespread taxa provide evidence of area relationships; cladistic relationships between taxa are ignored. Under the PAE protocol, the distribution table in Table II transforms into the same matrix as the BPA matrix in Table I. PAE is not a cladogram-based method and thus strictly spoken falls outside the scope of cladistic biogeography although it employs cladistic methodology to detect area relationships. PAE has been used by several biogeographers and palaeobiogeographers (e.g. Fortey & Mellish 1992, Morrone 1994a, da Silva & Oren 1996), and a very similar approach has found its way into synecology (Nel *et al.* 1998). A PAE-like method was suggested already by Legendre (1986), and more recently PAE has been recommended for delimiting the "areas of endemism" forming the units in cladistic biogeographical analysis (Morrone 1994b).

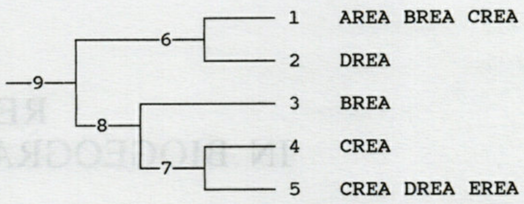

Fig. 1. – Taxon-area cladogram for taxa 1-5 in areas AREA-EREA. Ancestors are numbered 6-9.

The following discussion applies to both BPA and PAE. For parsimony analysis, an all-zero outgroup is added to the matrix, corresponding to a hypothetical area where the organisms in question do not occur at all. A non-zero root has been used by some authors, e.g van Welzen (1989) and Härlin (1996), but this "subspecies" of BPA is not considered here. To derive resolved are cladograms from the matrix, authors have routinely employed the simplest parsimony criterion, Wagner parsimony, in which characters are free to change back and forth with equal probabilities. Characters in biogeographical matrices are usually binary (but see Mayden 1988), issues regarding ordered characters are therefore not relevant.

HOMOPLASY IN BPA AND PAE

If characters (or, to be more specific: taxa and ancestors) are optimized on a RAC derived using BPA or PAE they may show homoplasy. Some taxa/ancestors may appear more than once on the RAC, and some may show reversals.

Taxa or ancestors appearing several times on the RAC can be interpreted in terms of dispersal (Wiley 1988, Brooks 1990, Page 1990). It should, however, be borne in mind that such interpretations, as far as BPA is concerned, founder on the lack of independence between the characters in the matrix (Page 1987, 1990, see also Mayden 1988): a character derived from an ancestor is not independent from characters derived from that ancestor's descendants. PAE does not suffer from this weakness because the taxa providing the characters can be regarded as independent evidence.

Reversals are interpreted as extinctions in BPA (Wiley 1988, Brooks 1990, Brooks & McLennan 1991, see also Ronquist & Nylin 1990): a taxon may be absent from an area because of extinction, and such an extinction may appear as a reversal on the RAC (but see Mayden 1988: 349-350 for a discussion of "apparent extinctions"). To minimize the number of reversals, Wiley (1988) recommended using DELTRAN optimization of characters.

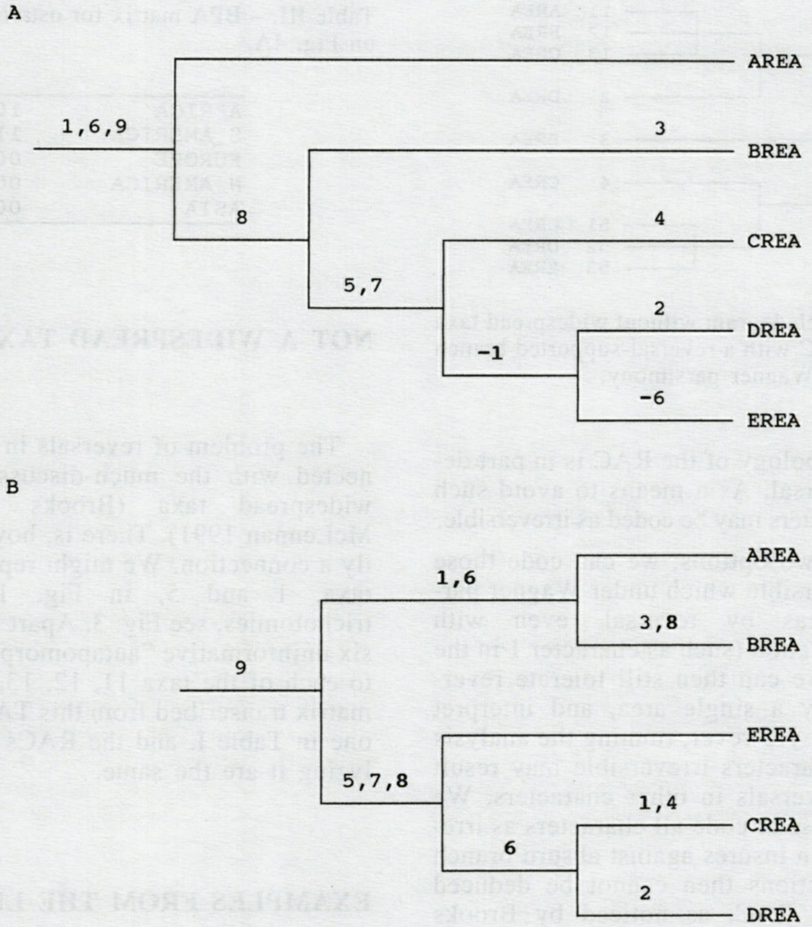

Fig. 2. – Most parsimonious trees (RAC) derived by BPA from the matrix in Table I. Numbers indicate characters supporting the branch below; negative numbers : reversals, bold numbers : characters showing convergence, negative bold number : non-terminal reversal. A, Single most parsimonious RAC found with Wagner parsimony. B, Single most parsimonious RAC found with all characters coded as irreversible.

REVERSALS AS SUPPORT FOR AREA RELATIONSHIPS

If a reversal occurs on a terminal branch of the RAC, it has no influence on RAC topology, irrespective of how it is interpreted *a posteriori*. If it occurs on a non-terminal branch, it may, however, contribute to determining RAC topology. Specifically, a reversal on a non-terminal branch of a RAC supports relationship among the areas united by this branch. This does not make sense because although such a non-terminal reversal might indeed represent extinction, and although one extinction in an "ancestral" area might be considered more parsimonious than independent extinctions in independent areas, the case for discarding independent extinction is much weaker than the opposite: discarding independent immigration in favour of shared ancestral presence in two or more areas: "A shared absence could be local extinction as a result of very different processes due to different causes...." (Nel *et al.* 1998: 175). This problem with BPA and PAE seems not to have been addressed so far but certainly deserves attention. Van Welzen (1989) discarded BPA in favour of component compatibility analysis (Zandee & Roos 1987) because some branches in his BPA-RACs were supported by absences of species or ancestors. Because of the non-zero rooting employed by van Welzen, these absences do, however, not correspond to reversals

Consider the TAC in Fig. 1. If the corresponding BPA matrix (which could equally well be a PAE matrix, *cf.* above) is analyzed with Wagner parsimony, e.g., using the branch and bound option of PAUP, version 3.1.1. (Swofford 1993), one tree, or RAC, is obtained (length 11, ci 0.818, ri 0.750), see Fig. 2A.

If we examine the support for the branches of this RAC, we find that the branch uniting areas DREA and EREA is supported only by a reversal in character 1. Areas DREA and EREA thus appear as sister areas only because they *lack* Taxon 1. In

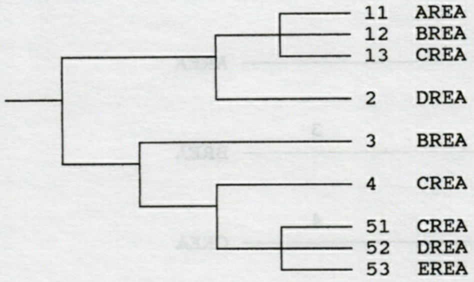

Fig. 3. – Taxon-area cladogram without widespread taxa but resulting in a RAC with a reversal-supported branch when analyzed with Wagner parsimony.

other words, the topology of the RAC is in part determined by a reversal. As a means to avoid such absurd RACs, characters may be coded as irreversible.

There now are two options: we can code those characters as irreversible which under Wagner parsimony unite areas by reversal, even with DELTRAN optimization (such as character 1 in the above example). We can then still tolerate reversals involving only a single area, and interpret them as extinctions. However, running the analysis with only some characters irreversible may result in non-terminal reversals in other characters. We may therefore choose to code all characters as irreversible. This option insures against absurd branch support, but extinctions then cannot be deduced from the resulting RAC, as noticed by Brooks (1990: 20).

Applying the first option to the matrix in Table I, coding only the reverting character 1 as irreversible, PAUP (branch and bound) finds 28 RACs (length 12 ci 0.750 ri 0.625) with a fully unresolved consensus, so in this case, this option is uninformative.

Applying the second option, coding all characters as irreversible, PAUP (branch and bound) finds one RAC (length 12, ci 0.750 ri 0.812), see Fig. 2B. This RAC is quite different from the one found with Wagner parsimony. In the "irreversible" RAC, the clade AREA+BREA is supported by character 1, which is parallelled in CREA, and by character 6, which is parallelled in CREA+DREA, the latter clade being only supported by character 6.

Whereas irreversible coding avoids branch support by reversals, it may thus increase the number of other problematical character optimisations in BPA. These problems with BPA were discussed by Wiley (1988), Brooks (1990), Brooks McLennan (1991) and Page (1990); they do not apply to PAE.

Irreversible coding in BPA has been suggested previously (Wiley 1988, Brooks 1990) but these authors did not specifically refer to the problem posed by branch support by non-terminal reversals in this connection.

Table III. – BPA matrix for ostariophysan fishes, based on Fig. 4A.

AFRICA	101011111
S_AMERICA	110111111
EUROPE	001010111
N_AMERICA	001010111
ASIA	001010111

NOT A WIDESPREAD TAXON PROBLEM

The problem of reversals in BPA has been connected with the much-discussed phenomenon of widespread taxa (Brooks 1990, Brooks & McLennan 1991). There is, however, not necessarily a connection. We might replace the widespread taxa, 1 and 5, in Fig. 1 with unresolved trichotomies, see Fig. 3. Apart from the addition of six uninformative "autapomorphies" corresponding to each of the taxa 11, 12, 13, 51, 52 and 53, the matrix transcribed from this TAC is identical to the one in Table I, and the RACs resulting from analyzing it are the same.

EXAMPLES FROM THE LITERATURE

Mayden (1988) analyzed relationships of North American drainage systems based on distributions and relationships of freshwater fishes. Two of his area clades (clade 15 and 16 in his fig. 5) are each supported by one reversal and one "positive" character (presence of a particular species of fish). Reanalysis with PAUP of Mayden's data matrix for the 15 areas forming his clade 10, using the original data coding and weighting scheme, shows that clade 15 is robust to irreversible coding of all characters but that clade 16 is not. With only the two reverting characters coded as irreversible, neither clade 15 nor 16 appears in the strict consensus. Reversals thus do play a role in determining the tree topology in this case.

Brooks & McLennan (1991: 235-237) reworked the analysis by Novacek and Marshall (1976) of the distribution of ostariophysan freshwater fishes. The TAC for this group (Fig. 4A) transcribes into the matrix in Table III. Brooks & McLennan (1991: fig. 7.31) gave two equally parsimonious RACs for this matrix (length 11 steps), see Fig. 4B-C. However, when analyzed with PAUP using Wagner parsimony two trees of length 10 are found, see Fig. 4D-E (inspection of fig. 7.31 of Brooks & McLennan also shows that one step can be saved by connecting AFRICA and S-AMERICA).

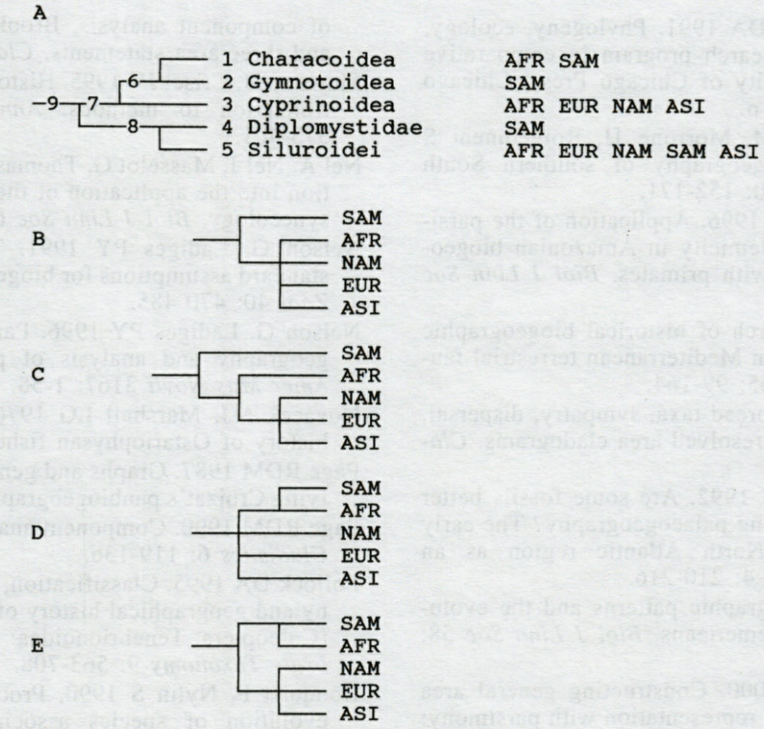

Fig. 4. – The case of the ostariophysan fishes. A, TAC for the group, without the basal lineage (Gonorhynchiformes). From Novacek & Marshall (1976), also reconstructable from fig. 7.30 and table 7.16 in Brooks & McLennan (1991), AFR = Africa, ASI = Asia, EUR = Europe, NAM= North America, SAM = South America. B-C, RACs of length 11 found by Brooks & McLennan (1991). D-E, RACs of length 10 found here.

Brooks & McLennan (1991: fig. 7.31) showed taxon/ancestor optimizations on their two RACs. Although they are not the shortest RACs it is interesting to note that on fig. 7.31b (= Fig. 4E here), the branch connecting N America, Europe and Asia is supported only by two reversals which seems not to bother the authors.

Van Welzen (1989: 121-124) analyzed relationships between 11 West Malesian areas, based on his own cladogram for the sapindacean shrub/tree genus *Guioa* Cav., using BPA and component compatibility analysis (Zandee & Roos 1987). The resulting RAC, which is the same for the two methods, has two branches exclusively supported by reversals (secondary absences). Curiously, van Welzen did not comment on this although branches supported by absences (which do not represent reversals due to the rooting method employed, *cf.* above) in some of van Welzen's other BPA-RACs were used to criticize BPA as a method.

CONCLUDING REMARKS

To the problems which have previously been recognized with BPA, that of reversal-supported branches should be added. Unlike some of the other problems with BPA, reversal-supported branches also causes problems for PAE, and users of the two methods should consider this difficulty.

To add to the confusion, it should be mentioned that Fortey & Mellish (1992), in order to avoid some types of "impossible" optimizations, suggested to code PAE characters as Dollo parsimonious, i.e. to explain *all* homoplasy by reversals. Their rationale for this procedure was to avoid "re-evolving" taxa on their RAC. Of course, Dollo coding will increase the problem of reversals, just as irreversible coding will increase the problem of independent appearances of taxa or ancestors.

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BIOGEOGRAPHY OF SOUTHERN POLAR BRYOZOANS

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ANTARCTICA
BRYOZOANS
POLAR FRONTAL ZONE
ZOOGEOGRAPHY

ABSTRACT. – Despite the central role of Antarctica in the history and dynamics of oceanography in mid to high latitudes of the southern hemisphere there remains a paucity of biogeographic investigation. Substantial monographs over the last century coupled with major recent revisions have removed many obstacles to modern evaluation of many taxa. Bryozoans, being particularly abundant and speciose in the Southern Ocean, have many useful traits for investigating biogeographic patterns in the southern polar region. They fossilise well, transitory morpho-stages between species are brief and most bryozoans have reduced dispersal opportunities due to possession of benthic larvae. Further to previously described broad faunistic patterns we demonstrate that bryozoans show sub-patterns within the Polar Frontal Zone. Four bryozoogeographical zones are recognised in Antarctica waters: East Antarctic seas, West Antarctic seas, the Antarctic Peninsula and the Scotia Arc. We discuss differences between species, genus and family level patterns in three marine orders (of differing geological age) and factors responsible for creation of such distributions.

ANTARCTIQUE
BRYOZOAIRES
ZONE FRONTALE POLAIRE
ZOOGÉOGRAPHIE

RÉSUME. – En dépit du rôle central de l'Antarctique dans l'histoire et la dynamique de l'océanographie des latitudes moyennes à élevées de l'hémisphère sud, les investigations en biogéographie restent rares. Les monographies substancielles des dernières décennies associées aux révisions majeures récentes ont levé divers obstacles dans l'évaluation moderne de nombreux taxons. Les Bryozoaires de l'Océan Sud, particulièrement abondants et riches en espèces, présentent de nombreux traits significatifs pour les investigations sur la distribution biogéographique dans la région polaire du Sud. Ils se fossilisent bien, les morpho-stades ontogénétiques sont brefs et la plupart des Bryozoaires offrent peu d'opportunités à la dispersion en raison de leurs larves benthiques. Au-delà des patterns à grande échelle déjà décrits, nous démontrons que les Bryozoaires présentent des sous-ensembles dans la Zone Frontale Polaire. Quatre zones zoogéographiques du groupe peuvent être reconnues dans les eaux antarctiques: les mers de l'Est et de l'Ouest antarctique, la Péninsule antarctique et l'Arc Scotia. Nous discutons des différences entre patterns au niveau des espèces, des genres et des familles appartenant à trois ordres marins (d'âge géologique différent) et des facteurs responsables d'une telle répartition.

INTRODUCTION

The continent of Antarctica and outlying subantarctic islands are isolated from most of the land and continental shelves of the globe both oceanographically (by the Antarctic Circumpolar Current) and bathymetry (by abyssal depths). Historically however, various plant and animal taxa common to the austral landmasses bear testimony to a period when South America, Africa and the southern Australasian islands formed the supercontinent Gondwana. Various attempts have been made at biogeographic investigations of the southern Austral marine flora (e.g. Clayton 1994) and fauna (Sara *et al.* 1992, Beu *et al.* 1997, Glasby & Alvarez 1999). Essentially, the results of these studies are in agreement with the biogeographic scheme proposed by Hedgpeth (1969) and further elaborated upon by Dell (1972). The basic feature of this scheme is three concentric zones denoting the High Antarctic region around the continent itself, the Antarctic Region extending to the Polar Frontal Zone (PFZ) and the Subantarctic Region north of the PFZ. Within this tripartite division, a series of districts is recognised, largely centred around the various islands groups of the Subantarctic Region. Bryozoans are potentially invaluable for historical zoogeographic comparisons, in view of their limited dispersal through a predominance of benthic short duration larvae abundance. Furthermore the taxon is highly abundant in Southern Ocean waters and is easily accessible due to its pre-dominance in shallow waters. Bryozoans have some interesting biogeographical links between the cool water margins of the southern Atlantic, Pacific and Indian Oceans (see Gordon 1989, Moyano 1996). Within Antarctic waters, bryozoan collections have been made for more than a century but from an early stage (Waters 1904) the diversity of the bryofauna was realised. Although major monographs were undertaken on some bryozoan groups, such as the Cyclostomatida (Borg 1926, 1944), others, such as the Cheilostomatida, were in a state of taxonomic flux. When combined with the level of Southern Ocean exploration, high rate of species discovery and description of new genera and lack of tertiary fossil knowledge it is unsurprising that comprehensive bryozoogeographical analyses have not been undertaken. The last few decades have seen a dramatic explosion of taxonomic and ecological work in southern polar waters for various reasons. Many new Antarctic cheilostomatid bryozoan species and genera have been described, whilst the taxonomic status of many others has been elucidated (see Hayward 1995 and references therein). Early collections from the subantarctic islands were studied by Busk (1884) and further explored by d'Hondt & Redier (1977) and d'Hondt (1984). In neighbouring regions Moyano (1974) and Lopez Gappa (1978) described Chilean and Argentinian species, whilst Hayward & Cook (1979, 1983) named South African species and Brown (1952), Powell (1967) and Gordon (1984, 1986, 1989) listed the rich fauna of New Zealand waters.

The Southern Ocean has been found, at certain depths, to be highly diverse (Brey *et al.* 1994) with certain groups such as the polycheates and bryozoans being particularly well represented (Clarke 1992) whilst other taxa most notably decapod and balanamorph crustaceans largely being absent south of 54°. Some (but few) bryozoan taxa are common to Antarctica, South America, South Africa and Australasia (Moyano 1985). The extensive work on Magellanic species have demonstrated whilst there are South American links with Antarctica, the two faunas are quite separate (Moyano 1982). One of the main differences is the (very) high level of Antarctic endemism. Even the Galapagos Islands bryozoans, also distinguished by high specific (though not generic) endemism, exhibit only half the proportion of species not found anywhere else (Banta & Redden 1990). Some explanations for commonality of Subantarctic islands with coastlines of southern portions of continents may lie with eastern drift along the circumpolar current. Both Moyano (1983) and Winston (1983) came to the conclusion that the ancestors of southern polar genera were in the Australian Tertiary fossil lineage.

Here we investigate the distributions and affinities of bryozoans south of 47° in the southern hemisphere, including Magellanic Chile, Argentina, the Falkland Islands, South Georgia, Bouvet Island, Crozet Islands, Prince Edward Islands, Kerguelen Islands, Heard Island, Campbell Islands, South Sandwhich Islands, South Orkney Islands, South Shetland Islands, Antarctic Peninsula, Weddell Sea, Bellingshausen Sea, Ross Sea and East Antarctic marine regions.

METHOD

The taxonomic reference material used in this study were the works of Busk (1884), Borg (1926, 1944), Hastings (1943), Brown (1952), Rogick (1965), Androsova (1968), Lopez Gappa (1978), d'Hondt & Redier (1977), d'Hondt (1984), Moyano (1982, 1983, 1985, 1991, 1996, 1999), Gordon (1984, 1986, 1989), the studies of Hayward and co-workers summarised in Hayward (1995) and Ostrovsky & Taylor (1996). In addition samples were collected over 8 years (from 1990-1998) from Tierra del Fuego, the Falkland Islands, South Georgia and Bird Island, the South Orkney Islands, the South Shetland Islands, the Northern Antarctic Peninsula and Southern Antarctic Peninsula. The main study localities and islands are shown in Fig. 1.

A species (presence-absence only) matrix by sites was constructed for Cheilostomatida, Ctenostomatida and Cyclostomatida separately. This matrix was subjected to Detrended Correspondence Analysis, as ordination techniques are more appropriate if the underlying structure in the data matrix consists of a gradient, rather than a more divisive structure. In common with all ordination techniques, DCA arranges the sites in a two-dimensional (or higher) space, in which the points (i.e. sites) are arranged such that the points close together correspond to sites with similar species composition and points that are far apart correspond to sites that are dissimilar in species composition. DCA is considered a more superior ordination technique, as it corrects for two of the major faults of earlier techniques, i.e. the fact that the ends of the axes are often compressed relative to the middle of the axes and the fact that the second axis often shows a systematic relation with the first axis. In the present analysis, only the first two axes were extracted (ease of graphical representation), which in all cases jointly accounted for more than 60 % of the total variance explained. In the Ctenostomatida data set, it was necessary to code for a universal dummy variable, as many of the sites held no species of this group (see Fig. 5). Thus a 1 (presence) was added to all regions for the dummy variable. In addition, the Cheilostomatida data set was subjected to TWINSPAN analysis, a polythetic divisive technique. Briefly, TWINSPAN produces a hierarchical classification based on successive dichotomous divisions of Reciprocal Averaging ordinations. Although a divisive technique may artificially split an underlying gradient structure, the technique is highly useful, as at each dichotomy the species responsible for the split are indicated, an aspect which is hard to glean from an ordination plot.

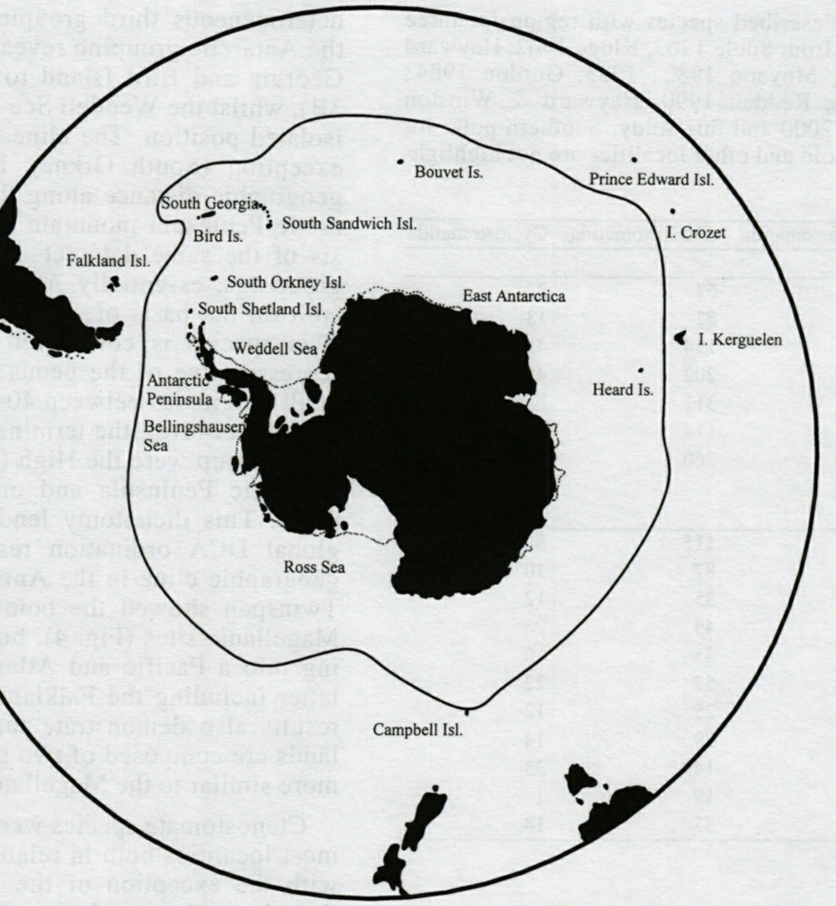

Fig. 1. – The Southern Ocean and associated land masses. All sites are named with the exception of Southern Chile, Southern Argentina and Tierra del Fuego or clarity. Sites which consist of a single island are given the postfix «Is» (or the prefix I. if French) whilst those consisting of an island group are given the postfix "Isl".

RESULTS

Species

The bryozoan fauna in the southern polar region or the area south of 47° investigated here comprises 501 species of which 410 were cheilostomates (81.8 %). The number and ratio of species representing the (3) marine bryozoan orders vary between regions both within and outside the Polar Frontal Zone (Table I). The proportion of Cheilostomatida to Ctenostomatida in the high Antarctic region (Ross Sea and Antarctic Peninsula in Table I) was very high compared to non polar regions because of the paucity of the latter taxa. Other isolated regions (islands in Table I) showed a similar pattern to a lesser degree, irrespective of latitude. The proportion of Cheilostomatida to Cyclostomatida was lowest in the Falkland Islands and the Ross Sea and highest around the Antarctic Peninsula and island groups of the Scotia Arc. The cheilostomate/cyclostomate values seem, therefore, to form a pattern with latitude and distance along the Andes-Scotian-Antarctic Peninsula mountains (Fig. 2).

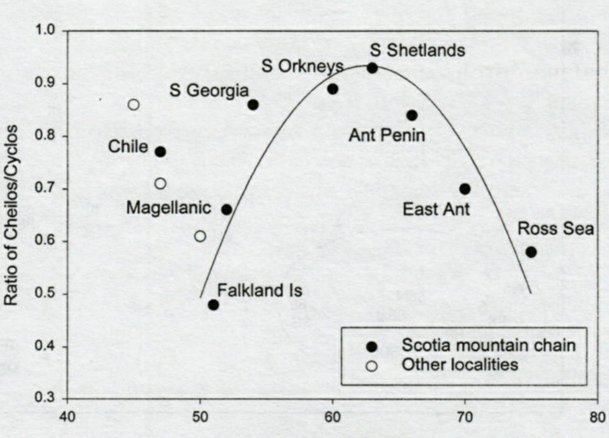

Fig. 2. – The number of cheilostomate/the number of cyclostomate species with latitude between 40 and 80 degrees South. Localities along the Scotia Arc mountain chain (linking the Andes to the Antarctic Peninsula) are shown as filled circles. Other sites are shown as open circles.

Table I.– Number of described species with region for three bryozoan orders. Data from Soule 1963, Kluge 1962, Hayward & Cook 1979; 1983, Moyano 1982; 1983, Gordon 1984; 1986; 1989, Banta & Redden 1990, Hayward & Winston 1994, Barnes & Dick 2000 and this study. Southern polar localities are shown in bold and other localities are not highlighted.

Region	Ctenostomatida	Cheilostomatida	Cyclostomatida
Ross Sea	**0**	**52**	**22**
Antarctic Penin	**0**	**82**	**13**
Magellanic	15	134	46
Chile	19	202	46
South Island (NZ)	13	311	ND
South Africa	1	114	16
Russian Arctic	33	260	73
Island groups			
South Shetlands	2	115	8
South Orkneys	0	87	10
South Georgia	1	85	12
Falkland Islands	2	49	26
Prince Edward	0	35	10
Kerguelen	3	57	22
Easter Island	0	25	12
Juan Fernandez	0	29	14
Galapagos	2	149	33
Cocos Island	0	19	1
Kodiac Island	3	57	14

Ordination of cheilostomate species revealed two homogenous site groupings, corresponding to an Antarctic and a Magellanic group (Fig. 3A), with the Subantarctic Islands forming a much more heterogeneous third grouping. Ordination of just the Antarctic grouping revealed a cline from South Georgia and Bird Island to East Antarctica (Fig. 3B), whilst the Weddell Sea occupied an extremely isolated position. The cline was ordered, with one exception (South Orkney Islands), according to geographic distance along the Andes-Scotian-Antarctic Peninsula mountain chain. Twinspan analysis of the same data set also revealed two major groupings, essentially Antarctic and Subantarctic, split on the basis of *Beania magellanica* (Fig. 4). This species is considered the most widespread representative of the genus occurring at localities at all longitudes between 40-55°S (Hayward 1995). At a lower level, the terminal divisions of the Antarctic group were the High (continental) Antarctic, Antarctic Peninsula and outlying Scotia Arc islands. This dichotomy lends support to both the global DCA ordination result and the observed geographic cline in the Antarctic group. Similarly Twinspan showed the homogenous nature of the Magellanic sites (Fig. 4), but also split this grouping into a Pacific and Atlantic coastal group, the latter including the Falkland Islands. TWINSPAN results also demonstrate that the Subantarctic islands are composed of two groups, one of which is more similar to the Magellanic site group (Fig. 4).

Ctenostomate species were poorly represented at most localities both in relative and absolute terms, with the exception of the Magellanic fauna. Although southern polar cyclostomate species were relatively species rich both by region (Table I) and absolute numbers (76), they represented only 15 % of the total bryozoans. Ordinations of both orders failed to establish any obvious groupings. The re-

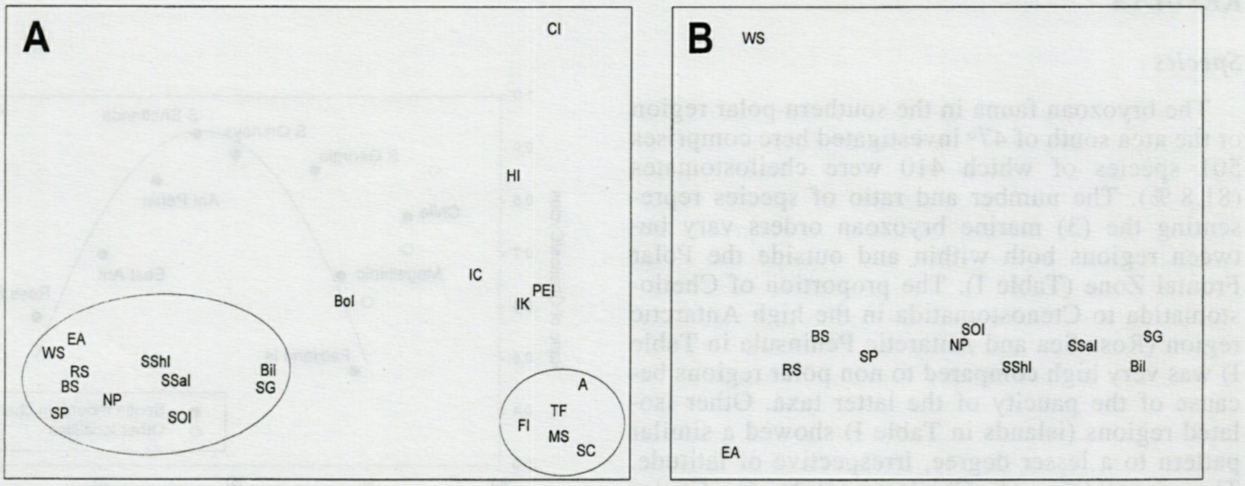

Fig. 3. – Detrended Correspondence Analysis (DCA) of sites using cheilostomate species. Island sites are positioned along the first two DCA axes, with symbols A (Argentina), Bellingshausen Sea (BS), Bird Island (BiI), Bouvet Island (BoI), Campbell Islands (CI), East Antarctica (EA), Falkland Islands (FI), Heard Island (HI), île Crozet (IC), îles Kerguelen (IK), Magellanic Strait (MS), Northern Antarctic Peninsula (NP), Prince Edward Islands (PEI), Ross Sea (RS), Southern Antarctic Peninsula (SP), Southern Chile (SC), South Orkney Islands (SOI), South Sandwhich Islands (SSaI), South Shetland Islands (SshI), Terra del Fuego (TF) and the Weddell Sea (WS). Ordination A includes all sites. Ordination B presents results of a further analysis exluding the Subantarctic Islands and Magellanic region from the matrix.

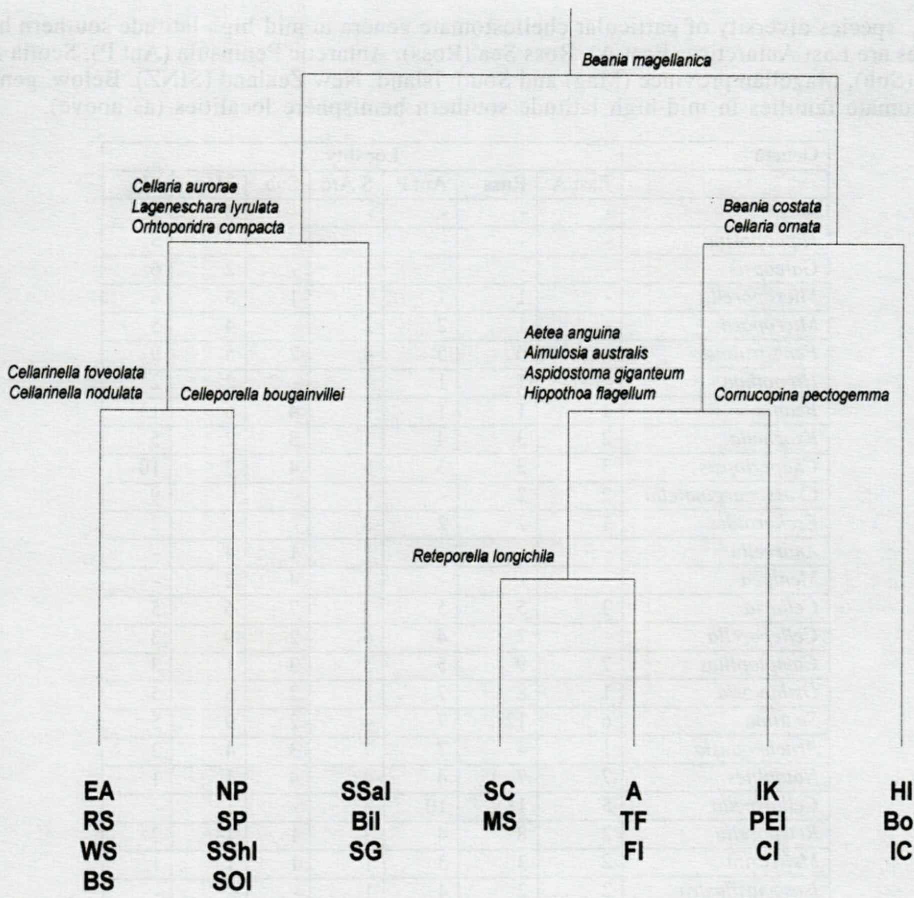

Fig. 4. – TWINSPAN dendrogram of sites showing species responsible for each dichotomous split. The symbols for the sites are as in Fig. 3.

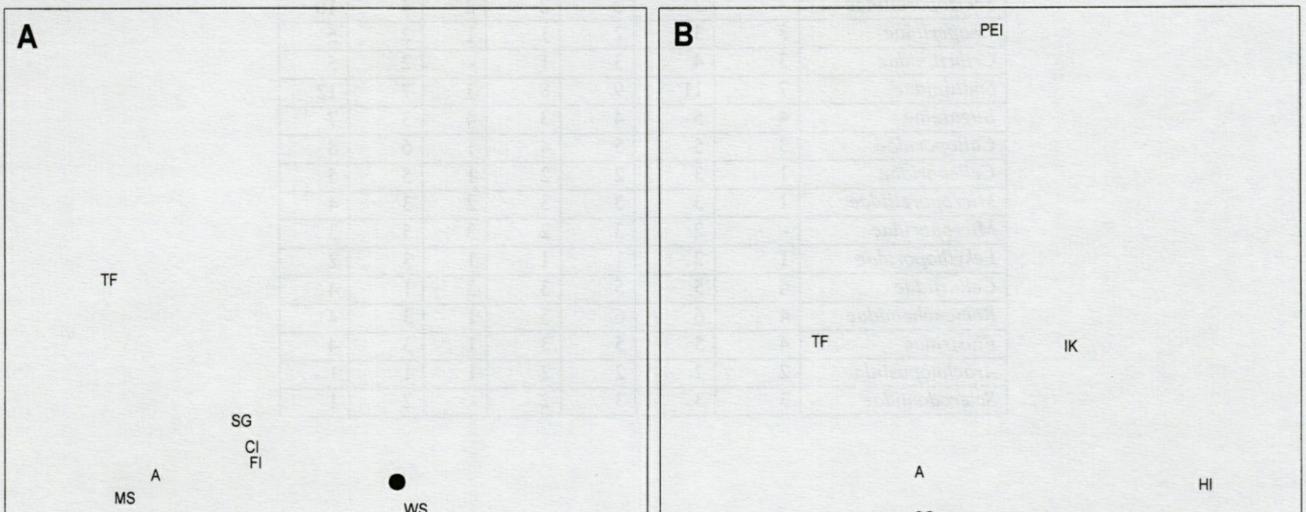

Fig. 5. – Detrended Correspondence Analysis (DCA) of sites using ctenostomate species (A) and cyclostomate species (B). Study sites are positioned along the first two DCA axes, with symbols as in fig. 2. The filled circle in (A) represents the position of all regions which harboured no ctenostomate species.

Table II. – Above, species diversity of particular cheilostomate genera in mid-high latitude southern hemisphere localities. The localities are East Antarctica (East A), Ross Sea (Ross), Antarctic Peninsula (Ant P), Scotia Arc (S Arc), Subantarctic islands (Sub), Magellan province (Mag) and South Island, New Zealand (SINZ). Below, generic diversity of particular cheilostomate families in mid-high latitude southern hemisphere localities (as above).

Genera	Locality						
	East A	Ross	Ant P	S Arc	Sub	Mag	SI_{NZ}
Aetea	-	-	-	-	-	3	3
Hippoporina	-	-	-	-	-	1	5
Galeopsis	-	-	-	1	-	2	6
Microporella	-	1	1	1	1	3	6
Micropora	-	1	2	2	-	4	5
Fenestrulina	-	6	5	4	2	5	9
Hippothoa	-	1	1	1	-	2	2
Beania	1	1	1	1	4	6	13
Exochella	2	3	4	1	3	2	5
Chaperiopsis	3	3	3	5	4	2	10
Crassimarginatella	2	2	-	-	-	-	9
Escharoides	1	2	2	3	-	-	2
Andreella	-	-	-	1	1	4	-
Menipea	-	-	-	1	4	2	-
Cellaria	3	5	5	3	7	6	5
Celleporella	-	2	4	6	2	9	3
Camptoplites	7	9	5	5	3	1	3
Osthimosia	1	8	7	5	2	5	5
Smittina	6	12	7	4	2	9	5
Arachnopusia	1	4	7	7	3	4	3
Notoplites	7	7	4	4	4	1	1
Cellarinella	5	11	10	3	-	1	-
Reteporella	2	8	4	3	1	1	2
Melicerita	2	3	3	1	1	1	1
Isosecuriflustra	2	2	4	1	-	-	-
Klugeflustra	3	2	4	2	-	-	-

Families

Phidoloporidae	1	1	1	2	1	2	7
Catenicellidae	-	1	-	-	-	1	9
Schizoporellidae	-	2	2	2	2	4	10
Chaperiidae	3	3	2	1	1	2	5
Cribrilinidae	3	4	3	1	-	2	5
Smittinidae	7	11	9	8	3	7	12
Bugulidae	4	5	4	3	4	3	7
Calloporidae	3	5	5	4	1	6	8
Celleporidae	1	3	2	2	1	5	5
Microporellidae	1	3	3	3	2	3	4
Microporidae	-	2	3	2	3	5	3
Lekythoporidae	1	2	1	1	1	3	2
Cellariidae	4	5	5	3	3	1	4
Romancheinidae	4	6	6	5	1	3	4
Flustridae	4	5	5	3	1	3	4
Arachnopusiidae	2	2	2	2	1	1	1
Sclerodomidae	3	3	3	2	-	2	1

sults of the ctenostomate species DCA does suggest a cline from West Antarctica to Southern Chile (Fig. 5A), with some evidence of a similar cline extending to East Antarctica in the cyclostomate (Fig. 5B), but to a larger extent the ctenostomate pattern was very unclear.

Genera

Evaluation of the number of species per cheilostomatid genus illustrates the richness of the New Zealand, and to a lesser extent the Magellanic fauna (Table II). Patterns of genus representation

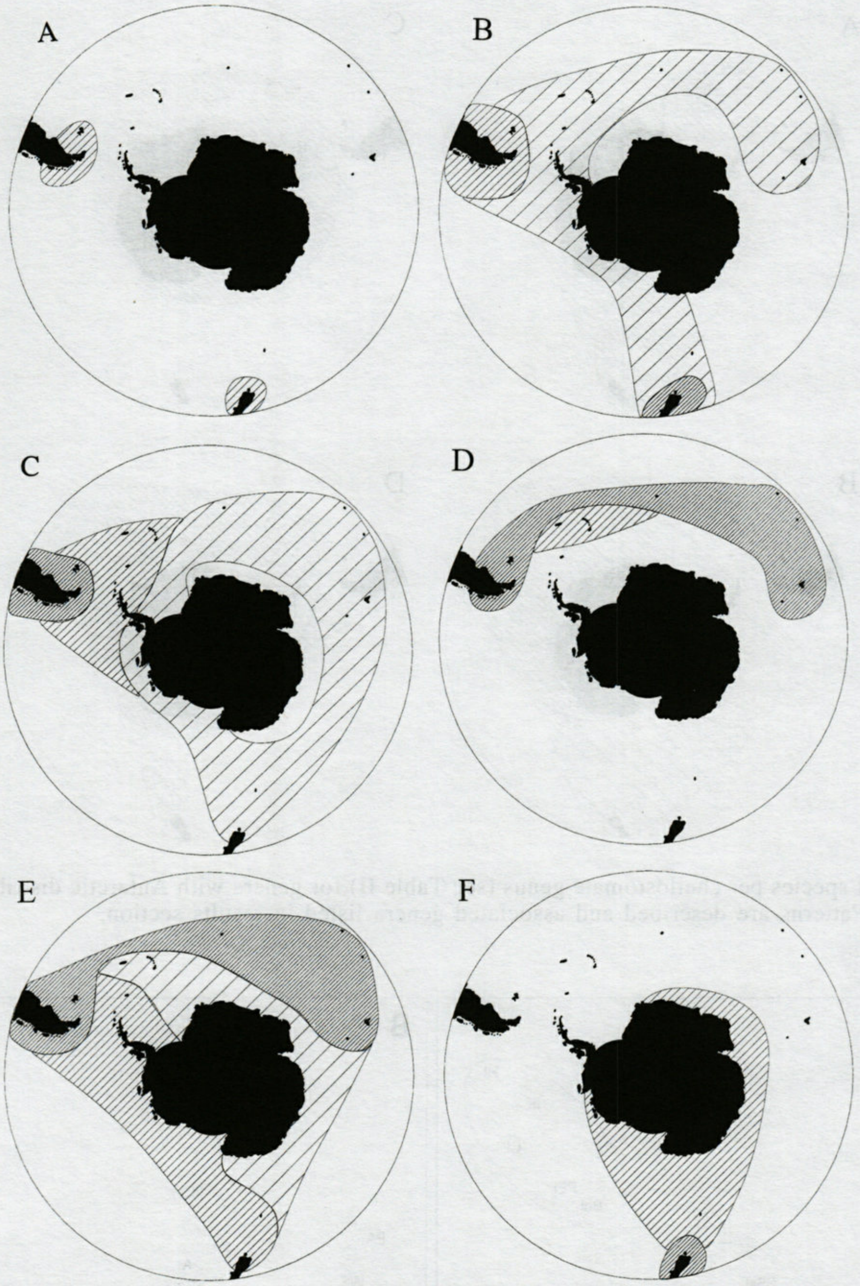

Fig. 6. – Number of species per cheilostomatid genus (see Table II) for genera with Non Antarctic distribution centres. Shading represents relative, not absolute, abundance; close hatching (high numbers), mid hatching (mid numbers), wide spaced hatching (few numbers) and no shading no species present. Patterns are described and associated genera listed in results section.

with region differed between genera but were generalised into 10 approximate trends. Whilst many genera were most speciose in either New Zealand or the Magellanic region, some were only present in one or both of these areas, for example *Aetea* (Fig. 6A). *Micropora, Microporella, Fenestrulina* and a number of other genera showed a similar pattern but with one or two representative species found in West Antarctica and the Subantarctic islands (Fig. 6B). The third pattern, only shown by *Celleporella*, was a cline from nine Magellanic species to none in East Antarctica (Fig. 6C). *Andreella* and *Menipea* also showed a cline from high species numbers in the Subantarctic (Fig. 6D) to few in the Scotia Arc and none in coastal Antarctica (or New Zealand). Like *Celleporella*, unique patterns (clines) were also shown by *Cellaria* (Fig. 6E) and *Crassimarginatella* (Fig. 6F).

In contrast to the high species endemicity (~80 %) there are few genera (~8 %) endemic to southern polar

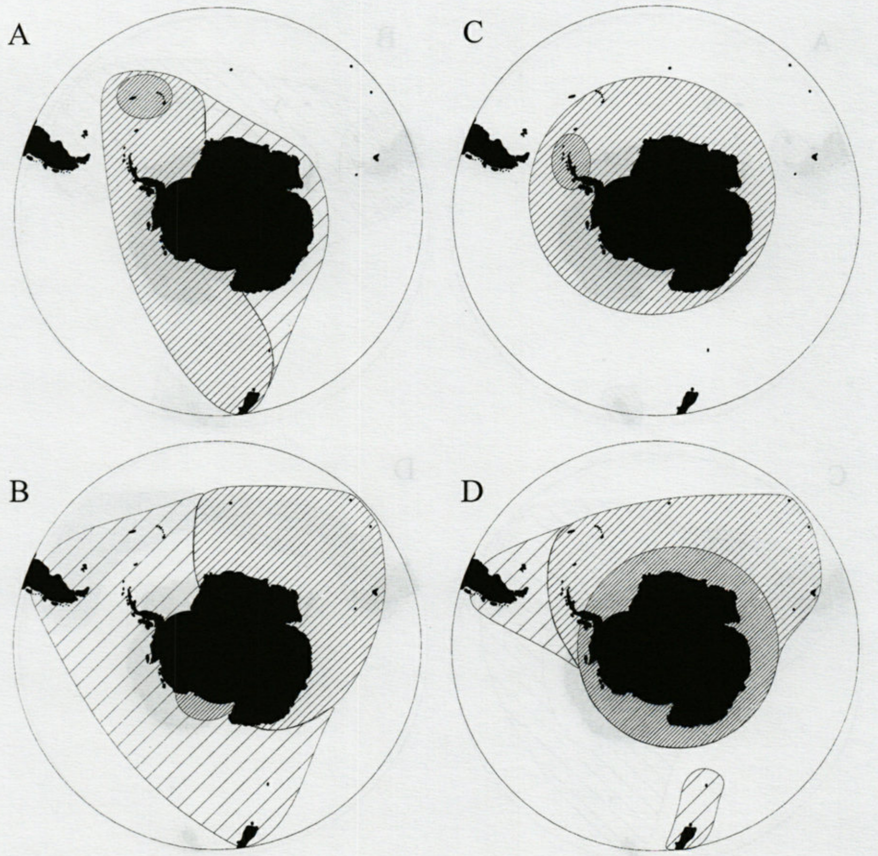

Fig. 7. – Number of species per cheilostomate genus (see Table II) for genera with Antarctic distribution centres. Shading as in Fig. 6. Patterns are described and associated genera listed in results section.

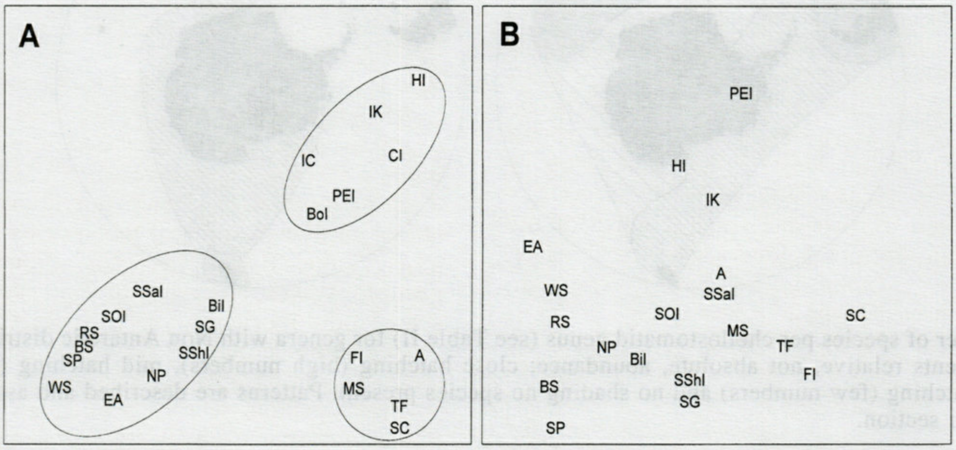

Fig. 8. – Detrended Correspondence Analysis (DCA) of sites using cheilostomate genera (A) and cyclostomate genera (B). Study sites are positioned along the first two DCA axes, with symbols as in Fig. 2. The circles in (A) enclose clusters of sites with high similarity.

waters. Other non-endemic southern polar genera are represented mostly by endemic species or unlike the patterns illustrated in Fig. 6 had highest species numbers centred in Antarctic waters. *Escharoides* was most speciose in the Scotia Arc but poorly represented north of the polar frontal zone (Fig. 7A). The genera *Osthimosia* and *Smittina* were most represented in the Ross Sea and least in the eastern Southern Ocean (Fig. 7B). The Antarctic Peninsula had the most species of two of the few endemic genera, *Isosecuriflustra* and *Klugeflustra* (Fig. 7C) and the genus *Arachnopusia*

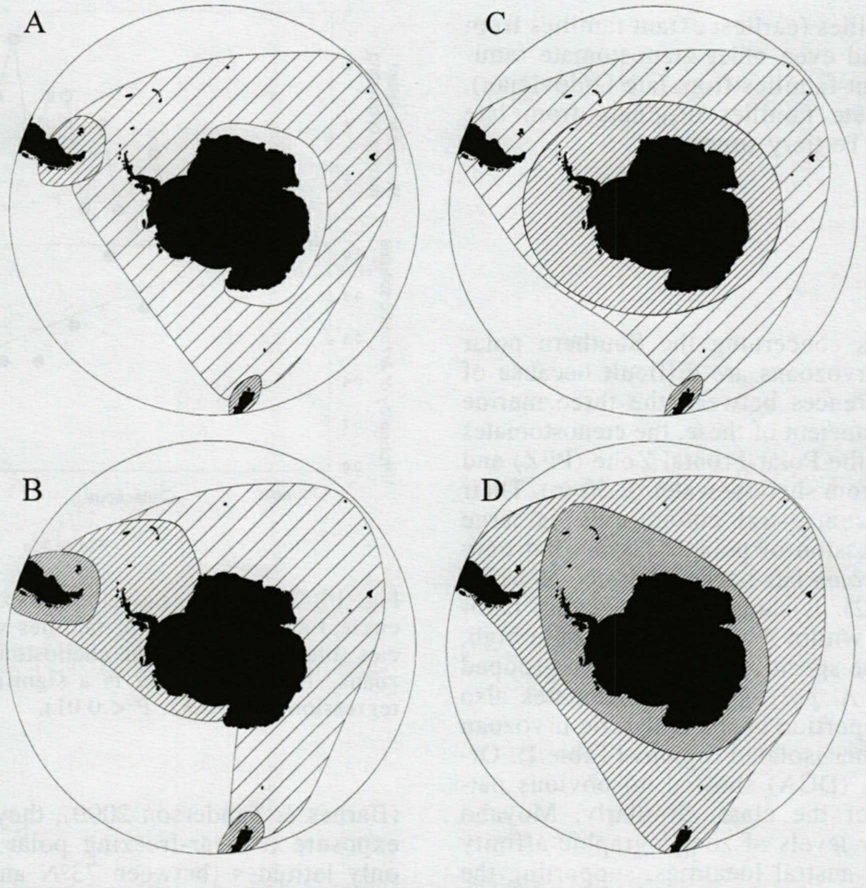

Fig. 9. – Number of genera per cheilostomate family (see Table III). Shading as in Fig. 6. Patterns are described in results section. Example families corresponding to patterns are Schizoporellidae (A), Celleporidae (B), Chaperiidae (C), Scleromidae (D).

for which the number of species declined outwards into the Magellanic and New Zealand regions. A number of genera, such as *Notoplites*, *Melicerita* and *Cellarinella*, were most speciose around coastal Antarctica and least represented north of the Subantarctic islands (Fig. 7D). These genera were represented by just one species north of the Southern Ocean, but other genera exhibiting a similar pattern, e.g. *Camptoplites* and *Reteporella*, have two or three non-polar species.

Ordination of cheilostomate genera showed a similar pattern to that of cheilostomate species, in that Antarctic and Magellanic sites formed distinct groupings (Fig. 8A). In addition, however, the Subantarctic islands also formed a homogenous grouping. Within both the Antarctic and Subantarctic island groupings there was evidence of clines along geographic gradients as with the patterns for cheilostomate species (see Fig. 3B). The geographically closest of the Subantarctic grouping, Bouvet Island, was most similar to the closest locality of the Antarctic and Magellanic clusters (South Georgia/Bird Island and Falkland Islands respectively). The cyclostomate generic pattern, like that at species level, revealed no distinct groupings (Fig. 8B).

Family

Although none of the 31 families represented in southern polar waters are endemic, most (sometimes > 90 %) of their constituent species are. Patterns of number of genera per family (Fig. 9) are not dissimilar to some of the species per genus patterns (Table II and Fig. 6,7). Four approximate groupings were recognised (but not illustrated). The Phidoloporidae typify a cluster of families mainly represented in New Zealand. Likewise a grouping including the Chaperiidae are dominated by New Zealand members but also have high generic importance in West Antarctica. The third cluster, typified by the Microporellidae, was fairly evenly represented across the study regions (with the exception of East Antarctica and the Subantarctic islands). As with certain generic patterns (Fig. 7) there were a number of families mainly represented in coastal Antarctic waters, such as the Romancheinidae. Virtually all of the most ancient cheilostomate families (mid Cretaceous or earlier in origin) have Antarctic representative species (Fig. 10). This proportion decreased from the mid Cretaceous only 10 % by the Quarternary period. In contrast to the older cyclostomate families (earliest extant families from early Triassic) and even older ctenostomate families (earliest extant families from late Ordovician), most Cheilostomate families originate from late Cretaceous/early Tertiary times.

DISCUSSION

Generalisations concerning the Southern polar and Antiboreal bryozoans are difficult because of the marked differences between the three marine orders. The most ancient of these, the ctenostomates are rare south of the Polar Frontal Zone (PFZ) and virtually absent from shallow water (< 50 m). Their potential for circumaustral colonisation is large through the possession of pelagic larvae, but only *Alcyonidium polyoum* has been confirmed as being so (Moyano 1982). It should be noted that taxonomic confusion within *Alcyonidium* is quite high, and more than one species may have been grouped under the name, *A. polyoum.* Cyclostomates also formed a low proportion of the Antarctic bryozoan fauna, as with other isolated regions (Table I). Ordination analyses (DCA) showed no obvious patterns or clines of the class. Similarly, Moyano (1996) found low levels of zoogeographic affinity between selected austral localities, supporting the present findings. In his study, despite low affinities, many cyclostomate species linked Antarctica to the Magellanic region (e.g. *Lichenopora canaliculata*), others New Zealand to the Magellanic region (e.g. *Bicrisia bicilliata)* and Antarctica to New Zealand (e.g. *Mesonea radians).* There were in addition some species which can be considered circumaustral such as *Disporella fimbriata*. In contrast to the present study, Banta & Redden (1990) found more distinct patterns in the Cyclostomatida (than in the Cheilostomatida) in the Galapagos fauna.

Although many Antiboreal cheilostomate species have been mistakenly reported from Antarctic waters (see Hayward 1995) there are still many confirmed as being circumaustral in distribution. The West-wind-Drift and Antarctic Circumpolar Current, and the convergent conditions caused, have been invoked as an explanation for such distribution patterns (Ekamn 1953, Briggs 1974). There are, in addition, a number of species, such as *Aetea anguina, Celleporella hyalina* and *Microporella ciliata* which are cosmopolitan. The existence of truly cosmopolitan species is generally doubted and poor taxonomy or modern dispersal through fouling vessels or drift debris are possible explanations. None of these potential cosmopolites, however, occur in southern polar waters (south of the Polar frontal Zone). Although bryozoans are a major component of fouling biotas at all latitudes and particularly so in cool waters (Barnes & Sanderson 2000), they may not survive exposure to near-freezing polar conditions. The only latitudes (between 73°N and 60°S) at which floating debris tends was found to be uncolonised were the polar seas.

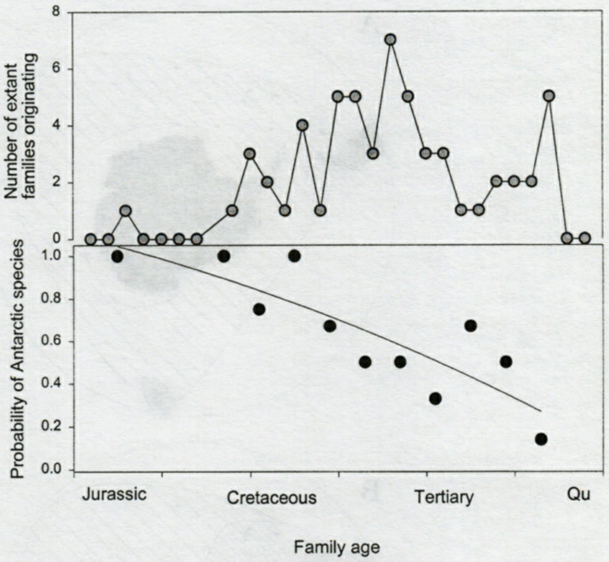

Fig. 10. Timing of origination of extent families (grey circles) and proportion of families with Antarctic species (black circles) in the cheilostomate order of bryozoans. The fitted curve is a significant second order regression ($r^2 = 0.82$, $P < 0.01$).

Many cheilostomatid families (compared to the Ctenostomatida or Cyclostomatida) have relatively modern (Tertiary) origins (Taylor 1993) (Fig. 10). Although the supercontinent Gondwana had fragmented much earlier than this, in very early Tertiary times Antarctica still formed a large continent attached to South America. Only since the Oligocene has Antarctica become isolated by the now large distances between it and the southern tips of other continents. The decrease in families with Antarctic species coincided with peak numbers of new families originating (Fig. 10) around the globe in a now fragmented Gondwanaland. Such a decrease in families with Antarctic representatives would be expected with the increased isolation of Antarctica and growing distances between shelf waters. However, the numbers of families with Antarctic species did (temporarily) increase at the time of the separation of South America and Antarctica.

Whilst East Antarctica has remained relatively stable with a large icecap since, there have been several phases of glaciation and melt in West Antarctica. Dispersal of species to and from each side of the Pacific Ocean seems to have occurred at pivotal points in southern polar geological history. Molluscs (Beu *et al.* 1997) dispersed both ways between New Zealand and South America with the formation of the Circumpolar current (Oligocene). Further pulses of Magellanic dispersal to New Zealand occurred during West Antarctic glaciation (Late Miocene and Pleistocene). Like the Arctic, the Magellanic region has been even more prone to environmental disturbance in the form of glaciation and precipitation. Such factors have been considered to explain the higher values of zoarial diversity and polymorphism of Antarctic versus Magellanic bryozoans (Moyano 1982). Such a hypothesis may be testable within polar waters by comparing bryozoans from East Antarctica with those from the less stable west.

Most previous analyses, whether bryozoological (Moyano 1996) or pertaining to other phyla (van Soest 1994, Canete *et al.* 1999), which have included localities south of the PFZ have only considered the Antarctic as one zone. Hedgepeth (1969) and Dell (1972) described a zone around continental Antarctica and another around the Subantarctic islands. In the present study the Antarctic and Magellanic Cheilostomatida form distinct clusters at both species and generic levels (Fig. 6,7) neither including the Subantarctic islands. TWINSPAN analysis suggested the many sites within the PFZ essentially form four Antarctic sub-zones: East Antarctica, West Antarctica (excluding the Antarctic Peninsula), the Antarctic Peninsula and the Scotia Arc. The centres of species and generic abundance support such regionalisation as there are examples of taxa, which are most speciose or are constituted by most species at each of these four areas (Fig. 7). Certain lower level taxa and the Cheilostomatida as a whole show a cline from the Magellanic through the Scotia Arc island chain and Antarctic Peninsula to East Antarctica.

The proportion of Antarctic endemic cheilostomatids was high at species level (82 %) but not at generic level (8 %), although both values were higher (in many cases by nearly an order of magnitude) than at other Antiboreal localities. Hexactinellid sponges show very similar patterns (83 % species and 28 % genera endemic to Antarctica) although Australasian endemism is slightly higher (Tabachnick 1994). The Bryozoa of the Antarctic region share high levels of endemism with other isolated but smaller areas such as the Galapagos Islands (Banta & Redden 1990) and Juan Fernandez Is. (Moyano 1996). None of the Subantarctic islands studied here had high levels of endemism but had fairly dissimilar bryofauna, for example Heard Is. (11.1 %), I. Kerguelen (8.7 %) and Prince Edward Is. (6.1 %). The geological history of the Subantarctic islands is little known and conclusions from the present study of their bryozoan fauna emerge as the least obvious affinities. All Subantarctic islands, including the Campbell Islands formed a homogenous group at the generic level (Fig. 8) reflecting presumably geographical proximity in early tertiary times but exhibited a much more heterogeneous pattern at species level (Fig. 3). Ordination results at this level, place the Campbell Isl. as distinct from all other sites, presumed to be caused by the strong biogeographical links between Campbell Isl. and New Zealand. Nevertheless, a biogeographical link exist between (see Fig. 4) the three islands within the PFZ (Bouvet Is., Heard Is., Campbell Isl.), quite possibly linked to the Antarctic Circumpolar Current, which is known to have been in existence since the Gondwana fragmentation, in approximately the same position as its present day track. The island groups outside of the PFZ, form a distinct grouping in the TWINSPAN analysis, biogeographically related the Magellanic region. This relationship can also be explained on the basis of ancient current patterns, in this case the West Wind Drift, which originates in the Magellanic region and circumnavigates the PFZ. Despite their relative close geographical proximity, Heard Is. and I. Kerguelen are biogeographically not closely related. Aside from the influence of currents, the Subantarctic island vary greatly in their ages (LeMasurier & Thomson 1990). The Prince Edward Islands are considerably younger than Heard Is. or I. Kerguelen which is reflected in the higher levels of endemism in the latter. However as only fragmentary exploration is available from the majority of the Subantarctic islands, the true level of endemism can only be speculated upon.

Bryozoans prove to be a particularly useful group for investigating biogeographic patterns in the southern polar region. Bryozoans are particularly abundant and speciose in the Southern Ocean and surrounding continental margins (Clarke 1992). Their taxonomy in the case of the Cheilostomatida has been recently and thoroughly reviewed (Hayward 1995) and current knowledge of them is beginning to reach an equivalent level to that in other seas (Winston 1992). A substantial fossil record of the phylum is known such that approximate ages have been established for most of the families (Taylor 1993). In addition there is evidence that the transition phase in species formation is brief (fossils of species intermediates are rare) so the history of species can be relatively precise (Jackson & Cheetham 1990). Finally most bryozoans have benthic larvae and as such have reduced potential of dispersal, but one group have pelagic larvae so are useful for comparison. Here the patterns found largely conform to the biogeographic scheme proposed by Hedgepeth (1969) and Dell (1972). However, we have demonstrated that there are sub-patterns within the PFZ. Antarctica and polar waters seem to have four zones from bryozoogeographical evidence; East Antarctic seas, West Antarctic seas, the Antarctic Peninsula and the Scotia Arc.

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SPATIAL AND TEMPORAL VARIABILITY IN CHLOROPHYLL-*a* AND DIATOM DISTRIBUTION IN THE SOUTH-EAST INDIAN OCEAN

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DIATOMS
BIOGEOGRAPHY
SUBTROPICAL CONVERGENCE
CHLOROPHYLL-*a*

ABSTRACT. – Cross frontal changes in chlorophyll-*a* (chl-a) concentration and diatom (> 20 µm) community species composition between South Africa and the Prince Edward Islands and in the mid-Indian Ocean were investigated during four cruises of the Marion Island Oceanographic Survey (MIOS I-IV) conducted in April/May between 1996 and 1999. Enhanced chl-*a* concentrations were recorded at stations occupied in the vicinity of the Subtropical Convergence (STC) south of Africa and in the vicinity of the Subantarctic Front (SAF) in 1998 and 1999. At these stations microphytoplankton (> 20 µm) comprised a substantial contribution (up to 15 %) of total chl-*a*. Outside these regions, however, total chl-*a* was almost entirely dominated by nano- and picophytoplankton. In the mid-Indian ocean no biological enhancement was associated with the STC. Species richness was highest in the region south of Africa (up to 44 species), particularly in the waters north of the STC. The high number of species recorded here can be related to the complex oceanographic regime. In the mid-Indian Ocean, species richness was consistently low, < 8 species. Numerical analyses indicated that south of Africa distinct diatom assemblages, separated by the major frontal systems, were associated with different water masses. South of Africa, the STC represented a strong biogeographic boundary to the distribution of diatom species. Within this region, a unique diatom assemblage was associated with the STC proper. In the mid-Indian Ocean, the STC did not act as a boundary to the distribution of diatoms, which is likely, the result of a reduced intensity of the front which allows for species to penetrate the front. During all four cruises, the SAF represented an important biogeographic boundary to the distribution of diatoms.

DIATOMÉES
BIOGÉOGRAPHIE
SUBTROPICAL
CONVERGENCE
CHLOROPHYLLE-*a*

RÉSUMÉ. – La comparaison des variations au niveau des fronts de la concentration en chlorophylle-*a* et de la composition spécifique des communautés de Diatomées (>20 µm) de l'Afrique du Sud aux Iles Prince Edwards d'une part, avec l'Océan Indien moyen d'autre part, a été étudiée au cours de quatre campagnes du Marion Island Oceanographic Survey (MIOS I-IV) conduites en avril-mai de 1996 à 1999. Des concentrations en chl-*a* élevées ont été relevées dans les sites situés à proximité de la Convergence Subtropicale (STC) au Sud de l'Afrique, ainsi que dans le voisinage du Front Subantarctique (SAF) en 1998 et 1999. Dans ces stations, le microphytoplancton (> 20 µm) représente une contribution importante (jusqu'à 15 %) à l'ensemble de la chlorophylle-*a* totale. Hors de ces régions, cependant, le nano– et le picoplancton dominent entièrement la chlorophylle-*a* totale. Dans l'Océan Indien moyen, aucune augmentation significative n'est associée à la STC. La richesse spécifique est la plus élevée dans la zone au sud de l'Afrique (jusqu'à 44 espèces), surtout dans les eaux au nord de la STC. Le nombre élevé d'espèces recensé dans cette région peut être lié au régime océanographique complexe. Dans l'Océan Indien moyen, la richesse spécifique est notoirement basse, inférieure à 8 espèces. Les analyses numériques montrant que les communautés de Diatomées du Sud de l'Afrique, séparées par les systèmes frontaux majeurs, sont associées aux différentes masses d'eau. Au sud de l'Afrique, la STC représente une importante barrière biogéographique à la distribution des espèces de Diatomées. Dans ces régions une seule communauté est associée à la STC. Dans l'Océan Indien moyen, la STC n'intervient pas comme barrière à la répartition des Diatomées qui est probablement le résultat d'une activité moindre du front qui permet aux espèces de le traverser. Pendant les quatre campagnes, le Front Subantarctique représente une barrière biogéographique importante à la distribution des Diatomées.

INTRODUCTION

The major oceanic frontal systems south of Africa are well defined for a number reasons. Firstly, they form part of the Antarctic Circumpolar Current that is not constricted such as in the region of New Zealand, thus allowing for their full development (Duncombe Rae 1989, Lutjeharms & Vallentine 1984, Belkin & Gordon 1996, Lutjeharms *et al.* 1993, in review). Secondly, the northern boundary of the Southern Ocean, the Subtropical Convergence (STC) is enhanced by the juxtaposition of the Agulhas Current (AC) and the Agulhas Return Current (ARC) (Lutjeharms & Valentine 1984, Weeks & Shillington 1994, 1996). As a consequence the frontal systems in this region have been the subject of extensive investigation (Lutjeharms & Emery 1983, Lutjeharms & McQuaid 1986, Lutjeharms *et al.* 1993). Results of these investigations have shown considerable variability in the position and intensity of the fronts (Lutjeharms & McQuaid 1986, Lutjeharms *et al.* 1993; Ansorge *et al.* 1999, Froneman *et al.* 1999, Pakhomov *et al.* 2000a). For example, the ARC that carries warm Subtropical surface waters may coalesce with the STC resulting in a frontal feature with a sharp transition in temperature and salinity (Pakhomov *et al.* 2000a). Similarly, the position of the Subantarctic Front (SAF) may vary as much as 100 km over a period of less than a month (Ansorge *et al.* 1999, Froneman *et al.* 1999, Lutjeharms *et al.*, in review). In contrast to the STC south of Africa, field data and Muliti-channell Sea Surface Temperature charts collected in the mid-Atlantic Ocean showed that STC was emphermeral and weak and was characterised by a poorly defined horizontal gradient in physicochemical parameters (Lutjeharms *et al.* 1993, Barange *et al.* 1998). There is evidence in the literature to suggest that the intensity of the STC in the mid-Indian Ocean also decreases (Belkin 1989).

Spatial distribution of diatoms (> 20 µm) south of Africa in austral summer has been the subject of extensive investigation on several occasions (Boden *et al.* 1988, Boden & Reid 1989, Froneman *et al.* 1995a, 1995b). Nutrient availability, light environment (Laubscher *et al.* 1993, Froneman *et al.* 1999) and biological factors such as grazing by zooplankton are implicated in determining the distribution of diatoms in the region (Froneman & Perissinotto 1996, Pakhomov & Perissinotto 1997). Boden *et al.*(1988) and others (see for example Froneman *et al.* 1995a, 1999) showed that distinct diatom assemblages were associated with different water masses or with hydrological features such as the Agulhas Return Current (ARC) and the STC south of Africa. The studies further showed that the major frontal systems south of Africa represented strong biogeographic boundaries to the distribution of diatoms. For example Boden *et al.* (1989) showed that the STC represented the southern boundary for the distribution of several subtropical zone diatom species including *Cerataulina pelagica* and *Hemialus hauckii*. More recently, Froneman *et al.* (1995) demonstrated that the SAF represented the southern boundary for the distribution of sub-antarctic diatom species such as *Pseudoeunotia doliolus* and *Thalassionema frauenfeldii*. The importance of the fronts as boundaries appeared to be the result of the sharp horizontal gradients in temperature associated with these features (Deacon 1982, Boden *et al.* 1988, Froneman *et al.* 1995a, 1995b). Subsequent studies conducted in the region have shown that the major frontal systems also represent important biogeographic barriers to the distribution of zooplankton (Pakhomov & McQuaid 1986, Pakhomov & Perissinotto 1997, Barange *et al.* 1998). A recent study showed a high degree of spatial variability of the STC as a biogeographic boundary, with the mid-Atlantic Ocean front representing a weak biogeographic boundary (Barange *et al.* 1998). The variability appeared to reflect changes in the intensity of the front in the open waters which allowed for species to be transported across the frontal system. It should be noted that although the STC represents a strong biogeographic boundary to the distribution of plankton south of Africa, warm core eddies shed from the Agulhas Return Current may at times transport plankton across the front (Froneman *et al.* 1997, Pakhomov & Perissinotto 1997).

The importance of the SAF as a barrier to the distribution of both phytoplankton and zooplankton in the Atlantic sector of the Southern Ocean in austral summer has been documented on several occasions (Deacon 1982, Froneman *et al.* 1995b; Pakhomov *et al.* 2000b). A recent study conducted in the Indian sector of the Southern Ocean in austral summer 1996 indicated that the SAF did not represent an important biogeographic boundary to the distribution of plankton (Froneman & Pakhomov 1998). The absence of this feature as a biogeographic boundary appeared to be related to cross frontal mixing which transported species across the front. These facts suggest strong spatial variability in the importance of the SAF as a biogeographic boundary.

During this study inter-annual variability of the importance of the major frontal systems south of Africa as biogeographic barriers to the distribution of microphytoplankton is investigated. These data are then compared with results obtained along a transect occupied in the mid-Indian Ocean to investigate spatial variability in biogeography of microphytoplankton.

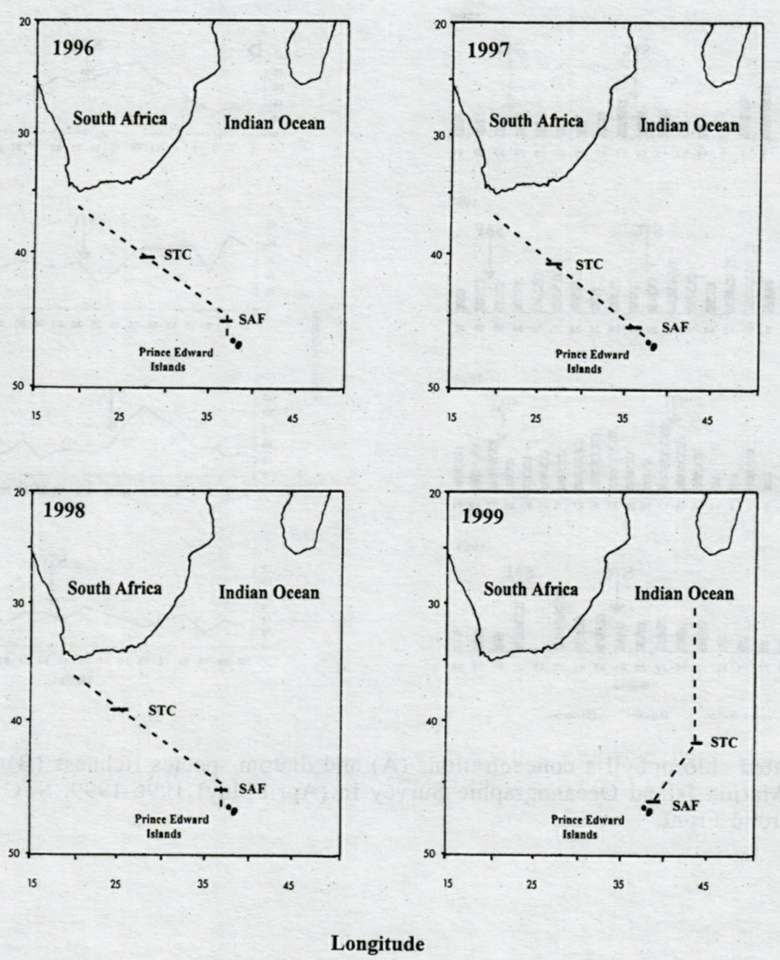

Fig. 1. – Cruise tracks during the four cruises of the Marion Island Oceanographic Survey conducted in April/May 1996-1999. STC = Subtropical Convergence; SAF = Subantarctic Front.

MATERIALS AND METHODS

Data for the study were collected during four cruises of the Marion Island Oceanographic Survey (MIOS I-IV) conducted in April/May over the period 1996 to 1999. Three transects were occupied in the region between South Africa and the Prince Edward Islands over the period 1996 to 1998 (Fig. 1). A single transect was also occupied in the south Indian Ocean between the Madagascar Ridge and the Prince Edward Islands in 1999 (Fig. 1)

To determine the position of the major frontal systems along each transect occupied, Sippican T7-XBT's (Expendable Bathythermograph) were deployed at 30 nautical mile intervals to a maximum depth of 760 m. Prior to the deployment, the XBT's were placed in a water bath for 5 minutes in order to minimise the difference between the probes storage temperature (25ºC) and that of the sea surface temperature. The position of the major oceanic fronts were defined by their subsurface temperature range and their subsurface axila temperature according to Park *et al.* (1993). These were as follows : Subtropical Convergence (STC) 8-12ºC, 10ºC; Subantarctic Front (SAF) 4-8ºC, 6ºC. Detailed discussion of the results are presented elsewhere (Ansorge *et al.* 1999, Pakhomov *et al.* 2000a, Lutjeharms *et al.* in review). The geographic position of the major frontal system during the four cruises is presented in Table I.

Water samples for the identification and enumeration of diatoms were collected at 30 nautical mile (± 55 km) intervals using a shipboard pump (Iwaki Magnetic

Table I. – Geographic position of the major oceanic fronts south of Africa and in the mid Indian Ocean in April/May 1996-1999.

Year	Subtropical Convergence (STC)	Sub-antarctic Front (SAF)
1996	42° 35'	45° 30'
1997	42° 50'	45°45'
1998	42° 15'	45° 45'
1999	43° 30'	45° 20'

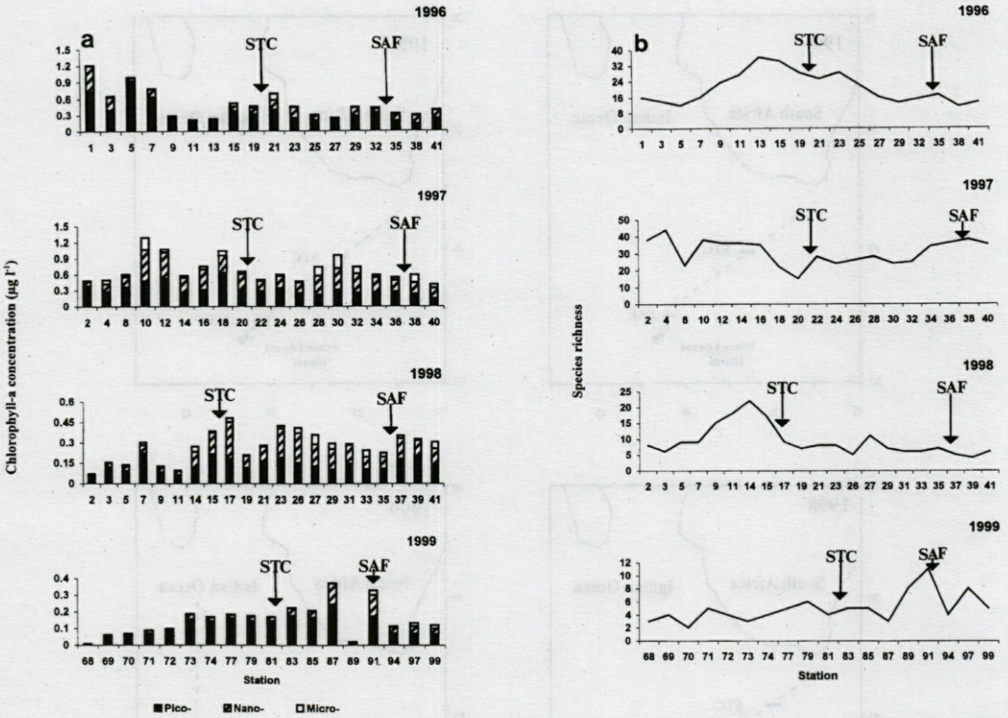

Fig. 2. – Size fractionated chlorophyll-a concentrations (A) and diatom species richness (B) during the four cruises conducted during the Marion Island Oceanographic Survey in (April/May) 1996-1999. STC = Subtropical Convergence; SAF = Subantarctic Front.

pump) made from polyvinylide flouride and ceramic materials, and operated at a flow rate of 4 litres per minute. The pump outlet was ± 5m below the sea surface and the seawater was supplied to the laboratory through PVC piping. Previous studies have shown that the collection of seawater samples using the shipboard pump does not significantly alter the diatoms community structure as a result of cell rupture or breakage (Froneman *et al.* 1995a). For the taxonomic analysis of the diatom standing stock, a 20 µm mesh filtration unit was connected to the pump outlet and a constant volume of 20 litres of seawater was filtered at each station (Berman & Kimor 1983). The diatoms retained by the filter were preserved in 2 % buffered (hexamine) formalin and enumerated and identified in the laboratory using a Nikon TMS inverted microscope operated at X400 magnification. A minimum of 500 cells or the entire sample was counted from each station. Densities were then expressed as cells per litre. The diatoms were identified using the works of Tomas (1996) and Boden & Reid (1989).

To compare diatom communities during the different cruises, non-metric cluster analysis were used in conjunction with the Bray-Curtis similarity index after log transforming [log 10(x + 1)] species data. Significance levels and sources of difference between the diatom assemblages associated with the different groups of stations were tested using the similarity analysis programs SIMPER and ANOSIM of the Plymouth Routines in Multivariate Research (Primer, Clarke & Warwick 1994) computer package according to the procedure described by Field *et al.* (1982).

In addition to the diatom samples, size fractionated chlorophyll-*a* concentrations were determined at each station. A 250 ml aliquot seawater sample obtained from the shipboard pump was gently filtered (< 5 cm Hg) though serial filtration into pico– (< 2 µm), nano– (2-20 µm) and microphytoplankton (>20 µm) size fractions. Chlorophyll-*a* concentrations were then determined fluorometrically (Turner 10AU fluorometer) after extraction in 90 % acetone for 24h hours in the dark (Holm-Hansen & Riemann 1978).

RESULTS

Chlorophyll-a

During 1996, total surface chlorophyll-*a* (chl-*a*) concentrations ranged from 0.28 to 1.2 µg l^{-1} (Fig. 2a). Elevated chl-*a* biomass was recorded at stations occupied in the continental shelf waters south of Africa and in the vicinity of the STC. Here chl-*a* concentrations exceeded 0.7 µg l^{-1}. Outside these regions total chl-*a* concentrations were always < 0.5 µg l^{-1}. Picophytoplankton (< 2.0 µm) followed by nanophytoplankton (2-20 µm) were identified as the first and second largest contributors to total chl-*a* comprising between 58 and 85 % and between 13 and 42 % of the total pigment, respectively. Microphytoplankton generally comprised <

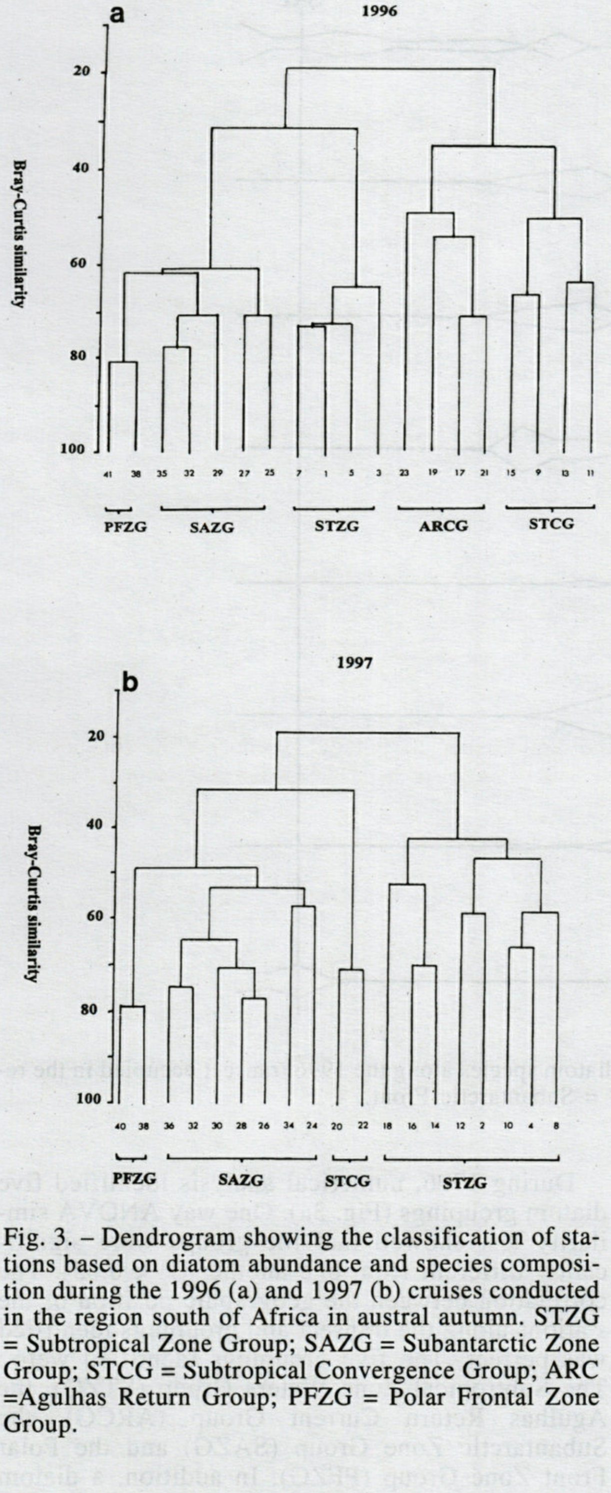

Fig. 3. – Dendrogram showing the classification of stations based on diatom abundance and species composition during the 1996 (a) and 1997 (b) cruises conducted in the region south of Africa in austral autumn. STZG = Subtropical Zone Group; SAZG = Subantarctic Zone Group; STCG = Subtropical Convergence Group; ARC =Agulhas Return Group; PFZG = Polar Frontal Zone Group.

5 % of total pigment. An exception was recorded at the station occupied in the vicinity of the STC (station 21) where microphytoplankton comprised 15 % of the total chl-*a* (Fig. 2a).

Along the 1997 transect total chl-*a* concentration ranged from 0.46 to 1.29 µg l^{-1} (Fig. 2a). Chlorophyll-*a* concentrations were again highest at stations occupied in the continental shelf waters south of Africa and in the region of the STC. In addition to these stations, a minor peak in chl-*a* concentration was also recorded at station 30 located in the Subantarctic Waters (Fig. 2a). Picophytoplankton generally dominated total chl-*a* during the cruise. Exceptions were recorded at stations occupied in the vicinity of the STC and at stations located at the southern boundary of the front where nanophytoplankton were identified as the largest contributor to total chl-*a* concentration. Generally, however, the contribution of nanophytoplankton total pigment was < 35 %. Microphytoplankton comprised < 10 % of the total pigment. Exceptions were recorded at stations 28 and 30 located in the waters north of the SAF and at station 10 located immediately north of the STC where microphytoplankton comprised > 15 % of the total pigment (Fig. 2a).

In 1998, total surface chl-*a* concentrations ranged from 0.09 to 0.47 µg l^{-1} (Fig. 2a). Elevated chl-*a* concentrations were again recorded at stations occupied in the region of the STC. In addition peaks in chl-*a* were also identified at stations located in the Subantarctic waters (stations 23 and 26) and at stations south of the SAF. At these stations nanophytoplankton were identified as the largest contributor to total chl-*a* concentration. Outside this region, however, picophytoplankton dominated total chl-*a* biomass. The contribution of microphytoplankton total pigment concentration was generally < 5 %. Exceptions were recorded at station 26 and 27 located at the southern boundary of the STC and at station 41 located in the waters surrounding the Prince Edward Islands where microphytoplankton comprised up to 10 % of the total pigment (Fig. 2a).

Total chlorophyll-*a* concentrations during the 1999 cruise ranged from 0.05 to 0.38 µg l^{-1} (Fig. 2a). No enhancement in chl-*a* concentration was observed at stations occupied in the vicinity of the STC (Fig. 2a). Highest chl-*a* concentration was recorded at station 87 located in the Subantarctic Zone Waters and at station 91 in the region of the SAF (Fig. 2). Throughout the cruise, picophytoplankton were identified as the largest contributor to total pigment comprising between 65 and 93 % of the total. Nanophytoplankton contribution ranged between 2 and 36 % of the total pigment. Microphytoplankton contribution to total pigment was always < 2 % of the total (Fig. 2a).

Species richness

Total number of diatom species identified during the four cruises was highly variable. Generally, the highest number of diatom species (up to 44 species) was recorded in the waters north of the STC, south of Africa (Fig. 2b). The lowest number of species, generally < 8, was consistently recorded along the transect occupied in the mid-Indian

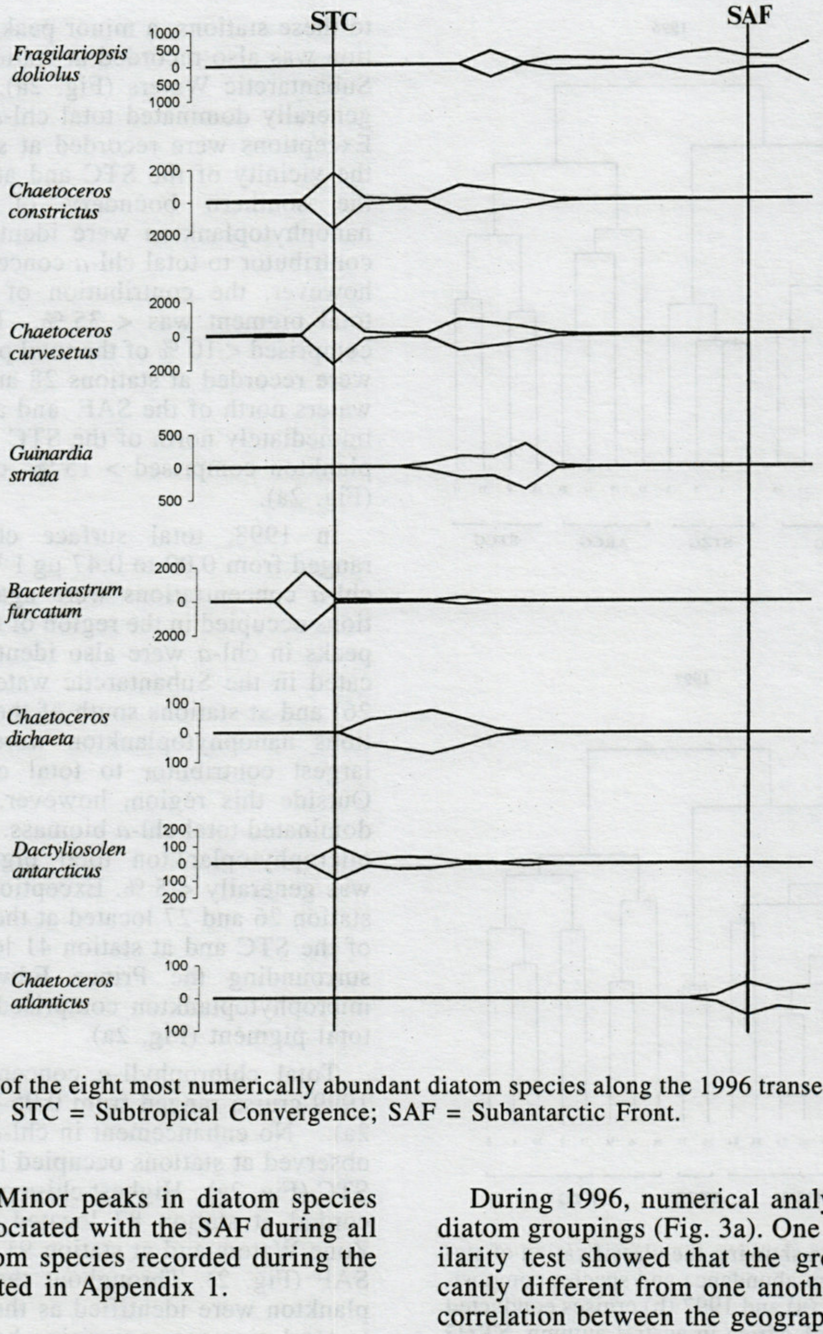

Fig. 4. – Distribution of the eight most numerically abundant diatom species along the 1996 transect occupied in the region south of Africa. STC = Subtropical Convergence; SAF = Subantarctic Front.

Ocean (Fig. 2b). Minor peaks in diatom species identified were associated with the SAF during all four cruises. Diatom species recorded during the four cruises are listed in Appendix 1.

Numerical analyses

Results of the numerical analyses conducted on the diatom data collected during the four cruises is shown in Fig. 3 and 6. Since the majority of the diatom groups were identified with a specific water mass or feature, the groups are designated by the name of the water mass or feature with which they are associated [water masses are identified after Hoffmann (1985) and Boden *et al.* (1988)]. Where groupings did not correspond to a specific oceanographic feature, the groupings are designated numerical values.

During 1996, numerical analysis identified five diatom groupings (Fig. 3a). One way ANOVA similarity test showed that the groups were significantly different from one another ($P < 0.05$). The correlation between the geographic position of the stations along the transect and groupings identified was perfect. The five groupings identified were : The Subtropical Zone Waters Group (STZG), the Agulhas Return Current Group (ARCG), the Subantarctic Zone Group (SAZG) and the Polar Front Zone Group (PFZG). In addition, a diatom grouping was associated with the STC proper and is as a consequence, designated the Subtropical Convergence Group (STCG). The distribution patterns of the eight most numerically abundant diatom species (average abundances within each grouping are indicated in brackets) is shown in Fig. 4. SIMPER analysis showed that these species accounted for up to 53 % of the dissimilarity between the groupings identified with the numerical analysis.

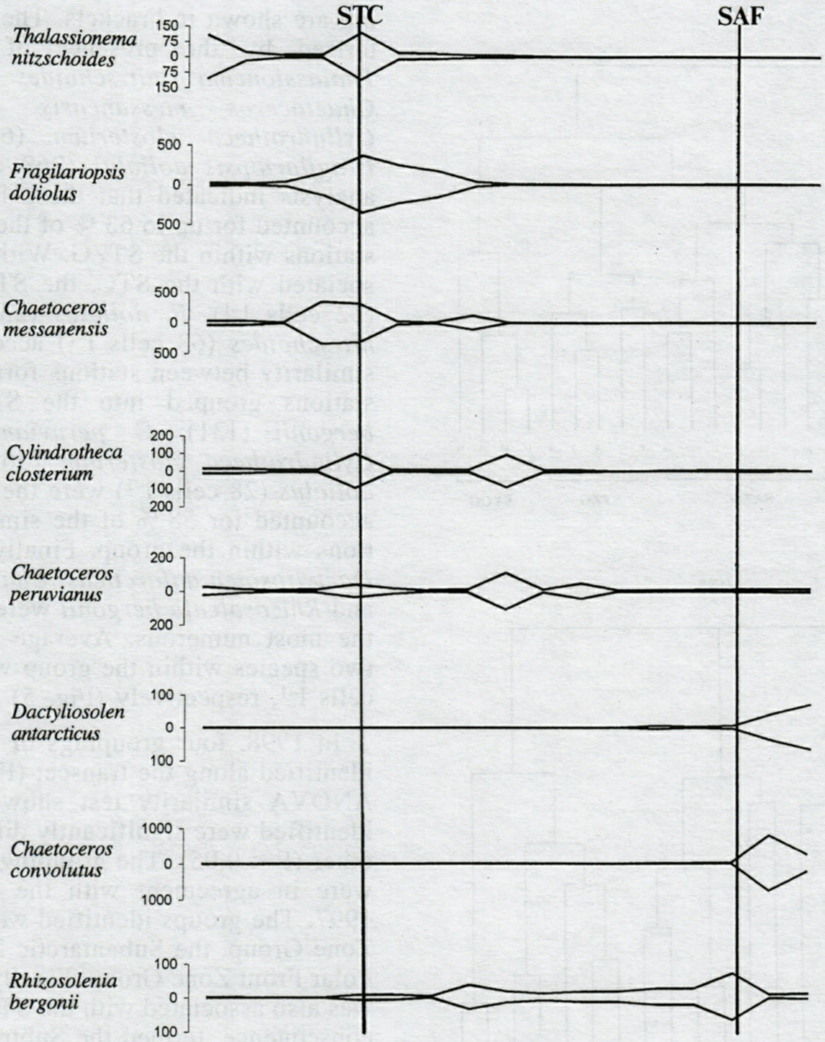

Fig. 5. – Distribution of the eight most numerically abundant diatom species along the 1997 transect occupied in the region south of Africa. STC = Subtropical Convergence; SAF = Subantarctic Front.

The STZG group was characterised by the predominance of three diatom species, *Bacteriastrum furcatum, Chaetoceros curvestus* and *Chaetoceros constrictus*. Average abundances of these three species within the group were 103, 198 and 90 cells l^{-1}, respectively. SIMPER analysis indicated that these three diatom species accounted for up to 43 % of the similarity between stations in the group. Within the grouping associated with the Agulhas Return Current (ARCG), diatom cells counts were almost entirely dominated by *B. furcatum*, *C. constrictus* and *C. curvestus*. The SAZG was dominated by four diatom species, *Guinardia striata (*238 cells l^{-1}*), Chaetoceros dichaeta (*68 cells l^{-1}*)* and *C.curvestus (*367 cells l^{-1}*)*, which accounted for up to 56 % of the similarity between stations within the group. The grouping of stations associated with the STC, the STCG, comprised three main species, *C. constrictus (*1350 cells l^{-1}*), C. curvestus* (1650 cells l^{-1}) and *Dactyliosolen antarcticus* (189 cells l^{-1}) (Fig. 4). Finally within the PFZG, two species predominated, *C. atlanticus* and *Fragilariopsis doliolus*. Average abundances of these two diatom species within the grouping were 90 and 286 cells l^{-1}, respectively. SIMPER analysis showed that these two diatom species accounted for up to 48 % of the similarity between stations within the grouping.

Hierachial cluster analysis identified four groupings of stations along the 1997 transect (Fig. 3b). One way ANOVA showed that all four groups identified were significantly different from one another ($P < 0.05$). The correlation between the geographic position and groupings identified was again, perfect. The first group contained all those stations found north of the STC and is, therefore, designated the Subtropical Zone Group. The second groupings comprised those stations which were in the immediate proximity to the STC and is therefore, designated the Subtropical Convergence

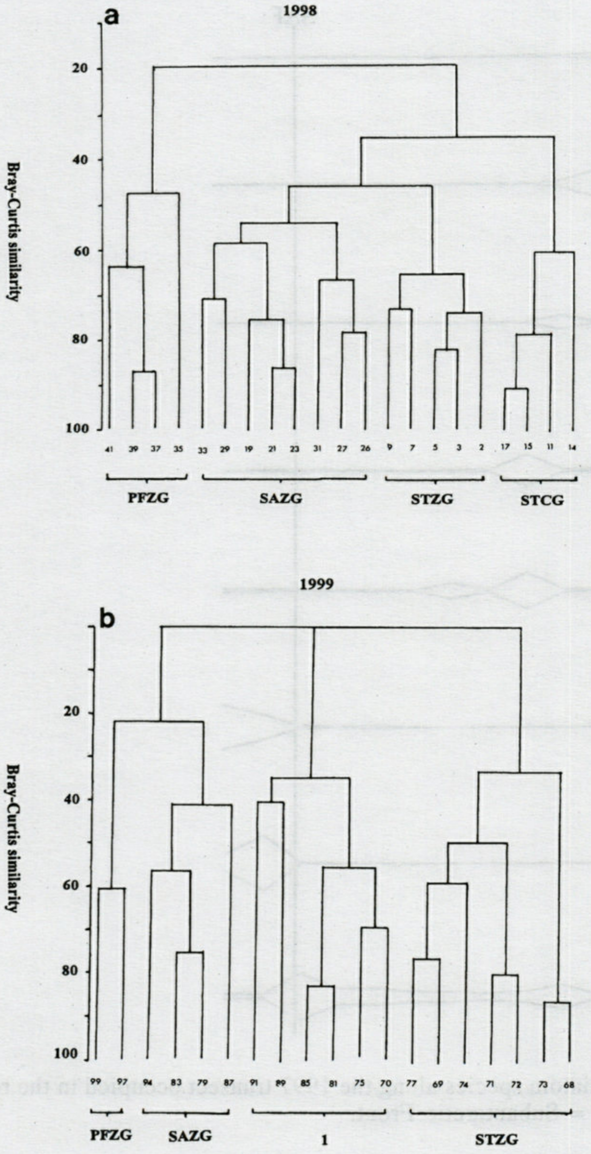

Fig. 6. – Dendrogram showing the classification of stations based on diatom abundance and species composition during the 1998 (A) and 1999 (B) cruises occupied in the region south of Africa and in the mid Indian Ocean in austral autumn. STZG = Subtropical Zone Group; SAZG = Subantarctic Zone Group; STCG = Subtropical Convergence Group; PFZG = Polar Frontal Zone Group.

Group (STCG). Finally groups three and four contained those stations located in the Subantarctic Zone and stations within the Polar Front Zone. As a consequence the two groups are designated the Subantarctic Zone and Polar Front Zone Groups (Fig. 3b).

The distribution patterns of the eight most numerically abundant diatom species accounting for up to 65 % of the dissimilarity between the diatom groupings identified is shown in Fig. 5. Average abundances of diatom species within each grouping are shown in brackets. The STZG was characterised by the presence of 4 main species, *Thalassionema nitzschoides* (84 cells l^{-1}), *Chaetoceros messanensis* (142 cells l^{-1}), *Cylindrotheca closterium* (65 cells l^{-1}) and *Fragilariopsis doliolus* (268 cells l^{-1}). SIMPER analysis indicated that these four diatom species accounted for up to 63 % of the similarity between stations within the STZG. Within the grouping associated with the STC, the STZG, *C. peruvianus* (32 cells l^{-1}), *F. doliolus* (230 cells l^{-1}) and *T. nitzschoides* (68 cells l^{-1}) accounted for 34 % of similarity between stations forming the STCG. At stations grouped into the SAZG, *Rhizosolenia bergonii* (131), *C. peruvianus* (67 cells l^{-1}), *Cylindrotheca closterium* (36 cells l^{-1}) and *F. doliolus* (28 cells l^{-1}) were the most abundant and accounted for 58 % of the similarity between stations within the group. Finally within the PFZG, *Dactyliosolen antarcticus*, *Chaetoceros convolutus* and *Rhizosolenia bergonii* were identified as being the most numerous. Average cells counts of the two species within the group were 63, 328 and 32 cells l^{-1}, respectively (Fig. 5)

In 1998, four groupings of stations were again identified along the transect (Fig. 6a). A one way ANOVA similarity test showed that the groups identified were significantly different from one another ($P < 0.05$). The groupings identified in 1998 were in agreement with the results obtained in 1997. The groups identified were : the Subtropical Zone Group, the Subantarctic Zone Group and the Polar Front Zone Group. Finally a diatom grouping was also associated with the STC proper and is as a consequence, termed the Subtropical Convergence Group (Fig. 6a).

Fig. 7 shows the distribution patterns of the eight most numerically abundant diatom species along the 1998 transect. SIMPER analysis indicated that these species were responsible for up to 53 % of the dissimilarity between groupings identified. In the STZG, three diatom species, *Dactyliosolen antarcticus* (170 cells l^{-1}), *Banquisia belagicae* (90 cells l^{-1}) and *Fragilariopsis kerguelensis* (1176 cells l^{-1}) dominated cells counts. Collectively, these species accounted for 39 % of the similarity between stations making up the STZG. Within the SAZG, *Rhizosolenia bergonii* (21 cells l^{-1}), *F. kerguelensis* (706 cells l^{-1}), *Thalassiosira antarcticus* (106 cells l^{-1}), *D. antarcticus* (131 cells l^{-1}) and *C. atlanticus* (108 cells l^{-1}) were identified as being the most numerous. These species accounted for 56 % of the similarity between stations making up the STZG. *Hemialus cuniforms* (66 cells l^{-1}), *C. atlanticus* (98 cells l^{-1}) and *F. kerguelensis* (767 cells l^{-1}) were identified as the most abundant at stations occupied within the PFZG (Fig. 7). Combined these three species accounted for up to 39 % of the similarity between stations within the group. Finally within

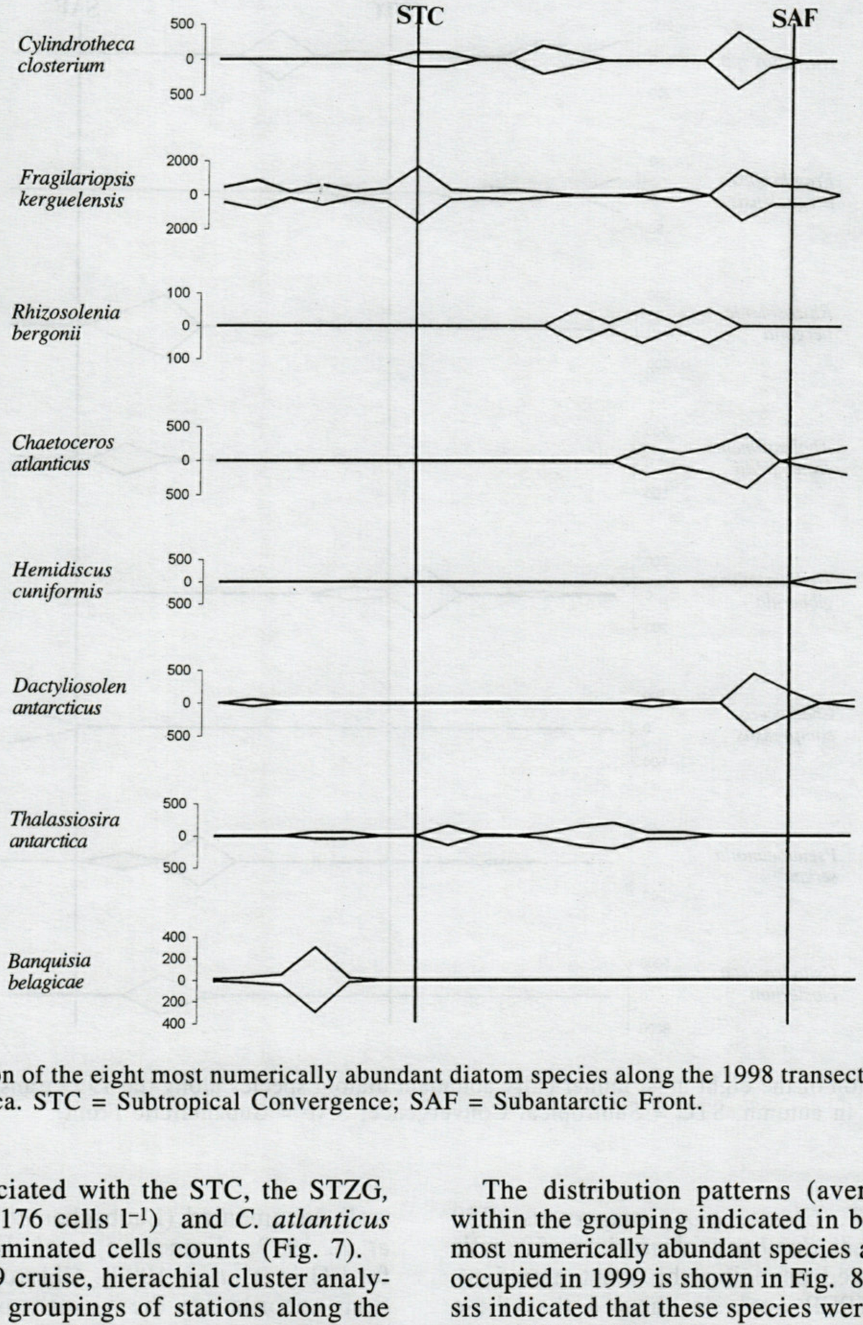

Fig. 7. – Distribution of the eight most numerically abundant diatom species along the 1998 transect occupied in the region south of Africa. STC = Subtropical Convergence; SAF = Subantarctic Front.

the grouping associated with the STC, the STZG, *F. kerguelensis* (1176 cells l^{-1}) and *C. atlanticus* (237 cells l^{-1}) dominated cells counts (Fig. 7).

During the 1999 cruise, hierachial cluster analysis identified four groupings of stations along the transect (Fig. 6b). The first group contained those stations located at the northerly section of the transect and is designated the Subtropical Zone Group (STZG). The second grouping comprised those stations located immediately north and south of the STC including those stations in the vicinity of the front. Since the grouping was not associated with any specific feature or water mass, the grouping is designated Group 1. Group three contained stations located within the Subantarctic Zone, and group 4 stations found south of the SAF. These groupings are designated as the Subantarctic Zone Group (SAZG) and the Polar Front Zone Group (PFZG). One way ANOVA similarity test showed that only STZG and PFZG were significantly different from one another ($P < 0.05$).

The distribution patterns (average abundances within the grouping indicated in brackets) of the 8 most numerically abundant species along the transect occupied in 1999 is shown in Fig. 8. SIMPER analysis indicated that these species were responsible for up to 38 % of the dissimilarity between the grouping identified. Within the STZG, *Fragilariopsis kerguelensis* (7 cells l^{-1}), *Thalassiosira gibberula* (31 cells l^{-1}) and *Nitszchia* spp. (33 cells l^{-1}) were identified as being the most abundant (Fig. 8). Combined these species accounted for 95 % of the similarity between stations making up the STZG. Within the grouping comprising stations located to the north and south of the STC, *T. gibberula*, *Rhizosolenia bergonii*, *Nitzschia* spp, *Thalassionema frauenfeldii* and *Pseudoeunotia seriata*. Average cells counts of these four species were 11, 135, 926, 86 and 926 cells l^{-1}, respectively. At stations comprising the SAZG, *Pseudoeunotia seriata*, *Cylindrotheca closterium*, *R. bergonii* and *Thalassionema frauenfeldii* dominated. Finally

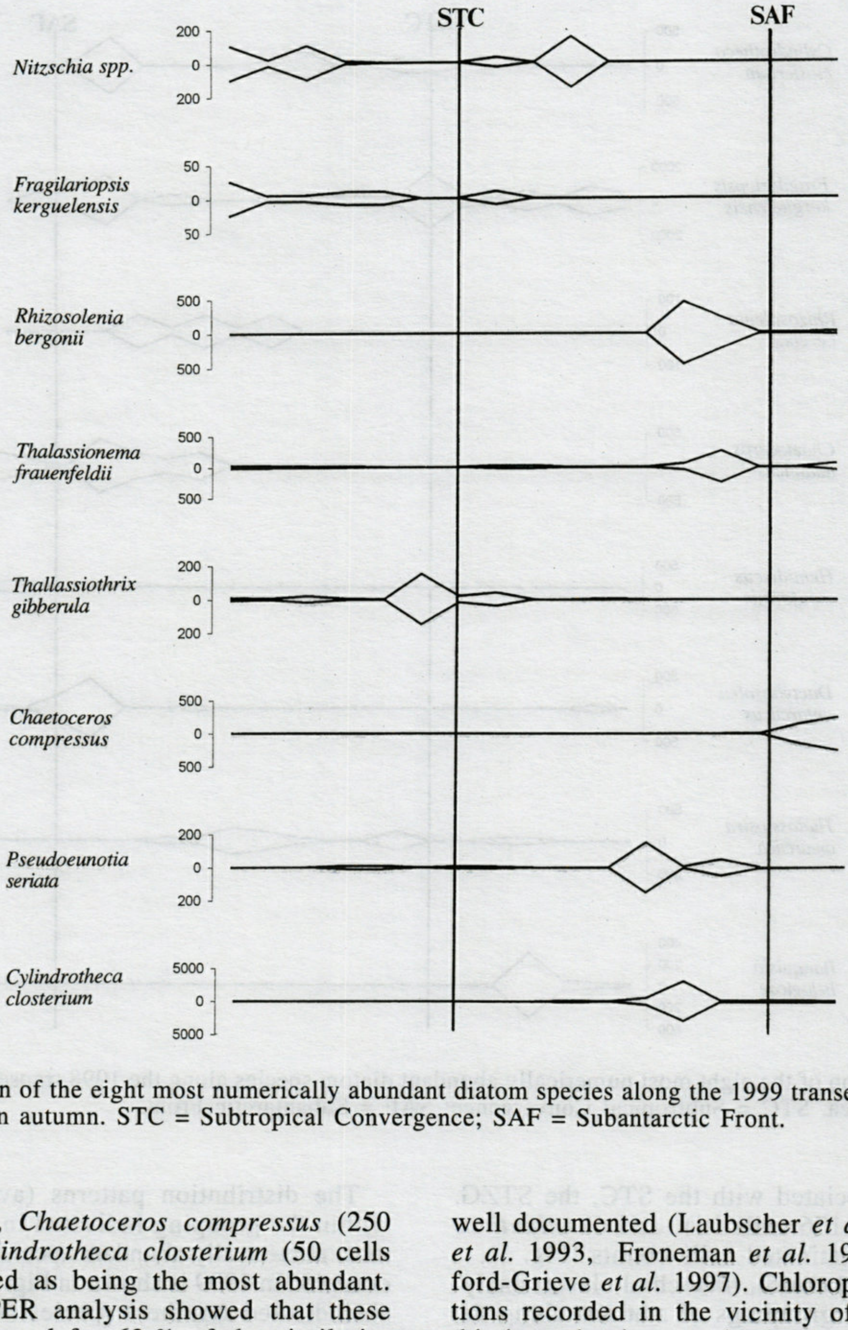

Fig. 8. – Distribution of the eight most numerically abundant diatom species along the 1999 transect conducted in the mid-Indian Ocean in autumn. STC = Subtropical Convergence; SAF = Subantarctic Front.

within the PFZG, *Chaetoceros compressus* (250 cells l^{-1}) and *Cylindrotheca closterium* (50 cells l^{-1}) were identified as being the most abundant. Combined SIMPER analysis showed that these two species accounted for 63 % of the similarity between stations within the group (Fig. 8).

DISCUSSION

Pigment concentrations

During the three transects occupied in the region south of Africa in autumn, enhanced chlorophyll-*a* (chl-*a*) concentrations were recorded in the vicinity of the Subtropical Convergence (STC) (Fig. 2a). Elevated biological activity in the vicinity of the STC in different sectors of the Southern Ocean is well documented (Laubscher *et al.* 1993, Sullivan *et al.* 1993, Froneman *et al.* 1995a, 1999, Bradford-Grieve *et al.* 1997). Chlorophyll-*a* concentrations recorded in the vicinity of the STC during this investigation, are in the same range as values reported in summer (Laubscher *et al.* 1993; Froneman *et al.* 1995a, 1995b) suggesting little seasonality in phytoplankton biomass. This result is in agreement with studies conducted in the vicinity of the STC in the region near New Zealand (Bradford-Grieve *et al.* 1997, Chang & Gall 1998). No biological enhancement was recorded in the vicinity of the STC in the mid-Indian Ocean. There is evidence to suggest that the elevated chl-*a* concentration recorded in the vicinity of the STC is the result of increase *in situ* phytoplankton production resulting from increased water column stability, macronutrient concentrations and iron availability (Laubscher *et al.* 1993, Comiso *et al.* 1993, Bradford-Grieve *et al.* 1997, Froneman *et al.* 1999).

While the absence of chl-*a* signal within the mid-Indian Ocean may reflect biological interactions such as grazing by zooplankton, preliminary data collected during the 1999 cruise suggested that zooplankton biomass in the region of the front was in the same order of magnitude as values reported in the region south of Africa (Pakhomov *et al.* 2000a). We can only speculate on the potential causes for the low chl-*a* concentrations recorded in vicinity of the STC in the mid-Indian Ocean. Weeks and Shillington (1994) proposed that the elevated chl-*a* concentrations recorded in the vicinity of the STC were the result of the mixing of warm-nutrient poor Subtropical waters with the colder Subantarctic waters which results in density stratification thus creating conditions favourable for phytoplankton growth. Indeed, chl-*a* concentrations in the region of the front have been shown to be strongly correlated to frontal intensity (Weeks & Shillington 1996). Belkin (1989) showed that the temperature gradient across the STC in the mid-Indian Ocean decreases. Under these conditions, density stratification would also be reduced resulting in less favourable conditions for phytoplankton growth. Alternatively, it is possible that the absence of a chl-*a* signal in the vicinity of the STC in the mid-Indian Ocean may reflect increased wind stress that would reduce phytoplankton growth (Weeks & Shillington, 1994, Froneman *et al.* 1999).

Finally the elevated chl-*a* concentrations recorded in the continental shelf waters south of Africa in 1996 is in agreement with previous studies conducted in the region (Laubscher *et al.* 1993; Froneman *et al.* 1999). According to Boden *et al.* (1988), the elevated chl-*a* concentrations recorded in continental shelf waters of southern Africa is the result of the transportation of phytoplankton cells in the Agulhas Current to the region. Alternatively, it is possible that the elevated chl-*a* concentrations recorded in the shallow continental shelf waters are the result of increased *in situ* phytoplankton production resulting from increased nutrient availability (Laubscher *et al.* 1993).

Species richness

Species richness during the four surveys was highest in the waters immediately north of the STC south of Africa (Fig. 2b). The increase in the number of diatom species in this region reflects the complex oceanographic regime. South of Africa, two oceanographic features are encountered, the Agulhas Current (which later retroflects to form the Agulhas Return Current (ARC)) and the Subtropical Convergence (Lutjeharms & Vallentine 1984, Duncombe Rae 1989, Lutjeharms *et al.* 1993). Boden *et al* (1988) showed that warm subtropical diatom species (for example *Ceratualina pelagica*) may be transported in the Agulhas Current to the region south of Africa. It is worth noting that in 1996, a distinct diatom grouping was associated with the Agulhas Return Current (Fig. 3a). The low number of diatom species recorded in the mid-Indian Ocean suggests that water mass modification may have occurred as no indicator species of Agulhas Current waters were recorded (Appendix 1). Following this, the low number of species recorded along the transect in mid-Indian Ocean likely reflects the low nutrient availability of Subtropical waters which limits the growth of large phytoplankton cells (Laubscher *et al.* 1993; Froneman *et al.* 1999).

The diatom species recorded during this investigation are similar to studies conducted in the region during summer (Boden *et al.* 1988; Froneman *et al.* 1995a, 1995b). It should be noted, however, that while similar species were recorded during the four cruises, there was considerable inter-annual variability in the dominants. In the absence of ecophysiological data, we cannot determine the cause of the variability in the dominants. However, the variability likely reflects the complex hydrological processes in the region that favour the growth of individual species.

Numerical analyses

Results of the numerical analysis indicate that distinct diatom groupings were associated with the different water masses in the south-east Indian Ocean. This result is in agreement with previous studies conducted in different sectors of the Southern Ocean during both summer and winter (Froneman *et al.* 1995a, 1995b, Fiala *et al.* 1998). Differences in the species composition within the different water masses reflect the spatial and temporal variations in the Southern Ocean pelagic ecosystem (Boden *et al.* 1988, Fiala *et al.* 1998).

In contrast to the region south of Africa, the STC did not appear to represent a biogeographic barrier to the distribution of diatoms in the mid-Indian Ocean. This result is in agreement with a similar study conducted in the mid-Atlantic Ocean (Barange *et al.* 1998). South of Africa, the STC is characterised by a sharp horizontal gradient in temperature which at times may be as high as 3°C per 10 km (Lutjeharms & Emery 1983). Given the extreme temperature gradient across the front, it is not surprising that it represents a strong biogeographic boundary to the distribution of plankton. In contrast in the mid-Indian Ocean, the temperature gradient across the STC decreases (Belkin 1989). Due to this decrease plankton species are able to penetrate the front. Alternatively, it is possible that the surface expression of the STC in the mid-Indian Ocean is intermittent rather than weak as demonstrated in the mid-Atlantic Ocean (Lutjeharms *et al.* 1993, Barange *et al.* 1998). Weeks and Shillington (1996) showed that pigment levels in the region of the STC were largely a function of the frontal intensity. The variability in intensity of the front may partially explain the inter-annual variability in pigment concentrations in the region of the STC as demonstrated by the Coastal Zone Color Scanner (CZCS) measurements (Weeks & Shillington 1994). It should be noted, however, that south of Africa diatoms may on occasions be transported across the STC by warm-core eddies shed from the Agulhas Return Current (Froneman *et al.* 1997).

Distinct diatom assemblages were associated with the STC proper during the three transects conducted south of Africa. This result is in agreement with a previous study conducted in the mid-Atlantic Ocean (Barange *et al.* 1998). Barange *et al.* (1998) suggested that the presence of a unique plankton community associated with the STC was the result of specific hydrological features of the frontal zone which allowed the presence of species from different water masses to occur in the immediate proximity of the front. During a study conducted in the Atlantic sector of the Southern Ocean, Froneman *et al.* (1995b) identified a distinct phytoplankton community associated with the Antarctic Polar Front (APF). The community associated with the front comprised species from the water masses to the north and south of the front. During the present study, the microphytoplankton groupings associated with the STC contained indicator species of both Subtropical Zone (*Hemialus hauckii*) and Subantarctic Zone waters (*Rhizosolenia bergonii*) (Boden *et al.* 1988). These data are consistent with the findings of Frontier (1977) who suggested that interaction of different water masses in the region of frontal systems may result in a unique and specific fauna.

The importance of the Subantarctic Front (SAF) as a barrier to the distribution of plankton in the Southern Ocean is not well documented. Although the front appears to represent an important barrier to the distribution of plankton in the Atlantic and Pacific sectors of the Southern Ocean (Froneman *et al.* 1995b, Pakhomov & McQuaid 1996, Pakhomov *et al.* 2000b), recent studies conducted in the region of the Prince Edward Islands in the Indian sector of the ocean failed to identify the front as a biogeographic boundary (Froneman & Pakhomov 1998). The absence of the front as a biogeographic boundary to the distribution of plankton appeared to be related to both cross frontal mixing and variability in the surface expression of the front, which transferred plankton across the front. Possibly, eddies generated by instabilities in the flow of the Antarctic Circumpolar Current may also have contributed to the transfer of species across the SAF (Ansorge *et al.* 1999, Froneman *et al.* 1999). During the present study the SAF always represented a strong biogeographic boundary to the distribution of diatoms. Oceanographic studies conducted in the vicinity of the Prince Edward Islands have demonstrated that the flow pattern of the ACC in the region of the islands comprises two distinct components. Upstream of the islands (west), the flow pattern of the ACC appears to be substantially affected by bathymetry (Froneman *et al.* 1999). This results in less disturbances in the flow pattern of the ACC (Froneman *et al.* 1999). As a consequence of the reduced disturbances, cross frontal mixing is less pronounced resulting in plankton not being transported across the SAF. In contrast, downstream (east) of the islands the flow of the ACC is highly disturbed. This disturbance generates cross frontal mixing and the formation of eddies which transfer plankton species across the SAF (Ansorge *et al.* 1999, Froneman *et al.* 1999). These facts highlight the spatio variability in the importance of fronts as barriers to the distribution of plankton.

CONCLUSION

Results of the study suggest that the major oceanic fronts south of Africa, in particular the STC, are characterised by biological enhancement and represent strong biogeographic boundaries to the distribution of diatoms. In contrast in the mid-Indian Ocean, the STC did not demonstrate increased chlorophyll-*a* concentrations and was not important in limiting the distribution of diatom species. Differences between the two regions appears to be related to the intensity of the STC. It is likely that the importance of the STC as biogeographic boundary to the distribution of diatoms in the mid-Indian Ocean will display marked spatial variability. For example in the region of the Crozet Plateau, the SAF converges with the STC resulting in a frontal feature with a sharp horizontal temperature gradient (Belkin 1989). Here, the coalescing of the two fronts would likely result in the feature representing a strong biogeographic barrier. Finally, although the data presented here represent only a small portion of the plankton community, it is worth noting that the results obtained here are in agreement with studies that have investigated the distribution of zooplankton across the major frontal regions of the Southern Ocean (Pakhomov & McQuaid 1996, Young *et al.* 1996, Barange *et al.* 1998, Pakhomov *et al.* 2000b).

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Appendix 1

1996

Actinocyclus octonarius Ehrenburg
Asteromphalus hookeri Ehrenburg
A. roperianus (Greyville) Ralfsin Prichard
Banquisia belgicae Paddock
Ceratualina pelagica Hendy
Chaetoceros affinis Lauder
C. atlanticus Cleve
C.convolutus Castracane
C.contrictus Gran
C. dichaeta Ehrenburg
C.didymus Ehrenburg
C.messanensis Castracane
C.peruvianus Brightwell
Corethron criophilum Castracane
Coscinodiscus concinniformis Simonsen
Cylindrotheca closterium Ehrenburg
Dactyliosolen antarticus Castracane
Fragilariopsis doliolus Medlin &Sims
F. kerguelensis Hustedt
Grammatophora marina Kutzing
G.angulosa H..Pergallo
Guinardia striata Hasle
G.cylindrus Hasle
Haslea gigantea Simonsen
Hemialus hauckii Grunow
Hemidiscus cuneiformis Wallich
Melosira sol Kutzing
Nitzschia bicapitata Cleve
Planktoniella sol Schutt
Proboscia alata Brightwell
P.indica Ehrenburg
Pseudo-nitzchia spp.
Pseuodeunotia seriata H.Pergallo
Pleurosigma directum Grunow
Rhizosolenia bergonii H.Pergallo
R.hebetata f. semispina Gran
R.simplex Karsten
Thalassionema nitzschiodes Grunow
T. frauenfeldii Hallegraeff
Thalassiothrix longissima Cleve & Grunow
T.antarctica Hasle

1997

Actinocyclus octonarius
Asteromphalus hookeri
A.marylandica Ehrenburg
A. roperianus
Banquisia belgicae
Ceratualina pelagica
Chaetoceros affinis
C. atlanticus
C.convolutus
C.*contrictus*
C. dichaeta
C.didymus
C.messanensi
C.peruvianus
Corethron criophilum
Coscinodiscus concinniformis
Cylindrotheca closterium
Ditylum sol Grunow
Dactyliosolen antarticus
Fragilariopsis doliolus
F. kerguelensis
Grammatophora marina
G.angulosa
Guinardia striata
G.cylindrus
Hemialus hauckii
Hemidiscus cuneiformis
Melosira sol
Nitzschia bicapitata
Planktoniella sol
Proboscia alata
P.indica Hasle
Pseuodeunotia spp.
Pseuodeunotia seriata
Pleurosigma directum
Rhizosolenia bergonii
R.hebetata f. semispina
Synedra indica Taylor
T*halassionema nitzschiodes*
T. frauenfeldii
Thalassiothrix longissima
T.antarctica
*T.heteromorpha*Hallegraeff

1998

Actinocyclus octonarius
Asteromphalus *marylandica*
Asteromphalus hookeri
A. roperianus
Bacteriastrum furcatum Shadbolf
Ceratualina pelagica
C. atlanticus
C.compressus
C.decepiens
C.didymus
C.messanensis
C.peruvianus
C.convolutus
Cerutalina pelagica
Corethron criophilum
Cosconodiscus spp
Cylindrotheca closterium
Dactyliosolen antarticus
Fragilariopsis spp
Fragilariopsis doliolus
F. kerguelensis
Guinardia striata
Haslea gigantea
Hemialus hauckii
Odontella longicruris Hoban
Planktoniella sol
Pleurosigma directum
Pseudoeunotia seriata
Rhizosolenia bergonni
Proboscia alata
P.indica
Skeltonema costatum Cleve
Synedra indica
Thalassionema nitzschiodes
T. frauenfeldii
Thalassiothrix longissima

1999

*Asteromphalus heptactis*Ralfs
Chaetoceros atlanticus
C.dichaeta
C.concavicornis Mangin
C.neglectus
Corethron criophilum
Dactlyliosolen antarcticus
Fragilariopsis kerguelensis
Nitzschia spp
N.bicaptata
Proboscia indica
Pseudoeunotia seriata
Rhizosolenia bergonni
Thalassionema nitzschiodes
Thalassiosira giberula Hasle
Thalassiothrix antarctica
T.longissima

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SPECIES BODY-SIZE DISTRIBUTION AND SPATIAL SCALE IN IBERIAN ANTS

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ANT ASSEMBLAGES
BODY SIZE
IBERIAN PENINSULA
MACROECOLOGY
SPATIAL SCALING

ABSTRACT – The specific body size distribution (BSD) for Iberian ants (workers) was compiled and compared to subsamples of that distribution at four smaller scales, from very local samples to species-lists for autonomous regions. The BSD of Iberian ants was right-skewed on a log scale and approached normality. The mean dry body mass ± s.d. was 0,93 ± 1,55 mg and the median 0,31 mg. Neither local samples nor samples at intermediate scales differed from random samples from the underlying Iberian distribution in median or skewness. Limited geographical scope or a misdirected measure (single individual mass) in this study could explain why we did not find the pattern of a previously reported difference in BSD of local samples as compared to regional samples in mammals. The BSD of local samples in Iberian ants was not influenced by latitude.

COMMUNAUTÉS DE FOURMIS
TAILLE CORPORELLE
PÉNINSULE IBÉRIQUE
MACROÉCOLOGIE
ÉCHELLE SPATIALE

RÉSUMÉ.– La distribution spécifique de la masse corporelle des ouvrières de Fourmis ibériques est recensée et comparée à celle de sous-échantillons à différentes échelles spatiales allant du niveau local au niveau de listes spécifiques de communautés régionales. La distribution des masses en logarithmes est biaisée à droite mais approche d'une normale. La moyenne (± p.s.) des masses corporelles (matière sèche) est de 0,93 ± 1,55 mg et la médiane de 0,31 mg. Les échantillons à différentes échelles ne diffèrent pas d'échantillons aléatoires de la distribution ibérique, en ce qui concerne la médiane et la skewness. La restriction géographique limitée à la Péninsule Ibérique, ou bien une mesure non appropriée dans notre étude pourraient expliquer l'absence du pattern connu chez les Mammifères, dans le sens d'une différence entre les masses corporelles des échantillons locaux comparées à celles des échantillons régionaux. La masse corporelle des Fourmis ibériques ne semble pas influencée par la latitude.

INTRODUCTION

The distribution of body size of many animal species, from mammals (Brown & Nicoletto 1991, Maurer *et al.* 1992), birds (Blackburn *et al.* 1990, Maurer *et al.* 1992, Blackburn & Gaston 1994a), fish (Brown *et al.* 1993) to insects (Schoener & Janzen 1968, Morse *et al.* 1988, Basset & Kitching 1991, Blackburn *et al.* 1990, Siemann *et al.* 1996, Novotny & Kindlmann 1996) and intertidal invertebrates (Navarrete & Menge 1997) shows a distinct skewed pattern. There are relatively more small than large species. This is invariable when body size is plotted on a log scale. Furthermore, when body-size distribution (BSD) on different spatial scales are compared, differences have emerged: BSD from local communities is markedly different from BSD on a larger or global scale. The shape of the BSD in North American mammals changes from log-skewed on a continental scale to log-uniform at smaller scales, with an intermediate pattern on a regional scale (Brown & Maurer 1989, Brown & Nicoletto 1991); this has also been indicated for Australian mammals (Blackburn & Gaston 1994b). A scale-related difference in BSD for aquatic communities has been shown by Fenchel (1993). We are not aware of other published analyses of systematic differences in BSD between local and regional assemblages. The generality of this scale-related pattern is unknown.

Here we document the interspecific body size distribution of Iberian ants and test the validity of the described pattern of change in the BSD with increasing spatial scale, from local habitats (< 1 km²) to Iberian Peninsula level (580.000 km²). Our study aimed to determine (1) the shape of the body size distribution for the ant species of the Iberian Peninsula, (2) trends of change of that distribution according to spatial scale, (3) discover possible methodological and temporal biases in the data base used.

MATERIAL AND METHODS

Peninsular assemblage of Iberian ants: a species list of Iberian ants was compiled, using different sources. The data base for the Iberian Peninsula was based on Collingwood (1978), updated with all posterior papers concerning Iberian ants, with descriptions of new species and/or revisions of species-groups. We added 9 still undescribed species. A two-step process was followed: (1) head length (HL) of workers was directly measured under the stereoscopic microscope to the nearest 0.006 mm for the smallest ants (up to 1.3 mm HL; n = 110 species) or nearest 0.013 mm for bigger ants (n = 32 species); for 95 species HL was taken directly from published information; (2) dry body mass was then obtained by applying the transformation from Kaspari & Weiser (1999): dry body mass in g $(M) = (4.7297 \times 10^{-4})$ $HL^{3.179}$. Data are presented in mg instead of g.

When analysing body size distributions authors use an average adult body mass, sometimes for a specific sex (females in birds, Blackburn & Gaston 1994). Roughly a third of Iberian species show a marked variation in size, originating from true polymorphism (sensu Wilson 1953) (38 species, from *Camponotus, Messor, Proformica, Cataglyphis, Pheidole*) or due to highly variable monomorphism (some *Tapinoma, Formica, Lasius, Aphaenogaster*). In polymorphic species, the minimum and maximum were taken and the mean used. It should be noted that in so doing three non-existent body sizes, from the purely dimorphic species of *Pheidole* were used; we assume that three in 237 is too small a proportion to change the shape of the BSD. Log-transformed body masses are used throughout the paper unless otherwise stated.

Local and other spatial scale assemblages of Iberian ants: Several distinct spatial scales were compared. The smallest scale (scale 1) studied was the range 1-10 km^2. 17 species lists were compiled from published information for local (=homogeneous habitat) samples and data restricted to those papers where an exhaustive effort had been made to detect the maximum number of species; usually covering at least one or more sampling years. A second scale (scale 2; n = 9) was from 100 to 1000 km^2, scale 3 (n = 6) from 1000 to 10000 km^2 and scale 4 (n = 4) from 10000 to 100000 km^2. Scale 5 comprised the entire Iberian Peninsula (581.600 km^2). A BSD for every sample at each different scale was generated, including the Iberian Peninsula data base.

Latitudinal trend: Geography may influence insect size patterns. Schoener & Janzen (1968) found temperate ants to be smaller than tropical ants. In Europe, Cushman *et al.* (1993) found that body size in European ants shows a latitudinal trend: body size increases significantly with increasing latitude. To determine whether this trend could interact with BSD we regressed mean body size against latitude. Only the very local samples (scale 1), assumed to be a single point (=without range) in space, were used.

Statistical analysis: A formal test of normality for the whole log-transformed BSD for Iberian ants was done with a Lilliefors test, an equivalent of the widely used Kolmogorov-Smirnov test, but preferable when the mean and s.d. of the normal distribution to which the data are compared are unknown and are estimated from the data (Sokal & Rohlf 1981: 711) with a Shapiro-Wilk *W* test. As shown by Loder *et al.* (1997) the slope of the frequency distribution for species in body size classes above the modal size class changes from –2.05 when 80 classes are used, to –2.4 for 40 classes and to –3.36 when just 5 size classes are used. In the absence of external justification, the number of classes used in the Lilliefors test is an arbitrary component and the Lilliefors test is sensitive to the number of classes used, but only for very big changes. Results of the Lilliefors test on Iberian ant BSD did not change for a range of 5 to 40 size classes. For visual presentations, inter-scale comparisons were done using the same number of size classes, that was set at 12.

There are several approaches to comparing BSD at different scales. Both central and dispersion parameters can be used. We have followed the same protocol as Brown & Nicoletto (1991): the BSD among species for local samples were compared with null models assuming that species were random samples from a larger-scale species pool. For each of the 17 local samples, 1000 bootstraps were done on the Iberian Peninsula BSD, with the number of species for that local sample and the distribution of medians and skewness of the simulated BSDs used to evaluate the null hypothesis of no difference of BSD for each local sample with the BSD for the Iberian Peninsula. The proportion of the 1000 simulations less than the observed value is the probability of failing to reject the null hypothesis. This procedure was repeated for the other scales, with the number of species per sample adjusted as needed. Analyses were done with Statistica 5.01 (Statsoft, Inc; Tulsa, OK) and Simstat for Windows 1.01 (Provalis Research, Montreal, QC).

RESULTS

Peninsular body-size distribution

There are currently 237 described Iberian ant species with workers. The BSD (Fig. 1) shows that most species are of intermediate size, with smaller numbers of both larger and smaller species. The very smallest species show the generally observed decline in frequency. The mean dry body mass ± s.d. was 0.93 ± 1.55 mg and the median 0.31 mg. The modal class was composed mainly of *Leptothorax* species. The largest size (9.76 mg; big workers of *Camponotus ligniperdus* (Latreille) was 2570 times the smallest one (0.0038 mg; *Leptanilla zaballosi* López, Martínez & Barandica). Though approaching normality, both the Lilliefors test (max $D = 0.076$; $P < 0.01$) and the Shapiro-Wilk

Table I. – Body mass of Iberian ants according to subfamily. Mean ± s.d. in mg. n: number of species. ANOVA, $F_{4,231} = 51,0$; $p < 0,001$. Different superscripts indicate statistical differences by a post-hoc Tukey's test.

Subfamily	Mean ± s.d.	n
Ponerinae^a	0.28 ± 0.32	9
Myrmicinae^a	0.41 ± 0.65	131
Dolichoderinae^a	0.18 ± 0.11	10
Formicinae^b	1.99 ± 2.15	81
Leptanillinae^c	0.008 ± 0.003	5

test ($W = 0.98$; $P = 0.024$) on log-transformed body mass showed that the BSD departed statistically from a normal distribution. There was a strong taxonomical component of variation in body size. When broken down by subfamily, body mass of Iberian ants were strongly divergent (Table I).

Local and other spatial scale assemblages of Iberian ants

A visual inspection of BSD for scale 1 samples (not presented) appears to show an almost uniform distribution but local samples did not differ —either in median or skewness–– from a random sample of the whole assemblage of Iberian ants (Table II). Two cases of local samples nested in levels 3 and 4 are presented in Fig. 2. The same results apply for scales 2 to 4 (Table III). The coefficients of variation (Table II, III) did not differ among scales (ANOVA $F_{3,32} = 0.58$; $P = 0.63$).

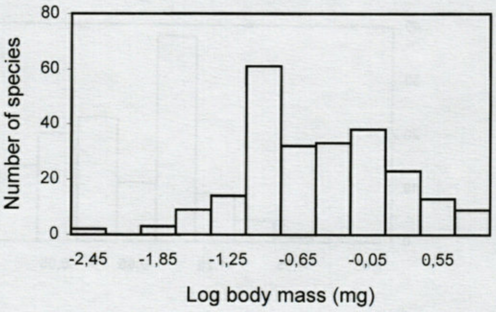

Fig. 1. – Frequency distribution (BSD) of log dry body mass of workers of Iberian ant species (n = 237). Mean dry body mass ± s.d. was 0.93 ± 1.55 mg and the median 0.31 mg. The modal class was composed mainly of *Leptothorax* species. Numbers indicate the lower limit for each class, that is 0.3 wide.

Latitudinal trend

The BSD of local samples was not influenced by latitude. Mean body mass showed no significant increase with latitude (mean dry body mass = – 0.02 + 0.01 latitude; $r^2 = 0.02$; $F = 0.35$; $P = 0.56$) suggesting that ant communities from more northern latitudes in the Iberian Peninsula do not have greater mean mass than those from southern latitudes.

DISCUSSION

The Iberian Peninsula ant fauna showed a greater number of small species and fewer larger

Table II. – Summary statistics for frequency distribution of Log_{10} of body mass (in mg) for Iberian ants in 17 local samples of homogeneous habitat (scale 1; surface 1-10 km^2). Median simulated: mean of the median for 1000 bootstraps of the Peninsular BSD with the number of species as needed for each locality. Skewness simulated: mean of the skewness for 1000 bootstraps of the Peninsular BSD with the number of species as needed for each locality. P is the proportion out of 1000 simulated bootstraps less than the observed value. C.V.: coefficient of variation (s.d.x 100/mean).

Locality	N	Median observed	Median simulated	P	Skewness observed	Skewness simulated	P	C.V.	Ref.
Güejar Sierra	11	-0.37	-0.49	0.53	-0.59	0.04	0.15	117	1
Sª Loja QL	14	-0.76	-0.46	0.26	0.77	0.07	0.89	99	2
Cenes de la Vega	15	-0.37	-0.54	0.57	0.17	0.07	0.54	207	3
Sabiote	15	-0.21	-0.51	0.65	-0.54	0.07	0.15	295	4
Sª Alfaguara QA	16	-0.55	-0.47	0.42	0.37	0.05	0.72	115	2
Arganda	16	-0.27	-0.49	0.67	-0.19	0.05	0.30	233	4
Sª Nevada EN	17	-0.27	-0.51	0.59	0.06	0.01	0.51	275	2
Sª Alfaguara RA	17	-0.16	-0.48	0.73	-0.27	0.03	0.27	355	2
Punta Entinas	19	-0.64	-0.47	0.41	0.11	0.05	0.51	118	9
Sª Nevada RN	21	-0.47	-0.50	0.53	0.30	-0.01	0.77	139	2
Valdelaguna	22	-0.38	-0.47	0.58	0.09	0.04	0.37	180	4
San Juan de la Peña	25	-0.37	-0.49	0.55	0.65	0.03	0.70	359	5
Sª de l'Obac	27	-0.31	-0.51	0.60	0.25	-0.00	0.70	162	6
Sant Cugat	27	-0.66	-0.42	0.39	0.31	0.00	0.73	120	8
Sariñena	30	-0.47	-0.49	0.50	0.42	-0.01	0.83	136	7
Sª Loja EL	30	-0.63	-0.45	0.44	0.37	0.01	0.81	108	2
Sª Nevada EA	35	-0.39	-0.48	0.55	0.15	0.05	0.55	157	2

Ref: 1: González *et al.* 1988; 2: Tinaut *et al.* 1994; 3: Tinaut 1982; 4: Serrano 1982; 5: Franch & Espadaler 1988; 6: Cerdá *et al.* 1989; 7: Espadaler 1986a; 8: Espadaler & López-Soria 1991. 9: Tinaut *et al.* 1995.

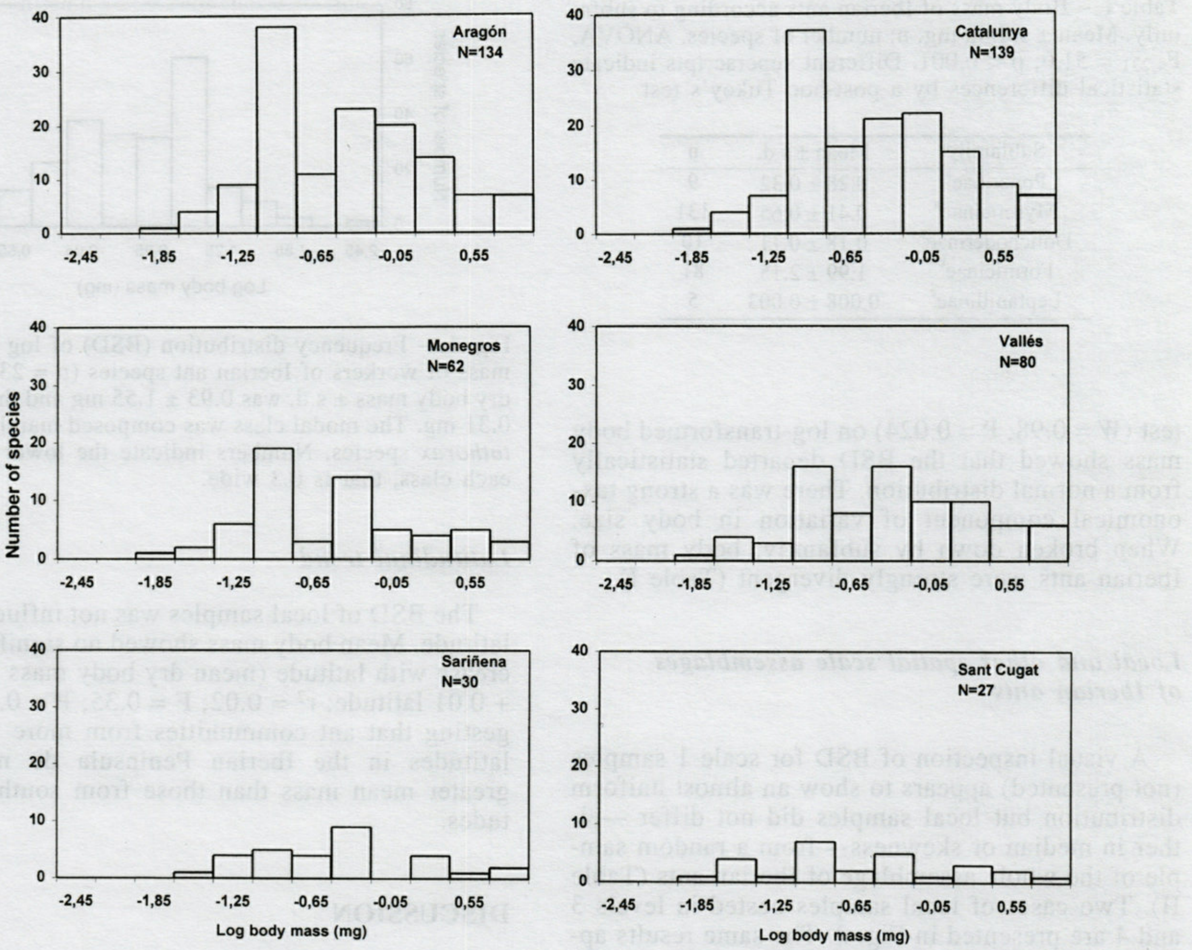

Fig. 2. – Frequency distribution (BSD) of log dry body mass of workers for two local samples (Scale 1: Sarinena and Sant Cugat) nested in their correspondingly higher level scale 3 (Monegros and Vallès) and 4 (Aragon and Catalunya). As scale gets smaller the BSD appears similar to a log uniform distribution but the median and skewness of scale 1 do not differ from random samples of its higher level BSD. N: number of species.

ant species, a pattern already detected for various assemblages by Hutchinson & MacArthur (1959). These authors also found few very small species, a rapid increase in number of species up to a modal size and a slow decline thereafter. Furthermore, bodysize distribution approached log-normal. In this way, our data do not depart from that described for a variety of taxa, from mammals to insects.

The relationships between species numbers, species abundance and body size are generally assumed to be strongly affected by the spatial scale at which studies are done (Blackburn & Gaston 1997, Brown & Maurer 1989). We studied the body-size distribution of Iberian ants, at a specific level. The range of variation of body size was virtually uniform at all scales and we could not detect any spatial effect on median body mass or skewness of the BSD. It follows, therefore, that there was no significant correlation (log s.d. = 0.705 – 0.042 $\log_{10}$ nº species; $r^2 = 0.07$; $p = 0.11$) between body size standard deviation and the logarithm of the number of species, as also found by Novotny & Kindlmann (1996) for a diverse group of taxocoenoses. The BSD of ant communities at varying nested scales seems to be no different from random samples from the underlying distribution at the largest studied scale (580.000 km^2). Neither could a significant increase in the mean size of ants from local samples with an increase in latitude be detected, an effect demonstrated by Cushman *et al.* (1993) for European ants. However, these authors considered a 20º latitude range, while the Iberian Peninsula range covers only 7º. This smaller geographical range may make it difficult to uncover a trend statistically. On a subfamily level, Formicines were also found to be bigger than Myrmicines, as these authors found for northern European ants. The principles that give rise to those distributions seem to act qualitatively the same on Iberian ant communities at disparate spatial scales. We feel it prema-

Table III. – Summary statistics for frequency distribution of Log_{10} of body mass (in mg) for Iberian ants in diverse assemblages (scale 2: surface 100-1000 km^2; scale 3: surface 1000-10000 km^2; scale 4: 10000-100000 km^2; scale 5: Iberian Peninsula, 581.000 km^2). C.V.: coefficient of variation (s.d.x 100/mean).

Locality	N	Median observed	Median simulated	P	Skewness observed	Skewness simulated	P	C.V.	Ref.
Scale 2									
Sª Morena	35	-0.16	-0.49	0.67	-0.45	0.00	0.14	314	1
Garraf	39	-0.27	-0.46	0.58	0.13	-0.03	0.66	237	2
Montnegre	40	-0.30	-0.44	0.62	-0.03	0.00	0.45	255	3
Collserola	42	-0.37	-0.49	0.60	0.39	0.00	0.87	167	4
Montseny	47	-0.21	-0.48	0.64	0.21	-0.02	0.75	275	5
Granada litoral	47	-0.47	-0.47	0.50	0.31	0.00	0.81	158	6
Gibraltar	54	-0.49	-0.47	0.47	0.29	-0.02	0.84	138	7
Sª Alfacar & others	59	-0.37	-0.44	0.52	0.10	-0.02	0.66	197	8
Sª Cazorla & others	71	-0.27	-0.48	0.59	0.21	-0.03	0.80	220	9
Scale 3									
Monegros	62	-0.48	-0.47	0.47	0.27	-0.02	0.84	145	10
Pyrenees (>1000 m)	68	-0.24	-0.51	0.70	0.03	-0.00	0.55	227	11
Sª Nevada	72	-0.31	-0.48	0.61	0.08	-0.03	0.65	187	12
Gavarres & others	80	-0.25	-0.46	0.68	0.18	-0.03	0.80	239	13
Vallès	80	-0.31	-0.48	0.62	-0.00	-0.02	0.56	194	14
Sª Guadarrama	100	-0.35	-0.45	0.60	-0.03	-0.02	0.49	171	15
Scale 4									
Valencia	82	-0.45	-0.48	0.51	0.19	-0.02	0.77	163	16
Portugal	98	-0.32	-0.51	0.65	0.07	-0.04	0.65	195	17
Aragón	134	-0.44	-0.44	0.48	0.19	-0.01	0.86	148	18
Catalonia	139	-0.40	-0.47	0.54	0.15	-0.04	0.84	157	16
Scale 5									
Iberian peninsula	237	-0.51			-0.04			138	see text

P is the proportion out of 1000 simulated bootstrapings that are less than the observed value. Ref: 1: Rodríguez 1981; 2: Espadaler 1992; 3: unpublished observations; 4: Lombarte *et al*. 1989, updated; 5: Espadaler 1986b, Espadaler & Ascaso 1990; 6: Ortiz 1985; 7: Tinaut 1989; 8: Pascual 1986; 9: Espadaler 1997a; 10: Espadaler 1997c; 11: Espadaler 1979, updated; 12: Tinaut 1981; 13: Suñer 1991; 14: Espadaler 1990; 15: Martínez 1987; 16: Espadaler 1997b; 17: Collingwood & Prince 1998; 18: Espadaler 1997c;

ture to propose mechanisms structuring the BSD, if there are any (Novotny & Kindlmann, 1996) until more comprehensive data bases are compiled.

Possible biases in the BSD

— Measurement errors. The BSD of Iberian ants covers three orders of magnitude, so it is assumed that measurement errors are likely to be very small in relation to interspecific body size variation. The variable size in polymorphic and monomorphic – but variable – ant species however, is undoubtably of greater importance. The correct parameter to use for species in which size is variable remains unresolved and largely unexplored (Blackburn & Gaston 1994b). How the frequency distribution of ant assemblages and their usually associated statistical parameters may vary according to which measure of body size is used (mean, median, maximum or the full range) is currently under scrutiny.

— The number of species known to be missing is not applicable here because data for the 237 described species from the Iberian Peninsula was available. Migrant species in local samples were probably absent or highly unlikely (nests are usually long lived in a given habitat).

— The number of undescribed species missing from the BSD is unlikely to alter the shape shown in Fig. 1. As a test for this possibility we compared the mean mass of recently (< 20 years) described species (n = 30 formally described + 9 still undescribed; head length ± s.d.: 0.91 ± 0.44 mm; dry body mass ± s.d: 0.69 ± 1.1 mg) with the mean mass of previously known species (head length ± s.d.: 1.02 ± 0.48 mm; dry body mass ± s.d.: 0.98 ± 1.62 mg). Body mass for both groups was not different (ANOVA on logmass; $F_{2,232} = 2.16$; $p = 0.11$). Thus, we are confident that no systematic biases have been introduced in the data base.

Ours is a restricted database of global ant body masses. In particular, large ants are lacking since these sizes come from tropical areas (viz. 115.4 mg for *Dinoponera gigantea* (Perty) or 94.5 mg for *Camponotus (Dinomyrmex) gigas* (Latreille)); Leptanillinae are amongst the smallest ants in the world and are included in our data. So the veil line, if this concept were to apply here, belongs on the right part of the distribution. The global ant BSD is probably skewed further to the right than that of Iberian ants.

Concluding remarks

As to why there seems to be no change in the BDS of Iberian ants at different spatial scales we envisage three possibilities: 1) the peninsular scale is not as big as it should be. Ours is a "partial" study (sensu Gaston & Blackburn 1996) since it concerns an area that embraces the entire geographical range of only a limited proportion of the species considered (30 %, Iberian endemics). If this was true, our analysis would effectively be limited to small and medium scales. This could explain the absence of a different pattern for local species assemblages which may appear if compared to more "comprehensive" studies (viz. whole European ants) that are at present lacking. 2) it could be that the smaller scales analysed are not sufficiently small, at the level of the world as perceived by ants. It has recently been proposed that ants perceive their habitat differently according to their size (size-grain hypothesis; Kaspari & Weiser 1999) and that patchiness at the 1-m^2 scale is a property of some ant communities (Kaspari 1996). We may not have reached the scale (grain level) appropriate to analyse ant body size distribution and uncover any flattening of BSD in local samples. This could be difficult to test since the number of species at very small habitat scales in the Iberian Peninsula would be so low that statistical problems (type II error) would be too important. Loder *et al*. (1997) recognised that "systematic differences between local and regional assemblages will be difficult to identify", particularly if differences appear to be non-existent, as is the case in Iberian ants. 3) a further hypothesis, considering that ants are social animals, is that worker size is not the appropriate variable to measure. Perhaps the colony, as an integrated operating unit within its natural environment (Hölldobler & Wilson 1990) would yield a distinct pattern when analysed. If this were so, the summed size distribution of the colony members would be the functionally appropriate "size" to measure. Unfortunately, reliable data on colony size are extremely difficult to obtain (but see Kaspari & Vargo, 1995, for a mainly tropical ants data base on colony size) and data for Iberian ants are lacking.

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BIOGEOGRAPHY AND DISPARITY WITHIN THE GENUS *CRYPTOCANDONA* (CRUSTACEA, OSTRACODA)

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BIOGEOGRAPHY
DISPARITY
EVOLUTION
OSTRACODA
CRYPTOCANDONA

ABSTRACT. – Information on carapace morphology of eight Recent ostracod species of the genus *Cryptocandona* (Candoninae, Candonidae, Cypridoidea), living in surface and groundwater habitats in Europe and Japan, allows to appreciate their pattern of disparity (i.e. morphological diversity). A morphometric analysis of the outlines of adult female valves using Elliptic Fourier Analysis is performed on individuals belonging to geographically separated populations. The data, displayed in a multidimensional morphospace, is analysed using Principal Component Analysis. It is shown that carapace shape patterns of the various species overlap within the *Cryptocandona* morphospace. The degree of morphological change of the carapaces of *Cryptocandona* species is evaluated within the context of their geographical and ecological distribution. Comparative data on various Candoninae lineages facilitate discussion on the limits of allocation of fossil candonines to the genus *Cryptocandona* using only carapace-shape criteria.

BIOGÉOGRAPHIE
DIVERSITÉ
MORPHOLOGIQUE
ÉVOLUTION
OSTRACODA
CRYPTOCANDONA

RÉSUMÉ. – Biogéographie et diversité morphologique à l'intérieur du genre *Cryptocandona* (Crustacea, Ostracoda). L'étude de la morphologie de la carapace de huit espèces actuelles d'Ostracodes appartenant au genre *Cryptocandona* (Candoninae, Candonidae, Cypridoidea), vivant dans des habitats aquatiques épigés et hypogés, en Europe et au Japon, permet d'apprécier leur type de diversité morphologique (i.e. disparité). L'analyse morphométrique utilisant la procédure de « Fourier Elliptique » sur le contour des valves des femelles adultes, a été réalisée à partir d'individus provenant de populations isolées géographiquement. Les données ont été représentées dans un espace morphologique multidimensionnel en utilisant l'Analyse en Composantes Principales. On montre que les patrons des formes de la carapace des différentes espèces de *Cryptocandona* se superposent à l'intérieur de l'espace morphologique. Le degré de changement morphologique à l'intérieur de *Cryptocandona* est évalué dans le contexte de leur distribution géographique et écologique. Des données comparatives sur différentes lignées de Candoninae facilitent la discussion sur les limites d'attribution des Candonines fossiles au genre *Cryptocandona* à partir des seuls critères de la forme générale de la carapace.

INTRODUCTION

C Delamare Deboutteville (1957) in a lecture delivered to the French "Société de Biogéographie" noted that one of the aims of the "Actual Biogeography" should be the reconstruction of natural histories of various animal lineages. Delamare Deboutteville (op. cit.) emphasised that the best way to achieve such a goal is through treating beside geographical information also data from other research directions like morphology, systematics, ecology and evolution. Our approach here is different, we will use geographical patterns of several species belonging to a non-marine ostracod group, the genus *Cryptocandona* Kaufmann (Candoninae, Candonidae, Cypridoidea), in order to better discuss the evolutionary problems related to morphological diversity, especially the disparity of the carapace shape, of these taxa.

The genus *Cryptocandona* Kaufmann, 1900 is an ostracod group, well defined by morphological traits of the limbs; the carapace is narrowly compressed, when seen in dorsal view, and the valves are weakly calcified and without ornamentation (Meisch 2000). Within the subfamily Candoninae it represents a primitive lineage, considering the fifth limb with three exopodial setae, the seventh limb with a seta on the second endopodial segment and a weekly internal sclerotised hemipenis (Danielopol 1980a, Namiotko & Danielopol 2001).

Since Kaufmann's publication (Kaufmann 1900), at least 15 species, Recent and fossil ones, are considered to belong to this genus (Kempf 1980). Most of them are distributed in Europe, one species (*Cryptocandona brehmi* (Klie)) was discovered in Japan (Klie 1934, Danielopol 1980a). Fossil species were described from the Tertiary and Quaternary deposits in Central Europe (e.g. Absolon 1973, 1978, Krstić 1972, Sokać 1978).

Recent *Cryptocandona* species colonise surface water habitats, those of lakes and springs but also the subsurface environment, riverbed sediments or porous groundwater in alluvial valleys (Meisch 2000). There are a series of exclusively groundwater dwelling species living either in porous groundwater or cave water habitats (see below). A limnetic environment is assumed for one Tertiary fossil species, *Cryptocandona nocens* (Krstić 1972).

The Recent *Cryptocandona* species we shall discuss here, taking in consideration their present-day geographical and ecological distributions (information in Löffler & Danielopol 1978, Danielopol 1980a, Meisch 2000, Namiotko & Danielopol 2001) belong to four distinct groups:

(1) Species which live mostly in Western and Central Europe inhabiting mainly epigean (benthic) habitats, seldom subsurface ones, i.e. *Cryptocandona reducta* (Alm).

(2) Species which are distributed over the whole Europe inhabiting both surface and subsurface habitats, in this latter case both shallow (hyporheal) and deep porous groundwater habitats, i.e. *Cryptocandona vavrai* Kaufmann.

(3) Species which live in porous groundwater habitats either mainly along the valleys of large rivers, like the Rhine, the Rhône, the Danube and their tributaries [i.e. *Cryptocandona kieferi* (Klie)] or mainly along the Carpathians (i.e. *Cryptocandona matris* (Sywula)).

(4) Species with restricted geographical distributions and occurring mainly in groundwater habitats, e.g. *Cryptocandona leruthi* (Klie) in Belgium, *Cryptocandona phreaticola* (Kiefer and Klie) in Slovakia, *Cryptocandona dudichi* (Klie) in Hungary and *Cryptocandona brehmi* (Klie) in Japan. These latter two species live in cave-water habitats. Note that *C. phreaticola* and *C. dudichi* were seldom found in surface water habitats connected to groundwater systems (springs) while the other two species were found in deep subsurface waters.

The carapace shape of the Candoninae is very diverse. One finds species with carapaces which approximates geometric shapes like the rectangular, trapezoidal or triangular ones (Danielopol 1978, 1980b). It was noted that often interstitial dwelling ostracods, especially those living in marine sands, display carapace shapes which are conspicuously more elongated than those belonging to epigean dwelling species (Elofson 1941, Hartmann 1973, Danielopol & Hartmann 1986). Non-marine ostracods which live in porous non-consolidated sediments have beside species with elongated carapaces also a rather high number of taxa displaying triangular and/or trapezoidal carapaces (Danielopol 1978, 1980b, Danielopol & Marmonier 1994). Another common feature of interstitial dwelling animals, beside their elongated body shapes, is also their more reduced size, as compared to those of related surface dwelling taxa (Giere 1993, Coineau 2000).

The questions addressed in this contribution are:

(1) Is the carapace shape of *Cryptocandona* taxa a valid taxonomic character ? For most organisms shape is under tight (phylo)genetic control making individuals within a lineage morphologically similar to each other. This is a feature that taxonomists have used since long time ago as the basis of their daily work. When morphologies (indeed a multidimensional trait) are arranged according to their relationships we obtain the so-called empirical morphological space (see McGhee 1999). It is expected for morphologically different species to occupy different positions in the morphospace. Unfortunately, not a single point but a cloud of them correspond to each species in the morphospace because shape is far from being an invariant trait. Genetic diversity, ecophenotypic variability and phenotypic plasticity all contribute to morphological disparity within a clade. Only when clouds of points representing species in the morphospace do not overlap, species can be safely discriminated on the basis of shape alone. Thus, understanding (and explaining) disparity patterns of *Cryptocandona,* as compared to other Candoninae would allow to progress toward better systematics of the Candoninae. It is well known that this latter scientific aspect is far from achieving the consensus of palaeontologists and neontologists. For instance one should compare the differences existing between the taxonomic system used by Mandelstam & Schneider (1963) and Krstić (1972) for the fossil candonines with those used by Danielopol (1978) or Meisch (2000) for Recent ones.

(2) Is morphological diversity of carapace shapes of *Cryptocandona* species related to any geographical pattern ? Because gene flow must be very reduced between populations living in patchy environments (for instance, groundwater habitats) a larger morphological disparity is expected.

Table I. – Material used for the morphological analysis (R-right, L-left, V-valve; see also text).

CODE	SPECIES	VALVES	LOCALITY	COUNTRY
1	*Candonopsis boui*	LV	Avalats	France
2	*Cryptocandona dudichi*	LV	Aggtelek	Hungary
3	*C. leruthi*	LV	Hermalle sous Argenteau	Belgium
4	*C. phreaticola*	LV	Tekovské Luzany	Slovakia
5	*C. nocens* (fossil)	LV	Belgrade	Yugoslavia
6	*C. brehmi*	LV	Hirowagara	Japan
7	*C. vavrai*	LV	Alas	France
8	"	LV	Clou de la Fou	France
9	"	2RV, LV	Arcine	France
10	"	RV, LV	Grumelange	Belgium
11	"	LV	Gentilino	Switzerland
12	"	RV, LV	Adamello-Brenta Park	Italy
13	"	RV	Harz	Germany
14	"	RV, LV	Dusznicka Bystrzycka	Poland
15	"	RV, LV	Şuncuiuş	Romania
16	"	LV	Sigiştel	Romania
17	"	RV, LV	Izverna	Romania
18	*C. reducta*	RV	Broadstone stream	UK
19	"	RV, LV	Ösling	Luxembourg
20	"	RV, 2LV	Hausruck	Austria
21	"	LV	Hut'	Czech Republic
22	"	RV, LV	Błażkowa	Poland
23	"	LV	Renö	Norway
24	*C. kieferi*	LV	Orgeux et Arcelot	France
25	"	LV	Saint Maurice de Gourdan	France
26	"	LV	Lutter	France
27	"	RV, 2LV	Lobau	Austria
28	"	LV	Blatnica	Slovakia
29	"	LV	Lumina	Romania
30	*C. matris*	RV, LV	Nierodzim	Poland
31	"	RV	Strwiąż stream	Poland
32	"	RV, LV	Bogdan Voda	Romania

(3) Is morphological diversity of carapace shapes of *Cryptocandona* species related to any ecological pattern ? Ecological conditions of groundwater habitats, especially the living space in porous systems, are assumed to be more homogenous and more constraining than those existing in benthic water habitats (Gibert *et al*. 1994, Coineau 2000). One could expect hence, that the carapace shapes of hypogean species living within non-consolidated porous sediments converge toward some adaptively functional type, e.g. the elongated and miniaturised one.

The present contribution belongs to a larger project dealing with the reconstruction of the evolutionary pathways of the *Cryptocandona* lineage. The revised morphology and systematics of the species assigned to this Candoninae genus will be published separately (e.g. Namiotko & Danielopol 2001, Marmonier *et al.* MS, etc).

MATERIAL AND METHODS

(1) Geographical and ecological information: We present briefly here the general geographical (Fig. 1) and ecological distribution of the species used for our morphometric analysis. For the special material which documents our contribution we add detailed information on the geographical location and the habitat type. The ostracod material discussed here is represented by carapaces and/or valves of adult females (Table I).

Cryptocandona vavrai Kaufmann, 1900 – The species is very common in the whole Europe (Löffler & Danielopol 1978, Meisch 2000). It occurs in both lentic habitats of lakes (littoral and the profundal ones) as well as in lotic habitats, springs, slow flowing streams; it colonises subsurface water both the shallow ones (the hyporheal of running waters) as well as deep groundwater in alluvial valleys. As the species is very eurythermal it occurs commonly in southern and northern Europe.

The original material of Kaufmann (and a figure of the valve here used from Kaufmann's monograph 1900) stems from a marshy area with helocrenes at Gentilino, W Lugano, Switzerland. We integrated in our data set also the outline of a specimen figured by Hartmann Hiller (1977) originating from the Harz area, Germany. The following material was directly investigated by us: (1) Grumelange in Belgium, near the boarder with Germany, a spring sampled by C Meisch; (2) hyporheal in the Dusznicka Bystrzycka stream, 15 km W Klodzko, Poland; (3) Şuncuiuş, a well accessing to porous groundwater, 45 km ESE Oradea, Romania; (4) Sigiştel, between Nucet and Ştei, a well accessing to porous

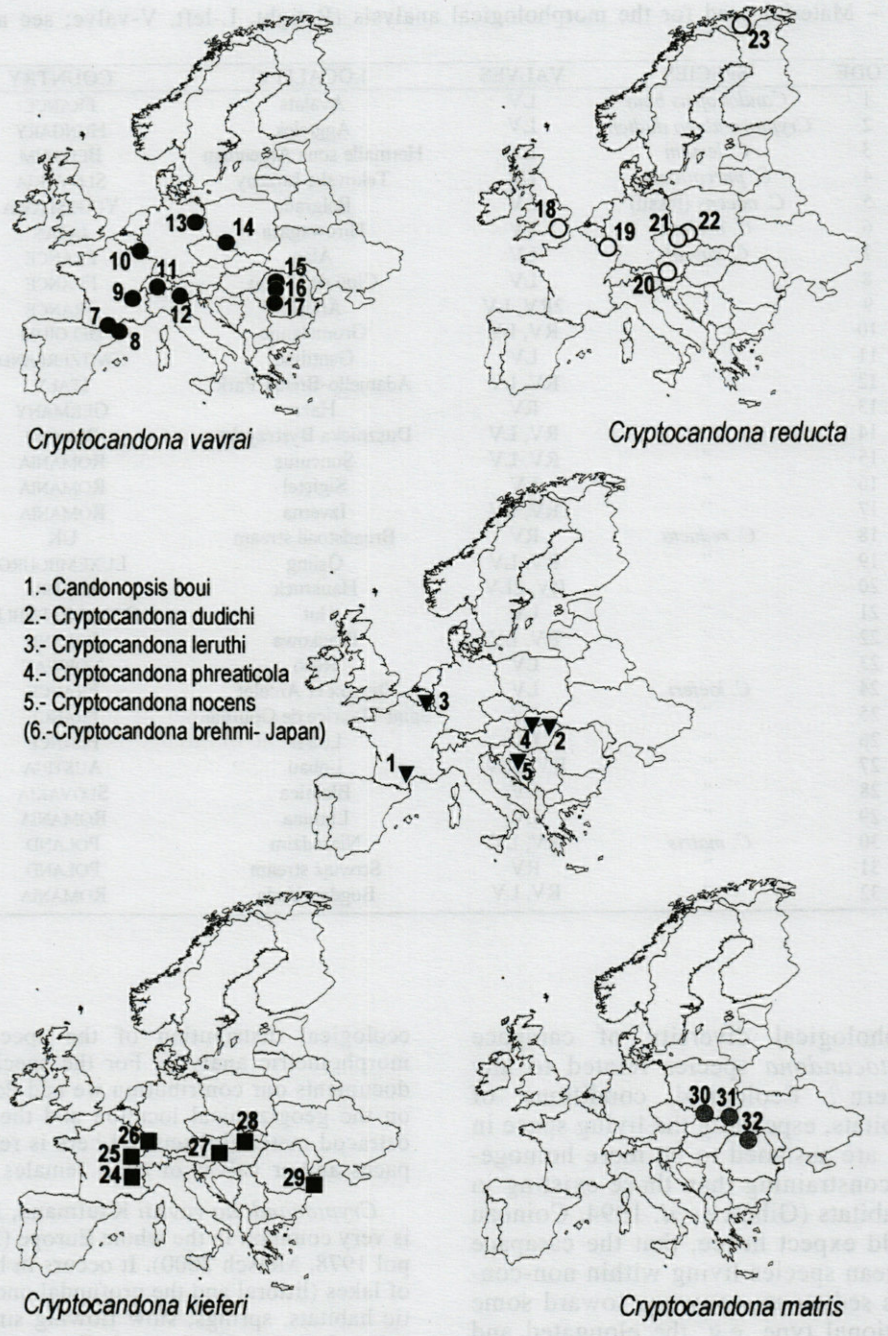

Fig. 1. – Maps showing localities from where ostracods have been collected. See text for a complete reference of material and literature sources.

groundwater, Romania; (5) Izverna, hyporheal in front of the Izverna cave, 15 km W Baia de Aramă, Romania; (6) Adamello-Brenta Natural Park, GA-1B spring, 40 km NW Trento, Italy; (7) Alas, hyporheal on the Lachein stream, 10 km SSW Saint-Girons, Ariège, France; (8) Arcine, a well accessing to porous groundwater, 20 km E Lyon, France; (9) Clou de la Fou, near Saint Paul de Fenouillet, marshy system, 30 km WNW Perpignan, France.

Cryptocandona reducta (Alm, 1914) – A mainly epigean dwelling species colonising various lotic and lentic habitats in the Western, Northern and Central Europe (Löffler & Danielopol 1978, Meisch 2000). It is a psychrophilic species which colonises also deep lakes like Loch Ness in Scotland (Griffiths *et al.* 1993); it occurs seldom in southern Europe e.g. in Auvergne, France (Scharf & Keyser 1991). *C. reducta* colonises infrequently groundwater habitats, i.e. the hyporheal of streams and porous groundwater in alluvial sediments along valleys. Alm (1914) described this species using material from springs at Renö in the province Finnmark (Norway). We used for the present contribution the outline of *C. reducta* published by Alm (1914). From Absolon's monograph on candonines (Absolon 1978) we used the outline of *C. reducta* drawn by this author from a female caught in a spring at Hut' near Jablonec nad Nisou, Czech Republic. Additional material used, stems from material deposited in our collections: (1, 2) two limnocrene springs (Q-98, D-94) at Hausruck, 15 km NNW Vöcklabruck, Upper Austria; (3) superficial sediments (a 10 cm deep layer below the bottom) of Broadstone Stream, 30 km NNE Brighton, East England, UK (the streambed at this site is dominated by fine sandy sediment, J. Araya– Schmid leg. and pers. comm. to DLD); (4) a well dug in alluvial sediments, 20 m inland from the River Bóbr at Błażkowa, 15 km W Wałbrzych, Poland (leg. T Sywula and pers comm to TN); (5) spring at Ösling, close to Bastendorf, Luxembourg (leg. C Meisch and pers. comm. to DLD and TN).

Cryptocandona kieferi (Klie, 1938) – This stygobite species was found in Western and Central Europe within the drainage basins of the Rhine, Rhône and the Danube (Klie 1938, Marmonier & Creuzé des Chatelliers 1992, Rogulj *et al.* 1993, Danielopol & Baltanás 1996, Meisch 2000). In Eastern Europe it occurs, near the Black Sea Coast, in Romania (see below). It lives mainly in porous groundwater of shallow and deep alluvial sediments. It occurs seldom in springs or at the surface of gravelly sediments when groundwater strongly exfiltrates (Danielopol *et al.* 2000).

For this species we used drawings from Absolon (1978), Marmonier (1988) and Marmonier *et al.* (MS) as well as material from DLD collection. Material from following six sites were studied: (1) a groundwater sample at Blatnica, 15 km S Martin in Slovakia (Absolon 1978); (2) a limnocrene spring at Lutter, near Benfeld on the Rhine, 30 km S Strasbourg, France (Marmonier *et al.* MS); (3) porous groundwater of alluvial sediments near Orgeux et Arcelot, in the Saône plain, 30 km N Dijon, France (Marmonier 1988); (4) porous groundwater of alluvial sediments of an abandoned channel of the Ain, closely located to the Rhône river, at Saint Maurice de Gourdan, 15 km NE Lyon, France (Marmonier *et al.* MS); (5) porous groundwater in alluvial sediments of the Danube floodplain at Vienna, samples from Lobau (the piezometres A-1, in Danielopol 1983 and A-81, in Pospisil 1994), Austria; (6) porous groundwater from clastic sediments deposited in the village Lumina, 15 km NW Constanţa, Romania.

Cryptocandona matris (Sywula, 1976) – A stygobitic species occurring mainly along the Carpathians in Poland and in north-eastern Romania. It was also found in a number of wells accessing to groundwater in alluvial sediments of the river Vistula in the Lublin Upland, Poland (Skalski 1982). The type material came from a well dug in alluvial sediments in Cisna (Bieszczady Mountains). The material used here originates from 2 sites in Poland (1-2) and one in Romania (3): (1) a well dug in alluvial sediments at Nierodzim, 20 km W Bielsko Biała; (2) a hyporheic site on Strwiąż stream, 30 km SSE Sanok; (3) a well accessing to the alluvial sediments at Bogdan Voda (Cuhea) in the Iza Valley, 55 km E Baia Mare.

Cryptocandona leruthi (Klie, 1936) – A stygobitic species from Belgium, living in the groundwater of the alluvial sediments of the Meuse (Maas) river, at Hermalle sous Argenteau, 15 km N Liège. Additional information in Namiotko & Danielopol (2001). The material here used belongs to the type series of the species, deposited at the Zoological Museum of the University of Hamburg (ZMH 341).

Cryptocandona phreaticola (Kiefer & Klie, 1927) – An apparently stygobitic species from Slovakia, found in porous groundwater habitats, a well at Tekovské Luzany (40 km SE Nitra), in riverbed sediments at Zliechov and in two springs located about 150 km N from the type locality. Additional information in Namiotko & Danielopol (2001). The material here used belongs to the type series of the species, deposited at the Zoological Museum of the University of Hamburg (ZMH 344).

Cryptocandona dudichi (Klie, 1930) – A troglobitic species from Hungary, found on the bottom of a drip-pool in the Barlang cave, at Aggtelek, 45 km NE from Miskolc (Klie 1930). The material here used represents valves from the type series of the species, deposited at the Zoological Museum of the University of Hamburg (ZMH 340). *C. duduchi* were found recently in a karstic spring closely located to the above mentioned cave (Z Gido leg, pers comm C Meisch to us).

Cryptocandona brehmi (Klie, 1934) – A troglobitic species from Japan, found on the Island Honshu, 120 km NW Tokyo in the cave Hirowagara (on the bottom of a drip-pool). The figure used here is redrawn from Klie (1934). As comparative material we used published information on the carapace or valves for the following species:

Cryptocandona nocens (Krstić, 1972) – A fossil Tertiary species known only from limnic sediments stratigraphically identified as the Lower part of the Lower Pannonian, at Belgrade, Yugoslavia. The outline of the valve used here comes from the original description of Krstić (1972).

Candonopsis boui Danielopol, 1981 – A stygobitic species living in Southern France. It is known from the riverbed sediments (hyporheal) of the Tarn river at Avalats (the valve figured here) and alluvial sediments near Albi at Go (Danielopol 1981, Danielopol & Hartmann 1986).

Candona candida (O.F. Müller, 1776) and *Candona neglecta* Sars, 1887 – Both species are very common in Europe, living in both surface (lotic and lentic habitats) as well as in groundwater (Löffler & Danielopol 1978, Roca & Baltanás 1993, Meisch 2000). They are known as fossils especially in Quaternary deposits of Europe (e.g. Absolon 1978). The outlines of the female valves of these species used in our morphometric study where extracted from Absolon's monograph (1978: 23, 25). They belong to both Recent and fossil (Middle and Upper Pleistocene) material from various localities in Czech and Slovak Republics and one in Alberta, Canada.

2) Acquisition of data and morphometric analysis: Ostracod shape analysis can be addressed in different ways. Landmark methods, including Procustes approaches, have been extensively used with well ornamented species (Kaesler & Foster 1987, Reyment *et al.* 1988, Abe *et al.* 1988, Reyment & Bookstein 1993, Reyment 1995). However, difficulties for defining landmarks in smooth or poorly ornamented ostracods have favoured methods based on outlines (Kaesler & Waters 1972, Kaesler & Maddocks 1984, Schweitzer *et al.* 1986, Burke *et al.* 1987, Schweitzer & Lohmann 1990, Baltanás & Geiger 1998). Among outline methods, Elliptic Fourier analysis is known to produce reasonable results with biological shapes (Rohlf & Archie 1984, Lestrel 1997, McLellan & Endler 1998) and has been used here.

Outline data (400-600 points per contour) were acquired from drawings using tpsDig software (Rohlf 1998). Sources of drawings are detailed in section (1). The origin of coordinates describing each outline was placed at the centroid (centre of gravity) of each valve. In order to make left and right valves comparable left ones were flipped horizontally. Only female outlines were included in the raw data set. Sexual dimorphism is known to be large in some *Cryptocandona* species thus contributing to overall morphological variability. The aim of the study, however, is to explore patterns in morphological variability at the specific and the between-population levels, not within populations or between sexes.

Twenty harmonics were computed as descriptor for each outline rendering a total of 77 coefficients per specimen. These coefficients were mathematically normalised to be invariant to rotation and starting position of the outline trace (Ferson *et al.* 1985).

It is very important to stress that shape alone, not size, is the trait under enquiry. Size is a feature that changes among species and individuals too. And although allometric scaling suggests that some interplay must exist between size and shape in non-marine ostracods, such relationship has not been described yet. In order to remove size effect, Fourier coefficients have been normalised for size too (Ferson *et al.* 1985).

(3) Representation of the multidimensional morphospace: Fourier coefficients are but numerical descriptions of valve shape, so they can be used to define positions within a multidimensional space which describe morphological relationships among items in it. We call this an empirical morphospace (McGhee 1999). It is important to underline that a morphospace like that is context dependent, *i.e.* morphospace features and the positions of ostracods in it change according the amount and kind of objects under study. Building an empirical morphospace directly from our series of Fourier coefficients implies to end up with a high order morphospace (77-dimensions) which is difficult to visualise and of limited use. Ordination techniques, like principal component analysis (PCA), allow us to reduce dimensionality in the original morphospace so that most of the variance in the original data set is summarised in few dimensions. Therefore, a PCA has been performed on the covariance matrix of centered data (a total of 65 valves belonging to 12 species in 3 genera). Having the original data projected onto the new morphospace defined by PCA it is easy to explore relationships among shapes using euclidean distances because principal components are, by definition, uncorrelated (orthogonal). Multidimensional Scaling (MDS) arrange "objects" (valve outlines) in a two-dimensional space so as to reproduce the observed euclidean distances and, hence, relationships among them.

RESULTS

Shape comparisons

Fig. 2 shows items under study arranged on a two-dimensional morphospace. It has been produced by applying multidimensional scaling (MDS) on the matrix of euclidean distances measured on the space produced by PCA. Only 15 principal components were extracted given that they explain more than 99 % of total variation in the raw data set. Dimensions 1 and 2 in the plot have been scaled different, otherwise all the points would lined up along the horizontal axis given that variability in the vertical dimension is very low. Now, it is important to stress several points concerning how the methods here employed work. First, all the analyses are directed towards the identification of major quantitative changes. It means that subtle qualitative changes will be undervalued. Second, Fourier harmonics run from the general to the particular. In other words, lower-rank harmonics (order 1, 2,...) account for the general shape of the object considered (e.g. elongated, rounded, etc.) whereas higher-rank harmonics account for the small details in valve outline. Because lower-rank Fourier harmonics are associated with higher numbers and a large variability, their contribution to the final arrangement of items in the empirical morphospace is larger than the contribution of higher-rank harmonics. This is not an undesirable property of the method as far as it is reasonable to value changes in general shape more than changes in small fine details. But once similarities or differences in general shape has been established, a morphologist or a taxonomist will likely be highly interested in such fine details. That is why dimension-2 in the plot (Fig. 2) has been enhanced, because it directly refers to changes in shape which are of minor quantitative importance but which are qualitatively relevant. Differences existing between left and right outlines, those valves belonging to the same population (=locality) normally cluster close in the morphospace.

All *Cryptocandona* species cluster together in the MDS plot (Fig. 2). Still, *C. nocens* and *C. dudichi* seem to fall apart. It is adequate here to remember that distances (gaps) in the vertical dimension have been enhanced and do not reflect large quantitative changes but subtle ones. In those species for which several populations have been included degree of overlap is high. There is a gradient in shape (dimension 1) running from *C. reducta* to *C. vavrai*, with *C. kieferi* and *C. matris* in a central position. This gradient relates to changes in eccentricity of valve outline. Elongated valves (low height/length ratio) are placed on the right side of the plot, whereas more robust compact shapes (like those of *C. candida*) are in the left side (Fig. 3A). Dimension 2 in MDS plot relates to changes from quadrangular (lower part) to triangular (upper part) shape in valve outline (Fig. 3B). It is in this dimension that *Cryptocandona dudichi* and *C. nocens* differ from their relatives. *Cryptocandona dudichi* has asymmetric valves, the left one higher and with a ventral protruded margin in its central part, the right valve more straight and the ventral margin slightly concave. The dorsal margin of both valves is widely arched. The maximal height, less than 50 % of the length, is located in the anterior half of the valve. The posterior third of the valves is visibly more straight and acuminate than the anterior one.

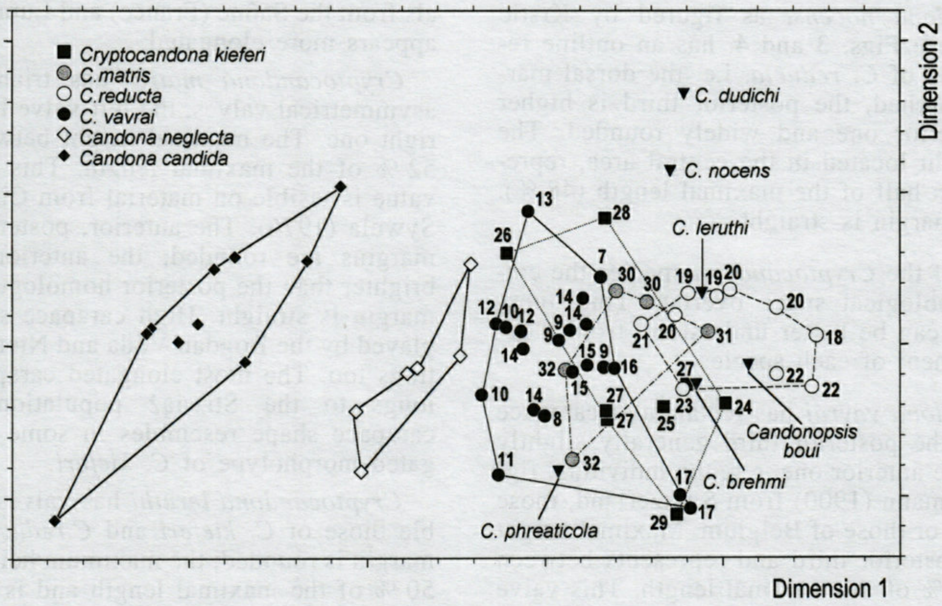

Fig. 2. – MDS plot summarising similarities in outline shapes among different populations in several *Cryptocandona* and *Candona* species. Numbers are for locality codes (see Table 1).

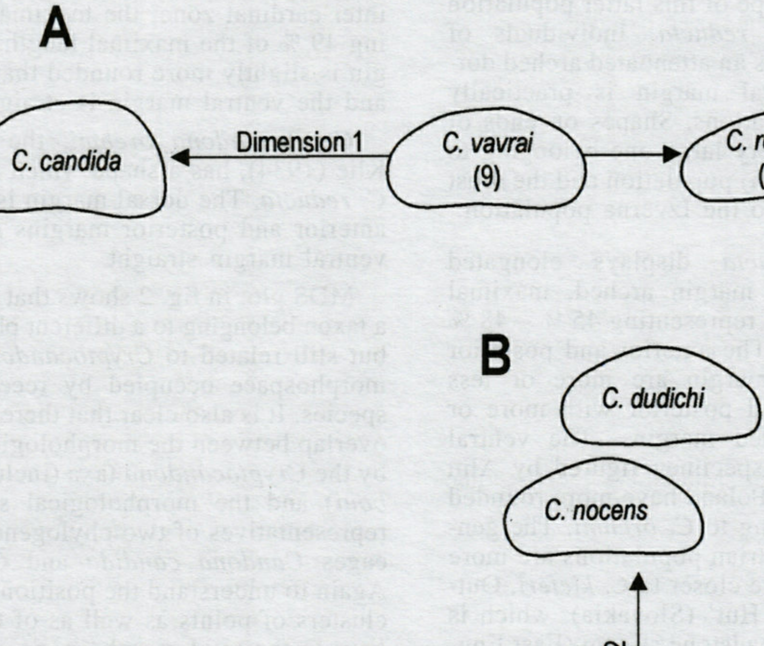

Fig. 3. – Main trends in shape change along dimensions displayed in MDS plot.

Cryptocandona nocens, as figured by Krstić (1972) and here Figs. 3 and 4, has an outline resembling those of *C. reducta,* i.e. the dorsal margin, clearly arched, the posterior third is higher than the anterior one and widely rounded. The maximal height located in the central area, represents less than half of the maximal length (48 %). The ventral margin is straight.

For most of the *Cryptocandona* species the empirical morphological space overlap. This unexpected effect can be better understood from a detailed assessment of each species.

Cryptocandona vavrai has rectangular carapace shapes with the posterior third generally slightly larger than the anterior one, e.g. the individual figured by Kaufmann (1900) from Switzerland, those of north Italy or those of Belgium. Maximal height lays in the posterior third and represents between 47 % and 51 % of the maximal length. This valve shape comes closer to those of *C. kieferi*. The dorsal margin can be angular in some populations like those of Sigiştel and Şuncuiuş with the angle formed at the maximal height of the valve or can be more rounded, like those of Arcine or those of Clou de la Fou. The valve shape of this latter population resemble those of *C. reducta*. Individuals of Izverna and Alas displays an attenuated arched dorsal margin. The ventral margin is practically straight in all the populations. Shapes on ends of the shape range are a very large one belonging to the Grumelange (Belgium) population and the most straight one belonging to the Izverna population.

Cryptocandona reducta displays elongated valves with the dorsal margin arched, maximal height in the central part representing 45 % – 48 % of the maximal length. The anterior and posterior sectors of the dorsal margin are more or less straight; the anterior and posterior with more or less symmetrical rounded margins. The ventral margin is straight. The specimen figured by Alm (op.cit.) and those from Poland have more rounded dorsal margins resembling to *C. brehmi*. The general carapace of the Austrian populations are more triangular appearing more closer to *C. kieferi*. Outermost shapes are from Hut' (Slovakia), which is the largest, and from Broadstone stream (East England) with the most elongated shape. Some of the *C. reducta* valves resemble those of *C. matris* due to their triangular appearance.

Cryptocandona kieferi has rectangular carapaces with the maximal height in the posterior third, 46 %-50 % of the maximal length; the dorsal margin widely convex, approaching a straight line in the inter-cardinal zone. The anterior and posterior margins broadly rounded while the ventral margin is straight. Individuals from Rhine and the Danube (Lobau, at Vienna) displays a more rounded and higher posterior third of the valves, while individuals from the Saône (France) and Lumina (Romania) appears more elongated.

Cryptocandona matris has triangular slightly asymmetrical valves, the left valve higher than the right one. The maximal height between 46 % and 52 % of the maximal length. This latter extreme value is visible on material from Cisna figured by Sywula (1976). The anterior, posterior and dorsal margins are rounded; the anterior one slightly brighter than the posterior homologue. The ventral margin is straight. High carapace shapes are displayed by the Bogdan Voda and Nierodzim populations too. The most elongated carapace shape belongs to the Strwiąż population. This latter carapace shape resembles in some sort the elongated morphotype of *C. kieferi.*

Cryptocandona leruthi has valves which resemble those of *C. kieferi* and *C.reducta*. The dorsal margin is rounded; the maximum height is less than 50 % of the maximal length and is located in the posterior part of the valve. The anterior and the posterior margins are rounded and symmetrically shaped. The ventral margin is straight.

Cryptocandona phreaticola appears more or less rectangular, with the dorsal margin straight in its inter-cardinal zone; the maximal height representing 49 % of the maximal length. The anterior margin is slightly more rounded than the posterior one and the ventral margin is straight.

Cryptocandona brehmi, the valve figured by Klie (1934), has a shape which resembles those of *C. reducta*. The dorsal margin is widely round, the anterior and posterior margins symmetric and the ventral margin straight.

MDS plot in fig. 2 shows that *Candonopsis boui,* a taxon belonging to a different phylogenetic lineage, but still related to *Cryptocandona*, lies within the morphospace occupied by recent *Cryptocandona* species. It is also clear that there is no continuity or overlap between the morphological space occupied by the *Cryptocandona* taxa (including *Candonopsis boui*) and the morphological space occupied by representatives of two phylogenetically distant lineages *Candona candida* and *Candona neglecta*. Again to understand the position of these latter two clusters of points as well as of those *Candonopsis boui* in the total morphospace we have to analyse further the detailed shape of these taxa.

Candonopsis boui has a carapace shape with the greatest height located in the posterior third; the dorsal inter-cardinal margin straight running downward to the anterior side. The ventral margin straight or slightly concave. The valves resemble those of *C. vavrai* from Şuncuiuş.

Candona candida displays more quadratic shapes with the maximal height located in the posterior third of the valve, representing always more than 50 % of the maximal length (sometimes up to 60 %). The inter-cardinal dorsal margin straight or

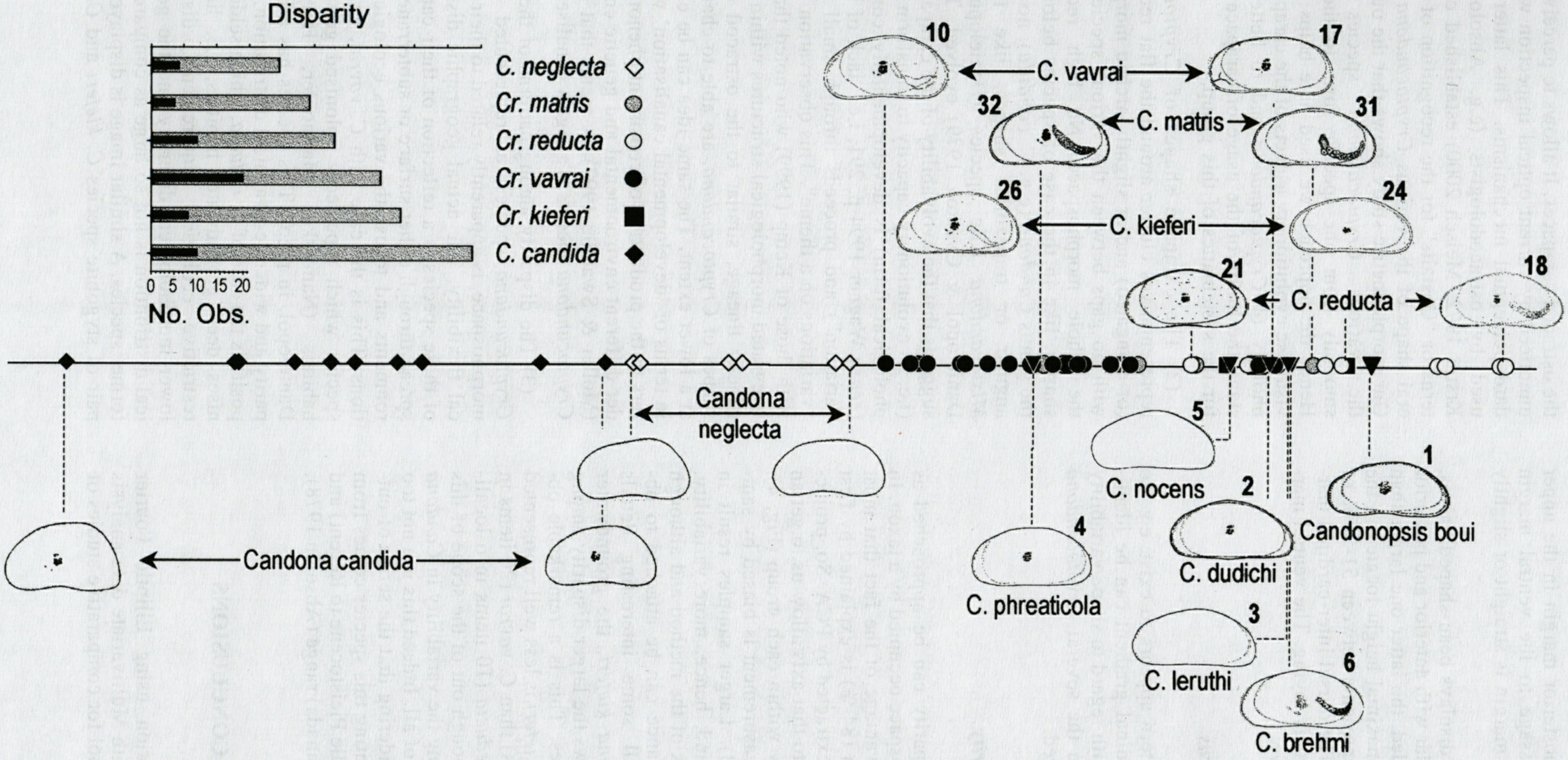

Fig. 4. – Disparity and shape trends in valve outlines displayed as their projections onto first principal component (84 % variance explained arranged). Disparity (inset upper left, grey bars) is measured as the amount of morphospace occupied (range of values in the axis). Sample size is also shown (black bars).

slightly arched, the posterior margin in the upper part straight, the passage to the ventral margin rounded. The ventral margin is straight or slightly concave.

Candona neglecta displays bean-shaped valves, more or less rectangular with anterior and posterior margins widely rounded, the latter one larger than the former one. The maximal height located in the posterior third and represents between 51-55 % of the maximal length. The dorsal inter-cardinal margin straight and obliquely laying. The ventral margin is slightly concave.

Biogeographic patterns

No geographic pattern appears to exist, e.g. no latitudinal or longitudinal gradient can be identified in the analyses with regard to shape variability among populations in the several *Cryptocandona* species here considered.

Morphological disparity

Morphological disparity can be approached as the amount of morphospace occupied by a taxon. In this case we took advantage of the fact that most variability in the data (84 %) is explained by first principal component extracted by PCA. So, projections of the valves onto that axis allow us to get an estimate of variability within each group (Fig. 4). Unfortunately this measurement is biased by sample size (Foote 1993). Larger samples result in larger shape ranges and, hence, more variability. Despite that drawback of the method and although no statistical significance can be attached to observed disparity, still some interesting details emerge. *Cryptocandona kieferi*, the groundwater dwelling species, shows the larger disparity among *Cryptocandona* species. This is a remarkable observation because *C. kieferi* is less well represented (8 items in 6 localities) than *C. vavrai* (20 items in 11 localities) or *C. reducta* (10 items in 6 localities) (Figs. 1, 4). Although out of the scope of this paper, it is worth noting the variability in *Candona candida* is the largest of all. Indeed this is a not too surprising result considering that the series of outlines used for representing this species comes from a wide temporal (middle Pleistocene to Recent) and spatial (Bohemia to Canada) range (Absolon 1978).

DISCUSSION AND CONCLUSIONS

(1) Shape description using Elliptic Fourier Analysis combined with Multivariate data analysis conform a powerful tool for comparative studies of the ostracod carapaces. It allows to perceive details unnoticed by current optical inspection with standard perceptual mechanisms. This latter process used by ostracodologists (e.g. Absolon 1978, Krstić 1972, Meisch 2000) established clear patterns or "Gestalts" for the recognition of the general shape of the various *Cryptocandona* species. Our morphometric study shows that the outlines of the various *Cryptocandona* species change smoothly from one specific form to the others. Hence the approach we used here helps to better visualise evolutionary aspects of the carapace morphology of *Cryptocandona* and to better understand the limits of the usage of carapace outlines for the systematics of this group.

(2) The carapace shapes of *Cryptocandona* representatives cluster around the flat rectangular (or elongated) and/or slightly arched morphotypes with no gaps between the various species within the whole morphospace. No high rectangular shapes, like in the case of species belonging to the genus *Candona* (e.g. *C. candida*), no high triangular or trapezoidal shapes, like those of *Mixtacandona* Klie species (Danielopol 1978, Danielopol & Cvetkov 1979) evolved. This fact suggests that the evolvability of the carapace shape (i.e. its evolutionary capacity to transform the morphological form) is developmentally constrained (*sensu* Wagner 1994 p. 291, i.e. "lack of heritable variation") and proceeds through small steps as "variations on a theme". This observation is in line with those of Kemp (1999) who noted that highly integrated morphological structures within a phylogenetic lineage, similar to the ostracod carapace shapes of *Cryptocandona*, are able to change only at a lower extent. The same idea can be expressed in terms of 'developmental canalisation' which refers to the production of consistent phenotypes under different environmental and genetic conditions (Møller & Swaddle 1997). It seems that shape in *Cryptocandona* species is a highly canalised trait.

(3) The disparity among patterns of the various *Cryptocandona* species, as represented by their morphospace, is apparently related to their ecological flexibility. The actual geographic distribution of these species is a reflection of their capacity to spread through either surface or subterranean environments and to use the various ecological situations. This is the case with *C. vavrai,* an epigean species which repeatedly colonised groundwater habitats (Namiotko, Marmonier, Horne and Danielopol, in prep). This species has a high disparity and wider geographical distribution. The opposite is the case of *C. reducta*, which seldom colonises deep groundwater habitats, i.e. has more restrictive ecological requirements, displays a lower morphological diversity and the geographical distribution is not so large as compared to the former species. A similar image is displayed by the pair of stygobite species *C. kieferi* and *C. matris*.

However in this latter case the reduced disparity of *C. matris* could be due to the low number of sites and populations represented here. From this information one could infer that the higher degree of disparity of outline shapes for species like *C. vavrai* or *C. kieferi* evolved as adaptive solutions to the local habitats where the different populations settled. Two epigean ostracods, *Eucypris virens* (Jurine 1820) and *Limnocythere inopinata* (Baird 1843) with both wide ecological and geographical distribution in Europe display similar wide morphological diversities of the valves (Baltanás & Geiger 1998, Yin *et al.* 1999, Baltanás *et al.* MS). The limits of our adaptive explanation will be here further discussed (see next paragraph).

(4) The convergent evolutionary state of the morphological form of animals in relation to their specific life habits and ecological space occupied was called by Remane (1943) "Lebensformtypus". Following Kühnelt (1969) typical animal life-forms for a specific environment (e.g. the porous sandy sediments) are the result of adaptive trends. The disparity of the *Cryptocandona,* as expressed by the various points within the empirical morphospace, does not show a directional trend from the most epigean dwelling species *C. reducta,* to the stygophile *C. vavrai*, leading finally to the exclusively interstitial dwelling species *C. kieferi* or *C. matris*. However, we noticed that within *C. vavrai* and *C. reducta*, the most elongated carapace shapes belong to interstitial dwelling populations. Within the exclusively interstitial species *C. kieferi* and *C. matris* one finds carapaces with both elongated and dorsally arched valves. One could interpret the convergent evolution of these "lebensformtypes" as a non experimental evidence of natural selection, shaping an adaptive solution for life within the porous space. This observation should stimulate groundwater ecologists to reinvestigate and better describe the local environment where these *Cryptocandona* populations with elongated valves live. Also laboratory experiments could be helpful to better understand the relationships between carapace shape and size of these ostracods and their movement through clastic sediments, within well controlled effective porosities.

Comparing the carapace shape of the cave dwelling species *C. brehmi* with those of epigean *C. reducta* populations and/or the interstitial dwelling *C. matris* we do not see distinct differences which could be interpreted as adaptive solutions to cave life.

The carapace of *C. dudichi* from a drip pool in the Barlang cave, displays a more acuminate posterior shape (as compared to the anterior part) than those of the other *Cryptocandona* investigated. This could be interpreted as an economy of material and space, an adaptive solution to the oligotrophic cave environment. However to corroborate or refute this hypothesis one needs additional ecological studies. One should note that the adult female of *C. dudichi* displays a carapace shape which resembles those of the 7th juvenile stage of *C. leruthi* (for this latter see Namiotko & Danielopol 2001). This observation suggests that *C. dudichi* with its posterior straight form of the valves is a paedomorphic species.

The fact that *Cryptocandona* populations with both slightly dorsally arched valves and those with a flat dorsal shape, live successfully within the interstitial space of various clastic sediments, suggests that external factors acting through directional selection are not strong enough to shape a distinctly elongated carapace form within this ostracod group. The dorsally arched morphotype exist in various epigean *Cryptocandona* populations too, hence one has to consider this type of carapace form an exaptation (*sensu* Gould & Vrba 1982). Rouch & Danielopol (1987) noted that the colonisation of subterranean habitats are favoured by epigean preadapted species.

The dorsally arched valves of *Cryptocandona* represent an excellent constructional solution for the strength of their thin calcified walls. Benson (1975) showed that such carapace types are build following the principle of a "catenary arch" in which the thrust in the calcified wall is well equilibrated, i.e. without making necessary additional mass to the extremity of the arch in order to avoid deformations. This latter situation can be seen in various Candoninae (Danielopol 1978, 1980b, 1990). Interesting enough, the principle of the "catenary arch", realised under natural conditions, was used by the Spanish architect Antonio Gaudi for the design of architectural objects, like those of the cathedral "Sagrada Familia" in Barcelona (Kemp 2000).

(5) The characterisation of the morphological form of the Candoninae valves represents an important aspect of the systematics of this group, especially when dealing with fossil species. Tertiary ostracod fauna, especially in or around the Paratethys in Central and Eastern Europe, is replete with Candoninae displaying a high morphological diversity (e.g. Krstić 1972, Sokač 1972, Olteanu 1995). The taxonomic characterisation of the fossil Candoninae using outline details proceeded in most of the cases by subjective and more or less impressionistic decisions. Hence the systematics of this group, as developed by many ostracodologists, reflects a high degree of arbitrariness. The analysis of valve outlines following the protocols used here allows higher degree of discrimination of morphological forms of Candoninae valves as compared to traditional methods mentioned above. In this way a more objective systematics of the Candoninae can be achieved !

Sbordoni (1993) suggested that the properties of a species can be better defined as a statistical cloud of traits, clustered within a multidimensional space. We suggest here that any taxonomic unit should be defined within a multidimensional morphospace as individualised groups separated from other similar groups by gaps. In our case (the examples used were chosen for comparative purposes only), the data of Recent *Cryptocandona* and *Candona* valve outlines, one could easily define a *Cryptocandona* pattern within which one could accommodate fossil species, like *C. nocens,* too. However the insertion within the empirical morphospace of *Cryptocandona* the carapace shape of *Candonopsis boui,* a candonid species belonging to a different phylogenetical lineage (Danielopol 1980a, 1981), forbids us to use solely the valve outline pattern of *Cryptocandona* as a generic characterisation. This means that fossil candonids with carapace outlines resembling living *Cryptocandona* species (e.g. *C. nocens*) can not be allocated, as did Krstić (1972), to this group using only the shape criterion of the valves.

(6) The morphometric method using the Elliptic Fourier algorithm applied on valve outlines gave us a general view on the extension of the variety of carapace shapes within the *Cryptocandona* group. We avoided to use these information for more specific phylogenetic inferences because of Zelditch *et al.* (1995) argumentation pointing out that most of the outline-based techniques (one exception being the thin-plate spline decomposed by its partial warps) are inappropriate for phylogenetical reconstructions. However, we intend for future studies on the Candoninae to combine outline methods with conventional Procrustes ones. These latter, using landmarks, were successfully used by Benson (1976, 1982, 1983) for evolutionary studies on Recent and fossil marine ostracods. We hope by combining these methods to unveil the biological homologies (*sensu* Wagner 1989) locked in the structure and the shape of the Candoninae carapaces and hence to reconstruct the evolutionary pathways of this group with more accuracy.

In conclusion, the usage of powerful morphometric and multivariate analysis applied to the carapace shapes of various *Cryptocandona* populations, combined with geographical and ecological information help us to better understand "what exactly, are these forms doing" as Bookstein (1992/1993, p 35) would say. It opens also new avenues for the improvement of the Candoninae systematics.

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The following persons have reviewed manuscripts published in volume 50. Their constructive comments have been valuable for the authors and are greatly appreciated by the editorial board:

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Les manuscrits, dactylographiés en double interligne sur le recto seulement des feuilles numérotées (ne pas excéder 20 pages) sont présentés en trois jeux complets, sous leur forme définitive.

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