Ashraf M.T. Elewa

Migration of Organisms

Climate · Geography · Ecology

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(Editor)

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With 67 Figures

Springer

Dr. Ashraf M. T. Elewa
Professor
Minia University
Faculty of Science
Geology Department
Egypt
E-mail: *aelewa@link.net*

Dedication

This book is dedicated to all people <u>who</u>

<u>Believe in</u> One God

<u>Believe in</u> Peace

<u>Believe in</u> Migration in the Way of God

To my father <u>who</u> died on Sunday, the 10th of April, 2005

Foreword

P. David Polly

School of Biological Sciences, Queen Mary, University of London,
London E1 4NS, UK, d.polly@qmul.ac.uk

Evolutionary biology journals of the 1950s and 60s were filled with musings on the improbable. Disjunct distributions of related organisms on continents separated by hundreds of miles of open ocean or in seas divided by mountainous barriers were a historical challenge. Pregnant porcupines were rafted across the South Atlantic on mangrove trunks to explain the presence of Palaeogene hystricomorph rodents in Africa and South America. Limpets were lofted across the Isthmus of Panama in the talons of birds to connect latter day Caribbean descendants with their Miocene Pacific ancestors. By the 70s continental drift lumbered into the paradigms of palaeontology and vicariance inserted itself as the null hypothesis – the evolutionary hegira was redefined as abduction by subduction. Dramatic finds like the Triassic vertebrate *Lystrosaurus* on the Antarctic mountains that once lay within the genus's now disjunct African and Indian range confirmed the predictive power of vicariance. In some instances, the vicariant sword grew so sharp that scenarios of circuitous continental conveyers became even wilder than earlier tales of drifting diaspora. By the end of the century, however, ideological battles between migrationists and vicariants had given way to more dialectic mixed model of biogeographic history.

   In the past decade, molecular phylogeography and geological isotope geochemistry have renewed interest in migration on much smaller temporal scales. Surveys of molecular diversity within species revealed that much geographic variation was phylogenetically structured. Pictures of species as panmictic gene pools have been redrawn so that speciation is no longer an event, but a never-ending narrative of the gradual breakdown in relationship. Rivers and hills, rather than oceans and mountains, separate subspecific clades. At the same time, geochemical evidence has revealed fine-scale wobbles in the Earth's climate. The Pleistocene, for example, is no longer the time when regal glaciers made stately advances and retreats across the continent, but a jumble of transient alternations of warm and cold overlain by more regular glacial and interglacial cycles. Warm spikes only hundreds of years long saw *Saiga* antelope sweep

horde-like from Central Asia as far as England, only to be driven back just as quickly. Phylogeographers and palaeontologists alike now talk of putative refugia and post-glacial recolonization to explain the biogeographic history of populations of seemingly continuously distributed continental species.

The present collection by Dr Ashraf Elewa of Minia University contains papers about migration that are as timely as the subject is traditional. Migration, it seems, is an ever-moving subject, and Elewa presents us with a sampling of some of its current trajectories. Reyment discusses the interpretation, and misinterpretation, of distributions of fossil marine organisms in light of pre- and post-mortem movements. Elewa, in two papers, considers the distribution of tiny but biostratigraphically important ostracods in relation to the changing reaches of the shallow sea that periodically inundated what is now northern Africa. Petrakis and Legakis investigate problems of detecting and understanding insect migration in Mediterranean ecosystems. Longer-term migration and adaptation in cold water Pacific mollusc faunas are described by Amano. Thompson and Russell take a particularly elegant look at phylogeographic structuring in the mtDNA in salamanders in the Pacific Northwest. The Miocene Vallesian Crisis, a time when the subtropical forest faunas of Europe virtually disappeared during a cooling episode, is used by Casanovas-Vilar et al. to investigate the geographic restructuring of entire faunas and floras. The final paper of the book, by Hortal et al., contains a creative quantitative study of the provincializing effect of basin and range structures in Iberia on mammalian communities and an extrapolation by GIS modelling to see whether the same provincial structure existed in the Palaeogene. Readers will get a flavour of the latest quantitative analyses – GIS, faunal clustering, mtDNA phylogenetics – and a sense of the breadth of international research in migration and biogeography.

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1 Introduction

Ashraf M. T. Elewa

Geology Department, Faculty of Science, Minia University, Egypt,
aelewa@link.net

Migration is commonly thought of as a mechanism by which organisms avoid unfavorable environments for more auspicious ones. Migration can be the seasonal movement of organisms from place to place or a more permanent dispersal from one region to another; either way, changing environmental conditions provide the impetus. But why do some organisms migrate and not others? How do the benefits of migration compare with the metabolic costs and hazards of the journey? Do differences between terrestrial and marine species in their interface with the environment have different effects on migration? What are the trade-offs between migration and evolutionary adaptation to local conditions?

Different species respond to environmental changes in different ways, partly based on their individual adaptations and range of tolerance. This phenomenon is most easily seen when comparing terrestrial and marine organisms, which have different relations to their environment. Terrestrial organisms are surrounded by low-density atmosphere and expend considerable energy moving and keeping themselves upright; marine organisms, in contrast, are surrounded by seawater, which has a density close to their own, making support and movement much less costly (Sverdrup et al. 2005). Thus, migration is likely to be more metabolically costly to a terrestrial animal than a marine one, all other things being equal. The factors affecting migration of land and sea species may therefore differ considerably, and one geologic episode may affect the two realms differently.

Terrestrial and marine organisms also differ in the environmental factors that affect them the most. Temperature and rainfall are major determinants on the land, but salinity is one of the most important in the sea. The difference in the salt content of seawater and bodily fluids affects the transport of water molecules through cell membranes in a process called osmosis; changes in salinity can have disastrous effects on the physiological balance of an organism. Temperature variation affects

marine organisms also, but in different ways than terrestrial ones. Changes in temperature affect water density, and therefore buoyancy and the ability of an organism to maintain its optimal position in the water column, positions that are important in terms of ambient pressure and available nutrients. Pressure in deep waters is so great that organisms must avoid it or evolve special adaptations to survive. Most life in the marine realm requires carbon dioxide and oxygen, whose concentrations vary with depth. Oceans can be divided into an upper photic zone, where sufficient sunlight penetrates to support photosynthesis, and a lower aphotic zone, where the intensity of sunlight is low or does not penetrate at all, so inhibiting photosynthetic activity. The constant motion of water in the oceans affects the distribution of organisms and patterns of productivity in the seas, both by transporting the nutrients and gases necessary for life and by carrying floating or drifting organisms with the currents.

Migration often serves as a short-term solution to variable environments, but adaptation can provide a long-term solution. Adaptation can thus be viewed as a parallel way for organisms to survive. Some groups have evolved bioluminescence to bring their own light to ocean depths. Such adaptations will have evolved through selection on favourable chance variants. Because some individual organisms possess genetic combinations that are particularly valuable for survival in a local environment, they will find the environment less antagonistic than do others. For example, for many organisms living in, on, or near the sea floor, the properties of the bottom material, or substrate, are very important for survival. In the vast oceanic environment, both the water and the sea floor are divided into specific zones that have distinct characteristics and support different populations of organisms. Depending on the circumstances, selection may favour adaptations to one of these, or it may favour generalized adaptations that permit movement from one to another. As conditions change, the organisms will either cope or move, and some species will be geographically localized and others widespread. A challenge for migration studies, especially in the fossil record, is to distinguish widespread species from species that migrate between localized environments (Taylor in Boardman et al. 1987).

Since the classic works of Schmidt-Koenig (1975), Schmidt-Koenig and Keeton (1978), Gauthreaux (1980) and Adley (1981), which contain valuable information on migration and quantitative approaches for its study, no edited book, to my knowledge, has considered migration in its broadest sense across different groups of organisms. Moreover, the quantitative analyses in these other works are now aging, with many new

approaches having been developed over the last decades. It is, however, worth noting that Dingle (1996) recently published an excellent textbook on migration, which covers all migratory organisms. The work focuses on the distinction between migration and dispersal and why the two should not be conflated. A second excellent book by Drake and Gatehouse (1995) is limited to insects and was an outgrowth of a symposium at the International Congress of Entomology in Beijing, China. A third recent book, was edited by Jones et al. (2004) with the title "Migrations and dispersal of marine organisms" and based on the proceedings of the 37th European Biology Symposium held in Reykjavík, Iceland, 5-9 August 2002. The main themes of the symposium were migrations and dispersal of marine organisms. Accordingly, no attention was paid to non-marine organisms.

To fill this gap, I have selected, in my opinion, a suitable collection of topics to explore migration in different groups of marine and non-marine organisms ranging from ostracodes and foraminifera (micro-invertebrates), then molluscs (macro-invertebrates), followed by insects, reptiles, amphibians, salamanders, birds, and finally mammals. Conceptually, these papers address a broad range of topics that have not been collected, I think, in any past single work:
1. The paleobiogeography and biogeography of organisms (both invertebrates and vertebrates);
2. The relation of ecological, paleoecological and other factors to migration;
3. The distinction between migration and species origination, extinction, and turnover;
4. Adaptability as a parallel way to migration for organisms to survive;
5. The ecological relation among species (predation, parasitism, commensalism, mutualism... etc.) and its effect on migration;
6. The application of modern quantitative techniques for constructing migration models.

This book should appeal to professionals and students at all levels. I hope this work represents an up to date summary of ideas in the field, as well as a useful summary of recent progress of the subject. In terms of authors, as in my previous book on morphometrics, I have invited a group of experts who present topics showing a broad diversity of organisms ranging from invertebrates to vertebrates, including popular groups such as insects, mammals, birds, reptiles and amphibians.

Additionally, as I am an ostracodologist, I have tried to highlight the importance of ostracodes for paleogeography. Pokorny in Haq and Boersma (1980) stated that marine ostracodes are not as well suited for interregional and intercontinental stratigraphic correlation as are other groups of planktonic microfossils, since benthic ostracodes have no planktonic larvae, therefore, the shallow, warm water species cannot easily cross geographic barriers (see also Keen et al. 1994; Elewa 2002). However, this limitation makes ostracodes excellent paleobiogeographical markers. Pokorny added that the deep-sea ostracodes of the Mediterranean province, studied by Benson and Sylvester-Bradley (1971), are of considerable paleogeographical interest. Examples are found in Paleocene to Middle Miocene and in Pliocene sediments from different areas of the Mediterranean province. Ostrocodes provided evidence that, in the Paleocene, there was a possibility in the southern Mediterranean for east-west migration through the Trans-Saharan Seaway (see Reyment and Reyment 1980; Reyment 1981; Elewa, chapter 3 of this volume). In the Late Miocene, the Mediterranean Sea was cut off from the Atlantic Ocean and transformed into a series of lagoons, as documented by endemic ostracode communities. At the beginning of the Pliocene, communication between the Mediterranean Sea and the Atlantic Ocean was re-established in the west, so that Atlantic euhaline species re-invaded the Mediterranean. Recent Mediterranean ostracodes are chiefly of Atlantic origin and differ from their Tertiary descendants. With the opening of the Suez Canal more than a hundred years ago, a migration route was established between the Indo-West Pacific and the Mediterranean. This is a special example of increasing human effect on the composition of naturally established regional faunas, as was emphasized by McKenzie (1973). Chapter 5 (this volume) by Elisabeth Brouwers presents valuable information about the migration of ostracodes along the northeast Pacific coast in response to temperature changes during glacial-interglacial cycles.

I would like to express my deep gratitude to all people who played an important role in the completion of this book. I especially acknowledge David Polly (UK) for writing the preface, as well as reviewing this introduction and two chapters for this book. The rest of the reviewers, an exceptional group of experts, are also thanked for their critical reviews of chapters in this book (Abdel Kireem and Bassiouni from Egypt; Blain from France; Rook from Italy; Tanabe from Japan; Campomanes, Hortal and Morales as well as an anonymous reviewer from Spain; Reyment and Savazzi from Sweden; Korner-Nievergelt from Switzerland; Whatley from UK; Cronin, Dodd, Finger and Peterson from USA; arranged alphabetically according to their countries). Thanks also to all of the

contributors for devoting their time in preparing their chapters for this book. They have done excellent work and without their contributions this project would not exist. A special word of thanks is due to the publishers of Springer-Verlag for their continuous help during the several steps of editing this book. I also appreciate the great help of the staff at Minia University in Egypt.

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2 Active migration and passive transport of marine organisms in the fossil record

Richard A. Reyment

Department of Paleozoology, Swedish Museum of Natural History, Stockholm, richard.reyment@nrm.se

2.1 Abstract

For the paleontologically oriented purposes of this review, migration can be conveniently considered from several aspects, some of which cannot be definitely identified nor definitely interpreted in the fossil record. In favourable circumstances, inference drawn from Schäfer's concept of "actuopaleontology" can provide enlightenment. Several *ad hoc* categories are briefly discussed here, to wit, seasonal migration, unidirectional migration driven by directed climatic, and or, geological factors, such as changes in the configuration of ocean basins, competition between species and the battle for survival and overpopulation, and enforced migration due to deep-sea oceanic currents. Additionally, and of particular paleontological consequence there is the contrasting circumstance of nekroplanktonic dispersal.

Keywords: Passive transport, directed migration, nekroplankton, eustasy, actuopaleontology, ammonites, ostracods.

2.2 Introduction

The problem posed of identifying cases of genuine migration in the fossil record is not as straightforward as it may seem on first thought. Migration may be viewed from several aspects. One of these concerns migratory patterns induced by seasonal factors and which is most clearly articulated in terms of the annual odysseys undertaken by many species of birds and a surprising number of cephalopod species (Schäfer 1962). Clearly, the possibilities of identifying this pattern are not great in paleontology. A second category concerns the unidirectional migration of organisms from

one geographical location to another in answer to such factors as tectonic influences, climatic deterioration, ephemeral island-bridges, the opening up of new areas for colonization, predation pressure, overpopulation, and competition. A good example of unidirectional migration is that of the "locked"arrival of *Elephas antiquus* on Cyprus and the evolution of this species into the dwarf species *Elephas falconeri (*Reyment 1983a)*. A similar example is the island evolution of the Columbian mammoth into a pygmy form. There are many such cases to be found in the literature on island speciation for deer, rodents, hippopotami (cf. Boekschoten and Sondaar 1972; Reyment 1983a; Thaler 1973). Another category is that of nekroplanktonic dispersal whereby befitting hard parts of dead organisms are dispersed as flotsam and jetsam by surface oceanic currents.

During the Cretaceous Period, for example, large-scale changes of sea level took place. In my experience, it is seldom appreciated that the level of the ocean does not oscillate about a chronologically stable average. The relevant stochastic model is, in effect, one of oscillations about a fluctuating, moving average; dominated by tectono-eustasy (Suess 1888, p. 364; 1892, pp. 465, 768; 1909, pp. 100-102), whereby the sea level changes slowly, but upon which minor oscillations are superimposed over a long time-period in answer to changes, and fluctuations, in the volume of the oceans occasioned by the growth of mid-oceanic ridges and their eventual subsidence (Thiede 1977). Glacial eustasy is another important factor in, for example, the Pleistocene and Holocene (Mörner 1976), which, however, in relation to tectono-eustasy is of fleeting significance time-wise. Reyment and Mörner (1977) examined the interplay between factors governing sea level change for the Upper Cretaceous. Additionally, vertical movements of the crust may play an important part at the local level. An example of this is the history of the coastal sedimentary basins of the Cretaceous South Atlantic Ocean (Reyment and Tait 1972; Reyment and Dingle 1987).

For the explicit purposes of the present note, we shall make a set of arbitrary distinctions between migrational models, passive and active. It will be apparent that these "categories" encompass the migration of individuals in their lifetime as well as long-term migration of a lineage and post-mortem dispersal. I have not been so bold as to provide unique labels for each case considered but rather retained a more anecdotal form - moreover, there no hard and fast marches can be drawn between them.

1. Seasonal migration from an overwintering site to a summer location. The bird paradigm for active North-South migration.

2. Active dispersal by living marine organisms such as occurs when a new *lebensraum* is being exploited. This may be exemplified by the gradual invasion by marine organisms into epicontinental seas (i.e. very

shallow seas of wide geographical extent that spread over surfaces of slight relief) formed by rising Suessian sea level (cf. Reyment 1996) which may be exemplified by the incursions into the vast, shallow epicontinental trans-Saharan seas of molluscs and crustaceans.

A special case of this design is the way in which Cretaceous and Tertiary ostracods were able to cross the South Atlantic from western Africa to south-eastern South America by a chain of mid-Atlantic islands (Reyment 1980a, 1980b, 1983b; Thiede 1977).

3. Enforced migration of living organisms by oceanic currents. Examples of this mode of migration are provided by ongoing research on deep sea-currents relocating the coelacanth *Latimeria* sp. to the Celebes (Sulawesi) in Indonesia together with *Nautilus pompilius*. Neither of these denizens of deeper waters are strong swimmers and cannot successfully hold their own against powerful westerly flowing submarine currents (television programme aired in 2004 in the *Discovery Science* Channel by Professor Hans W. Fricke (Max Planck Institute, Frankfurt/Main, and coworkers). This kind of migration would obviously be most difficult to prove for fossils.

4. Nekroplanktonic dispersal. The buoyant shells of dead organisms are transported by oceanic currents sometimes over thousands of kilometres from the habitat of the living animal.

5. There is also the category I call "spurious migration"; that is, well isolated occurrences of identical species of non-marine plants and animals, but for which land-separation due to continental drift and seafloor spreading are the cause. Western Africa and eastern South America provide an example of this category (Reyment and Tait 1972).

2.3 Seasonal Migration

The distribution of fossil cephalopod shells is often a source of puzzlement as to whether active or passive in origin, not least because of the paucity of information available for living representatives. Comparative information must be extrapolated obliquely, such as afforded by the following case-history for squids. Tinbergen and Verwey (1945) reported on the seasonal migratory behaviour of the squid *Loligo vulgaris* in the waters around Den Helder (Netherlands). Individuals are observed to arrive in great numbers in the Spring when they reproduce. Most animals do not live for longer periods but it is believed that some surviving individuals may overwinter in Portuguese waters. An excellent reference to marine seasonal migration of squids, and other marine animals, is the treatise by Schäfer (1962). On

the subject of the seasonal migration of dibranchiate cephalopods to and from the German tidal sea (Wattenmeer) he noted that most species exhibit migratory behaviour. He listed as being seasonal migratory the species: *Sepia officinalis, Loligo forbesi, L. vulgaris, Alloteuthis subulata* and *A.media. L vulgaris* arrives in June/July and departs in September. *L. forbesi* arrives somewhat later and leaves in October/November. Many individuals die during the reproductive period after which, the carcase rises to the surface where, according to the paleontologically germane observations of Schäfer (1962), it remains floating for about four days, on average, borne up by the gases of putrefaction. Many carcases strand along the maximum tidal shoreline, others disintegrate during advanced putrefaction.

The mass occurrences of dead calamars and squids on tidal flats of northern Europe are partly attributable to episodes heavy rainfall and the concomitant drop in salinity.

My own personal observations in the Danish wattenmeer around Esbjerg may be added to this general observation. Following on a violent out-of-season storm out of the North, thousands of lifeless cephalopods were observed to be strewn widely over the tidal flats. Transferring this observation to the past supports the interpretation of mass mortality of ammonites in the Saharan Cenomano-Turonian shallow epicontinental environment as having been caused by salinity-shock in connexion with the effect heavy rainstorms on stenohaline organisms (Reyment 1980a, 2003; Courville and Thierry 1993; Mathey et al. 1991; Mathey et al. 1995).

Whether or not shell-bearing tetrabranchiate cephalopods migrated according to some seasonal pattern is a difficult question to answer. A possible clue is the observation by Talavara and Faustino (1931) made for several areas around the Philippines that *Nautilus pompilius* appears periodically with a maximum during the summer months. In the light of current knowledge, this periodicity could possibly be due to local vertical migration and not to an active geographical displacement. In any event, the energy required for seasonal migration over vast distances cannot conceivably be mustered by shell-bearing cephalopods as has been demonstrated by a method of energy bookkeeping by Reyment (1988). A potentially useful type of simulation has recently been ventilated by Brayard et al. (2004), which may in the future turn out to be adaptable to aspects of the situation outlined above.

The seasonal migration of birds that inhabit a freshwater swamp environment is thought to be a distributional vector for ostracods via eggs trapped in mud attached to some part of the body of the bird. As far as I am aware this hypothesis has never been proven by direct observation. Hartmann (1988a, p. 792) attributed the arrival of Alaskan *Cyprideis* in

Hawaii to this intermediary. In this connexion it should be borne in mind that the eggs of marine ostracods quickly dehydrate when exposed to the air and thus lose their viability, whereas those of freshwater species can survive for many years. Many of the non-marine species described by G. O. Sars were obtained from eggs in ancient mud-samples stored in the Bergen Museum.

2.4 Active unidirectional migration

Here I shall present tow case-histories, one of which (the ammonites) harbours perforce an element of speculation. The second (the ostracods) is more firmly anchored in reasonable assumptions and confirmatory observations.
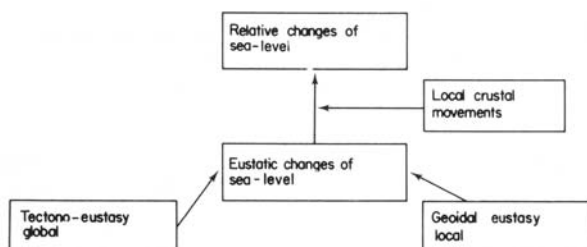
Fig. 1. Schematic representation of the factors underlying marine transgressional episodes and relative changes in sea level; these may occur singly or in various combinations. After Reyment and Mörner (1977)

In order to appreciate the forces at work it is necessary to consider how changes in sea level can and do occur. Figure 1 gives a schematic appraisal of the variables of significance for the development of epicontinental transgressional episodes. The main force driving the dispersal of marine organisms across the vast trans-Saharan inland sea was tectono-eustasy, fuelled by the growth of mid-oceanic ridges and seafloor spreading causing changes in the volume of ocean basins. The effects of geoidal eustasy (Mörner 1976) would have been negligible (glacial eustasy does not appear to have entered into the equation on an appreciable scale).

On the Atlantic side of the epicontinental transgression, local crustal movements played an important part, coupled with the growth of the mid-Atlantic ridge (Reyment and Dingle 1987). The field evidence and distribution of species points to the invasion of the sea having been mainly from the north.

2.4.1 The Ammonites of the Saharan Turonian (Cretaceous)

Reyment and Mörner (1977) dissected the elements of fluctuations in sea level in the light of factors that are directly related to the rise and fall of sea level on a mondial scale (Fig. 1). The Cretaceous sea level record for the South Atlantic region encompasses five major transgressive cycles of which three are well known to be of major global significance; the tectono-eustatic event that took place during the Late Cenomanian-Early Turonian has attracted most interest. It was on this episode that Suess (1888-1909) elaborated his classical concept of eustasy (known specifically today as tectono-eustasy). Locally, earth movements caused by faulting may be responsible for significant, though isolated, relative changes of sea level, such as occurred in the inland sedimentary basins of West Africa (Louis 1970, 1977). The Cenomano-Turonian was a particularly active phase of ridge growth and seafloor spreading connected with accelerated movement apart of South America and Africa and a paucity of geomagnetic reversals (Reyment 1974, 1976, 1980e). Gebhardt (1997) concluded from an analysis of foraminiferal associations that the water depth can hardly have exceeded 50 m in the area with which he was concerned. Viewed in a wider context (cf. Louis 1970, 1978) it is however obvious that greater depths existed off the "Saharan ramp" (Reyment 2003) and that these formed a Caspian Sea type of environment during falls of sea level related to phases of ridge-subsidence.

The seeming proliferation of "species" in Nigerian and North African vascoceratid ammonites seems to be best explained as deriving from ecophenotypic reactions to a variable and often inhospitable epicontinental environment (Courville and Thierry 1993a, 1993b; Reyment 2003). The founder forms followed the sea advancing from the Tethys and, during the acme of the epicontinental transgression, were able to enter the unfolding South Atlantic via the Nigerian coastal basin. The morphometric analyses tend to indicate that the most abundant elements of the Nigerian paleofauna consisted of two highly variable species, *Thomasites (Thomasites) gongilensis* (Woods) and *Thomasites (Bauchioceras) nigeriensis* (Woods) and that the latter evolved from the former early in the history of the Saharan mid-Cretaceous epicontinental sea (Reyment 2003). In addition to the effects of ecologically triggered polymorphism or polyphenism, sparked off by episodes of fragmentation in ephemerally isolated "Balkhash-type" basins, there are intimations of polymorphism, possibly relatable to sexual dimorphism. This eventuality deserves to be given detailed study on the basis of more comprehensive material obtained from the abundance of virtually unexplored sites in Nigeria, Niger, and Chad (Faure 1966).

2.4.2 The early Turonian ammonite genus *Benueites* in the South Atlantic Ocean

The distribution of species of *Benueites* in the late early Turonian (Upper Cretaceous) seems to accord with a model of unidirectional migration with speciation in a situation in which tectono-eustasy did not provide the main driving force and is therefore a rare example of a case-history where an interpretable migrational pattern, accompanied by evolutionary events, can be established for ammonites. The oldest occurrence of the species, *B. benuensis* Reyment and its dimorph, seems to be in Nigeria (the Wadatta limestone which directly overlies older Turonian beds with vascoceratids) near Makurdi (Reyment 1955), and, presumably, in beds of the same age in northeastern Brazil (Reyment 1971). The same species, and a new one, *B. reymenti* were recorded by Collignon (1966) from the Tarfaya Basin of southern Morocco. The same two species (and dimorphs) occur in Trinidad (Reyment 1971). *B. benueensis* (and dimorph) were figured by Reyment (1971) from Colombia together with a third new dimorphic species, *B. colombiensis* Reyment. The locations are marked schematically in Fig. 2. A plausible explanation of the distribution of the three known species of the genus would seem to lie with the oceanographical effects associated with the continued opening of the South Atlantic Ocean and a diverging pattern of northerly migration. The fact that all three species occur in an *in situ* dimorphic association speaks against the likelihood of their having been spread nekroplanktonically on a large scale.

2.4.3 Ostracoda of the North African Paleocene

During the Early Paleocene, possibly latest Maastrichtian, the last of the extensive tectono-eustatic trans-Saharan epicontinental transgressions began (Reyment 1982a). At its acme in Late Paleocene time, the sea stretched from the north of Africa to Nigeria and from the Gulf of Guinea probably through the Kontagora syneclise (Fig. 3).

An impressive paleobiological feature of this is the wide distribution of many species of ostracods. There are at least 24 West African species in common with the Paleocene of Libya (Reyment and Reyment 1980). The main thrust of the Paleocene epicontinental transgression proceeded in a manner similar to the earlier ones, that is the advance of the sea was more rapid from the north than from the south. Evidence for this lies with the indication of a multivariate progression for carapace volume for several species. An example for the abundantly occurring *Bairdia ilaroensis* Reyment and Reyment is shown schematically in Fig. 2.

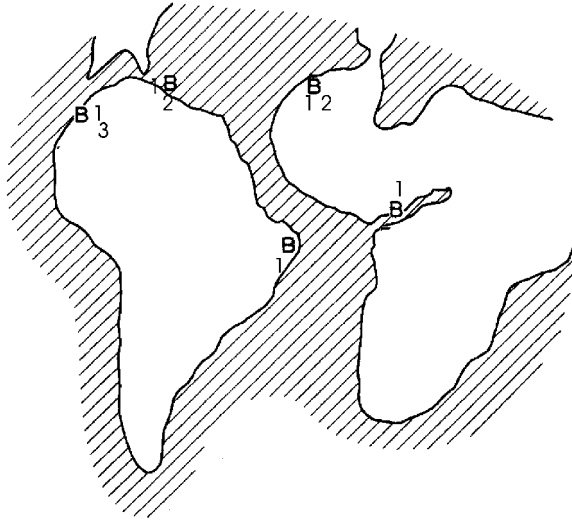**Fig. 2.** Distribution of species of *Benueites* in the South Atlantic realm in the Early Turonian shown schematically. Key: 1: *Benueites benueensis* 2: *Benueites reymenti* 3: *Benueites colombiensis*
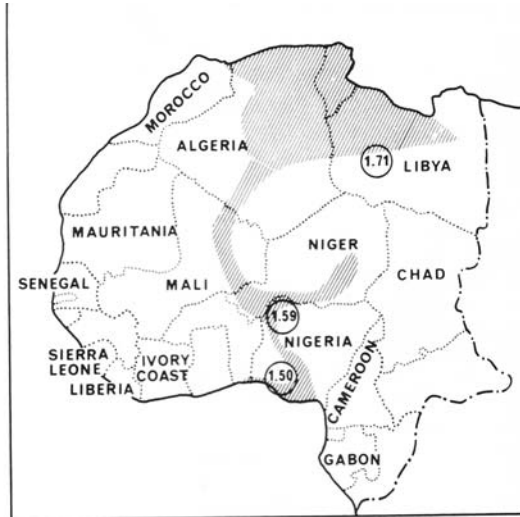

Fig. 3. Three discriminant scores for carapace volume for *Bairdia ilaroensis* showing a gradual shift from north to south. The shaded area delineates the maximum extent of the trans-Saharan Paleocene epicontinental sea

There is a statistically significant decrease in volume of the carapace over time as the transgression advanced, carrying the evolving association in its wake.

By way of comparison, ostracods were dispersed from the Tethys during the Coniacian Saharan transgression (Reyment 1980d); this incursion of the sea seems to have been of short duration.

2.4.4 South Atlantic Island-Hopping

Nigerian Paleocene and Eocene ostracods have been reported from Argentina (Bertels 1969, 1977). We shall now briefly examine a likely mechanism for this distributional pattern, granted that by Paleocene times, the southern Atlantic had attained a respectable width and under normal marine conditions it would not be possible for shallow-water benthic organisms to cross from one side to the other. A variety of "island hopping" would seem to afford a likely agent.

In the early Maastrichtian, and again in the early Paleocene, ostracods followed the last two major epicontinental transgressions across the Sahara, spreading through the Saharan system of tectonically controlled basins to the expanding South Atlantic Ocean (Reyment 1980b, 1983b).

A logical explanation for the agreement in coastal marine ostracod faunas between West Africa and eastern South America would seem to lie with the migration of shallow-water species by a chain of islands and high-grounds (Thiede 1977).

A schematic reconstruction of the situation is given in Fig. 4. The occurrence of West African shallow-water Cretaceous marine ostracod species in South America has been recorded by Reyment and Neufville (1974) and Neufville (1973).

An additional factor of importance for ostracods and some other animals relates to passive transport on algae. The passive migration of many species, including ostracods, across the Pacific Ocean, is known to occur in this manner (Hartmann 1982a, 1982b). My own observations made in Tahitian waters in 1986 confirmed the occurrence of ostracod "demes" being transported on floating algae in accordance with Hartmann's observations.

Fig. 4. Reconstruction of the averaged southern Atlantic Ocean in Maastrichtian and Paleocene time. The schematically denoted shallow region between southern Brazil and southern Africa seems to have provided a migrational route for benthic organisms, in particular ostracods. The trans-Saharan transgressions around the Cretaceous-Cenozoic boundary contain elements in common with Brazil and Argentina. Based on the paleo-oceanological results of Thiede (1977) and for faunistic aspects on Neufville (1973) and Reyment (1980b)

2.5 Imposed dispersion by submarine currents

In a recently aired television programme *(Discovery Science)* deriving from the submarine biological research of Professor Hans Fricke (*vide* p. 2), it was made reasonably apparent that individuals of the newly

discovered Pacific coelacanths are transported by submarine currents that bring isolated individuals to northern Sulawesi (Indonesia) from the island complexes of the South Pacific, thence further westward, from some as yet unidentified centre of distribution in the southern Pacific Ocean. It was also illustrated that co-occurring individuals of *Nautilus pompilius* s. l. are presumably dragged from their natural habitat to Indonesian islands in the same manner (e.g. northern Sulawesi). Notwithstanding that species of *Nautilus* occur widely throughout the Pacific and Indian oceans, albeit patchily distributed (Fig. 5), it is certainly quite reasonable to accept the possibility of forced dispersal in relation to such relatively poorly endowed swimmers as the coelacanth and the pearly nautilus. It has been suggested on these grounds that the reported occurrences of living nautilus in the eastern reaches of the Indian Ocean could be the result of imposed dispersal by powerful (intermittent?) subsurface currents. Indeed, the distributional pattern being established for *Latimeria* is persuasively close to those of *Nautilus*, not least in the far western reaches of the Indian Ocean.
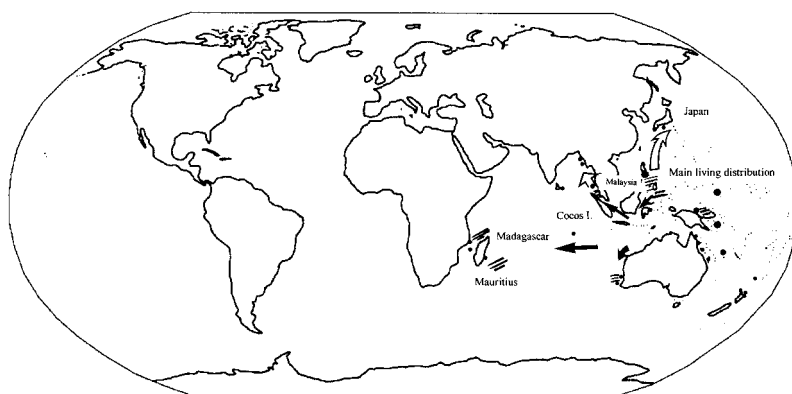
Fig. 5. Sketch map showing the distribution of living species of *Nautilus* in the Indian and Pacific Oceans and places where nekroplanktonically drifted shells occur. The black arrows indicate approximately the dispersal directions of living individuals, the open arrow marks the direction taken by floating shells borne by the Kuroshio current. The black dots mark stranding sites of shells. Based on Reyment (1973a), supplemented with information obtained from recent records

This aspect of submarine oceanology holds promise of yielding results of far-reaching significance (cf. Fricke and Hissman 1994; Fricke 1998). The tantalizing significance of this research for understanding the dispersal

of fossil cephalopods with properties analogous to living nautiloids remains to be exploited.

2.6 Nekroplanktonic dispersal

The post-mortem distribution of the remains of organisms is of trivial significance in neontology but of great importance to the paleoecologist. Schäfer (1962, p. 570) discussed, and illustrated the effects of, the post-mortem distribution of gas-floated marine mammals in the Jadebucht, northern Germany. This is a potentially important factor and one that deserves more attention in the paleoecological literature than it has received. I note, in passing, that rock paintings made by past and present Australian aboriginal people correctly, and elegantly, depict the post-mortem deformation of water-transported vertebrate carcases. From the standpoint of the paleontologist it is, however, the fossil cephalopods that claim pride of precedence.

Despite the constantly accruing weight of evidence in favour of nekroplanktonic dispersal of the shells of species of the pearly nautilus, there still seems to me to be an aura of reluctance associated with accepting the practical consequences for paleobiogeographical interpretations. There is, however, a logical *non sequitur* here in that what the animals did in life has nothing to do with what happened with their remains after death, when outrageous fortune reigns supreme. The post-mortem distribution of nautiloid shells is well documented. Reyment (1958) made a survey of the existing literature, and original observations. Since then, records of stranded shells have been published by Toriyama et al. (1965) for beaches around western Thailand, Teichert (1970) for drifting shells in the Bay of Bengal and 250 km SW of Sri Lanka, Reyment (1973, pp. 35-39) for western Malaysia, Fiji, the Philippines (stranded shells and shells inhabited by hermit crabs), the Solomon Islands (study due to Mr. C. F. Fowler, reported in Reyment 1973a), Great Barrier Reef (reported by Dr. J. S. Hynd in Reyment 1973a), Mauritius, Zanzibar. The floating behaviour of various models of nekroplanktonic shell-types has been analysed and illustrated by Reyment (1980c).

Reyment (1967) discussed the post-mortem transport of rare nautiloid shells in the Paleocene proto-South Atlantic by the forerunner to the Benguella current, from southern Africa to the Niger Embayment. An analogous example of post-mortem transport has been reported by Chirat (2000) for Paleogene nautiloids. Reyment (1968) and Laufeld (1974) described preferred orientation in stranded orthocones in the Ordovician

and Silurian of Sweden. These shells occur in great numbers and it is clear that they must have in life inhabited a shallow, strand-near environment.

Not only cephalopod remains are carried nekroplanktonically. Reyment (1986) recorded a floating "mummified" shell of a regular echinoid floating 100 m offshore off Estepona, Spain. This observation is analogous to the record of floating gastropod shells by Krejci-Graf (1935) and to the rafting of reef-coral and other organisms (Jokiel 1989).

The total body of evidence reporting the widespread post-mortem transport of fossil cephalopod shells is extensive, too extensive to attempt a review here. References to published information on the topic are given in Reyment (1958, 1971, 1973a, 1980c).

2.7 Spurious migration

In what must be one of the most important contributions ever to ostracodology and paleobiogeography, Krömmelbein (1970) and Krömmelbein and Wenger (1966), demonstrated that the fresh-water Neocomian ostracod faunas of northeastern Brazil and Gabon shared a common geographical origin. Of the 40 species of ostracods known from the Cocobeach Formation of Gabon and 90 species from northeastern Brazil, 33 occur in both regions. This result was fundamental to establishing the existence of a land connexion between South America and Africa in the lowermost Cretaceous and for delineating the rift-controlled freshwater inland seas in the Gabon, Congo and northeastern Brazilian contact zones. It is stimulating to observe how Krömmelbein gradually, over a spate of years, arrived by skilful deduction at the conclusion that the Brazilian and Gabon ostracod sequences had once inhabited the same sequence of rift-valley lakes and that the impression of lateral migration was not a viable concept. Transport by migrating birds as a possible mechanism was soon discredited since experience shows that birds migrate along a N-S-N axis and not in an E-W-E direction, which would be a pointless exercise from the bioclimatic standpoint (Hartmann 1988b). A referee suggested that this may not have been so in the past. Be this as it may, there is no evidence known to me that gainsays Krömmelbein (1970) and Hartmann (1988) and, moreover, the question has scant bearing on the geological facts before us. The fact that a great number of the known Wealden ostracod species of Gabon and eastern Brazil are common to both areas was used by Reyment and Tait (1972) and Reyment and Dingle (1987) in their reconstruction of the rift-valley phase of the South Atlantic Ocean. They also compiled a detailed reconstruction of the relative