

CRUSTACEAN ISSUES 4

CRUSTACEAN BIOGEOGRAPHY

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Edited by

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A.A.BALKEMA/ROTTERDAM/BOSTON/1986

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG

Crustacean

Crustacean biogeography / ed. by Robert H. Gore & Kenneth L. Heck. — Rotterdam [etc.] :

Balkema. — Ill. — (Crustacean issues, ISSN 0168-6356; 4)

ISBN 90-6191-593-7 bound

SISO 597.6 UDC 574.9:595.3

Subject heading: crustaceans; biogeography.

ISSN 0168-6356

ISBN 90 6191 593 7

© 1986 A.A.Balkema, P.O.Box 1675, 3000 BR Rotterdam, Netherlands

Distributed in USA & Canada by: A.A.Balkema Publishers, P.O.Box 230, Accord, MA 02018

Printed in the Netherlands

Preface

It is a pleasure to acknowledge the following persons or their institutions for helping make the presented papers session in Biogeography of the Crustacea a success. Foremost acknowledgment must go to the Academy of Natural Sciences of Philadelphia for providing funds, personnel and aid before, during and after the Symposium. Particular thanks are jointly extended by the editors to the Division of Ecology and Limnology, and the Department of Malacology. Among the individuals who contributed time, space, or aid are Dr George M. Davis, Chairman, Department of Malacology, and his staff, all of whom made the first editor's tenure at the Academy such a rewarding experience. Mss Sandy Devan and Helen Anderson provided clerical aid above and beyond the call of duty. Special thanks also go to Mary Wiley, business manager of the American Society of Zoologists for her untiring help in formulating the arrangements for both the Symposium papers session, and the contributed papers session on the following day. Dr F. Lynn Carpenter, Chairwoman, Division of Ecology, ASZ, generously provided some funding allowing partial defrayment of travel expenses for some participants. Dr Patsy A. McLaughlin, program officer for the Crustacean Society, first approached one of us (R.H.G.) with the idea for the symposium and helped initiate the requisite action to see it through. The support of the presiding officers of the Crustacean Society, and many of the members, is also appreciated; the Symposium would certainly have been less successful without such help. The first editor (R.H.G.) also wishes to express a very special thanks to Kim A. Wilson, for her tolerance and forbearance for so long. Finally, of course, we gratefully acknowledge all of the participants at the Symposium papers session, and particularly those authors whose papers appear herein. In the final analysis it will be they who are responsible for the success of this volume.

Introduction

This symposium had its origin in a simple and easily observed fact. One need only scan the recent pages of several well-known journals or textbooks that treat biogeography to see the often heated debate, acrimonious rhetoric, and fervent exhortations as to which process, or functioning geological or biological event, would more adequately explain the distribution of this animal or the dispersal of that plant. One is reminded of Victorian missionaries attempting to proselytize a large, and unruly group of all too recalcitrant natives who often are more interested in how to carve up the proselytizer for their colleagues' philosophical dinner table than in paying attention to the way, the truth and light of vicariantist or dispersalist dogma. Yet, in these controversies crustaceans have played but a minor role, if they played any role at all. A perusal of several recent and classical texts in biogeography shows that if crustaceans are referenced at all in the literature cited, they are usually noted as species-listings or other taxonomic-oriented publications, or in an ecological or ethological framework. We believe that the time has come to change this, and this volume is intended to be a positive step in this direction.

A wag, commenting on biogeography in general and crustacean zoogeography in particular, once said 'The more we investigate the distribution of crustaceans, the more it seems they occur'. There is a nugget of truth in this facetious statement. Crustaceans do indeed occur; from the hadal oceanic trenches to the highest mountains; in stygian terrestrial caves on continents as well as on mid-oceanic islands; in anchialine pools, ephemeral desert ponds, hot springs, deep wells, glaciated lakes, swift montane creeks, on sawgrass prairies, brackish sloughs, hypersaline lagoons and major continental rivers. They are found under rocks, in burrows, tubes, and crevices; in shells, on, in, and with other crustaceans as well as members of other invertebrate and vertebrate phyla; they live in sponges, on stony corals, under seastars, between the spines of echinoids, clinging to holothurians, sharing worm tubes, attached to seagrasses, hitching rides on turtles, fouling almost every conceivable type of hard (and many soft) substrates; they curl up in the dirt of household potted plants, engage in explosive population growth in swimming pools, destroy pilings, climb trees, and inhabit epiphytes on other trees. They are as close as one's backyard or as remote as Ascension or Kerguelen Island, in areas as easily collectable as the seashore, or as difficult to sample as hydrothermal vents. In short, Crustacea are ubiquitous. If they do not now occur in a specific habitat, the chances are that they did at one time in their history, or will in their future if given half a chance.

In the papers that comprise this volume we will be given fascinating and intriguing

glimpses of some of this ubiquity. Papers treating palaeontological distributions will be balanced by those examining historical, and even man-made dispersals. Distributional explanations or hypotheses will range from groundwater transport to planktonic dispersal, from overland migrations to piggyback radiation via parasitized hosts. Biotopes from the darkest subterranean caves to the hadal depths of the ocean will be treated herein, using fresh, brackish and marine water forms as well as terrestrial groups. Traditional dispersalist views will be defended, but vicariance explanations will also be proposed, to account for the observed distributions. Even a melding of these two often antithetically opposed hypotheses will be given consideration.

In assembling the participants for this volume we leaned towards neither dispersalist nor vicariantist viewpoints, accepting both for the sake of arguments but adhering toward neither. Spatial limitations prevented treating every crustacean group, but we hope that those groups which are addressed might provide some indicative concepts toward the phylum Crustacea in general. After editing the 12 papers that comprise this volume it has become clear to us that the data supporting one viewpoint in one group may outweigh those in another, but that the proposed explanations may also only be valid for the particular group being considered. This is, of course, not unexpected, given that the Crustacea are a large, phylogenetically complex, geologically old, geographically widespread taxon. During the course of their evolutionary history they have evolved numerous, often unique, methods to move around on this planet, and once in place, to ensure that they stay there. Today, if distributions seem disjunct, if ranges seemed skewed, if populations appear to be curiously relict, these may all be the joint results of the animal's efforts to remain in place, and nature's attempts to undo these efforts.

Our task, as biogeographers, is to attempt to make some sense out of these distributions, and in so doing, to ask pertinent questions as to how such distributions might have taken place. A major problem, and a recurring one, will be the generation of acceptable and testable hypotheses. Because the fossil record is often poor, patchy or incomplete, many previous ranges can only be suspected, many distributions only implied. For all of our records both fossil and recent, we are seeing only the remnant, the collectable specimens, and not always the complete previous ranges.

Whether we believe one group to have dispersed from a center of origin or radiation, or another to have undergone a vicariant sundering, we should not lose track among the general tracks of the primary goal in biogeography — the attempt to explain the distribution of organisms as we see such today. It may be, for example, that present day ranges are a combination of both dispersal and vicariance, as some have suggested in the papers that follow. If so, can we say that one occurred before the other? Can not a dispersal event take place after a vicariant event, as well as before? Are not all vicariant distributions a consequence of a previous, and much older dispersion? Is not every dispersion a potential vicariance event — be it a behavioral, physiological, ecological, or reproductive sundering? Does not isolation occur intrapopulationally as well as extrapopulationally? What are the upper and lower limits of any biogeographic event, whether it is a dispersal or a vicariant determination? These are but a few of the philosophical questions that might be applied to any biogeographical study, regardless of the (often almost religiously held) convictions of the researcher.

We may also ask in what way does it matter, if it matters at all. Organisms are notoriously disrespectful of man-imposed boundaries, and man-delimited ranges. If biogeography is to be a dynamic discipline rather than a static recording of ranges we must take every

factor of the organism's biology into consideration. Certainly, crustaceans have employed many factors, either during larval stages, or in adulthood, or perhaps during both, to arrive where we find them today. To ignore such factors is to produce incomplete assessments not only of the organism's distributions, but of its ecological responses, biological relationships within the distribution, and indeed even the ability to distribute.

We are indeed fortunate to have assembled such a varied slate of authors to address these and other topics within *Crustacean Biogeography*. When the participants were solicited for the oral presentations during the 1984 meeting of the American Society of Zoologists at Philadelphia, and later for the chapters that appear herein, one important stipulation was made. All contributors were requested to let their imaginations run a little more freely than perhaps they were accustomed to doing. We wanted ideas, perhaps unpopular — speculations, perhaps bold or even tenuous — and conclusions, perhaps controversial. Our goal was not only to inform, but more importantly, to make the student of biogeography think, or even rethink, previously held (and perhaps all too sacred) concepts. Herein we have radiation, centers of origin, island biogeography; but also herein are body size factors in relation to environmental constraints, Lessepsian migrations and tracks, global conclusions, and false cosmopolitanism. In editing these papers, and we hope in the reader's assessment of each, it seems apparent that the field of *Crustacean Biogeography* is ripe for forment, for controversy, and most of all for change. We believe that the Crustacea can and will play a major role, of increasing importance, in the field of biogeography as a whole. We trust that the contributions in this volume will foster continued interest in this regard.

Robert H. Gore
Kenneth L. Heck

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1 Realized distributions

Prologue

While not intending to categorize or assign any of the authors who have contributed to this volume by lumping them under one title or another, we believe that the contributions can be separated into three main categories. In Part I five authors examine zoogeographical aspects of Decapoda, Cirrepedia, Syncarida, Peracarida and Coepoda primarily from the position of what may best be called 'realized distributions'. Thus, Rodney Feldmann's paper provides new data and insight into possible palaeozoogeographic distributions of some rather poorly known decapod taxa, including a novel hypothesis which employs both plate tectonics and a generalized track of dispersal to explain the occurrences of marine raninid, and freshwater aeglid crabs within the southern hemisphere. His data support similar distributions seen in the Mollusca within the same region.

William Newman's paper takes the position that the Hawaiian biota is probably best explained as the result of long range dispersal from the Indo-Pacific. He examines this concept in relation to several factors, including extinction and island integration, using the Cirrepedia. The hypothesis of high and low island stepping stones, which occurred during eustatic lowering and raising of sea levels across the Pleistocene, is promulgated. The question as to whether island raising or lowering is truly indicative of a dispersal, rather than a vicariant, event should spark some controversy in future studies.

Gilberto Rodriguez discusses the freshwater terrestrial regions of Central America where he investigates the present day occurrences of pseudothelphusid and trichodactylid freshwater crabs. Using a suite of cladistically derived characters, Rodriguez suggests that shared synapomorphies in the respiratory structures of these crabs strongly imply a monophyletic origin for the families. However, both a vicariant and a dispersalist viewpoint are advanced, in which a Gondwanan distribution was severed by one or more vicariant events during the mid-Cretaceous, followed by further dispersal and subsequent vicariant events in the Pliocene. The latter phenomenon is invoked to explain a puzzling disjunct distribution of some pseudothelphusids between the Greater Antilles and the distributional center of northern South America. Rodriguez' paper does much to reconcile the polarity that too often occurs between dispersal and vicariance zoogeographers.

However, migrations certainly have their place in understanding the biogeography of the Crustacea, as is amply shown by Dov Por's concise summary of dispersal and vicariance events in the Levantine landbridge. The formation of this barrier was important in that it severed a once-continuous Tethys Sea, isolating peracaridan and syncaridan groups (among others) from their taxonomic relatives. This more or less ongoing series of events in the

Triassic, coupled with the eventual salinity crisis and a nearly complete drying out of the Mediterranean sea was followed by later transgressions, all of which left indelible marks on many previously united crustacean groups. The establishment of the Suez Canal has again affected distributions, allowing some groups to migrate back into the Mediterranean. Por examines the several aspects of these events using subterranean, interstitial and epigaeic forms, and follows their distributions from the Red Sea-Levantine area into the Mediterranean.

On another continent on the other side of the world John Holsinger also uses subterranean distributions, in this case of amphipods, to show that three major zoogeographic patterns can be discerned: an ancient freshwater distribution of forms that extends possibly from the early Mesozoic; a marine relict distribution which is postulated to be the result of a stranding of ancestral forms previously marine during late Cretaceous-Tertiary times; and an island-associated group of taxa living fully marine to marginally freshwater in or on West Indian islands, which are also hypothesized to have become isolated during island emergence in the Cenozoic. Holsinger invokes both early Laurasian-Pangaeic vicariant events, and subsequent destruction of groundwater habitats by glaciation (as another vicariant sundering of distributions) to explain present day distributions of some groups. Other groups are postulated to have radiated from deep groundwater refugia beneath glacial ice coverings. Holsinger's paper is a compilation of fascinating vicariant and dispersal events within an extremely interesting group of familial taxa, most of which are stygobionts that apparently colonize much of their ranges either by remaining subterranean, or by becoming stranded and eventually adapting to freshwater during events of island emergence.

None of these authors can be considered strict dispersalists or vicariance biogeographers. Instead, they have incorporated both concepts to suggest some plausible explanations for distributions seen today. As such, these papers form an ample springboard to jump as deeply as one might wish into the complexities involved with the novel vicariant concepts and reconciliations with traditional dispersals from centers of origins.

Paleobiogeography of two decapod crustacean taxa in the Southern Hemisphere: Global conclusions with sparse data

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ABSTRACT

Examination of the fossil record of two decapod crustacean groups, the Aegliidae and the raninid genus *Lyreidus*, shows that they originated in the southern circum-Pacific region in Late Cretaceous and Eocene time, respectively, and that dispersal into lower latitudes probably occurred in the early Oligocene. Fragmentation of the southern Pacific landmass, dominated by Antarctica and Australia, and concomitant development of the circum-Antarctic current system severely reduced the probability of further dispersals along this route. These interpretations, based on extremely limited fossil data, parallel conclusions drawn regarding the paleobiogeographic distribution of mollusks in the early Tertiary Wedellian Province.

1 INTRODUCTION

Ortmann (1902a) introduced an article on the zoogeography of freshwater decapods by emphasizing that the final goal of zoogeography was, 'the retracing of the present animal distribution to its beginning in the past . . . a corollary of this is the reconstruction of the ancient physical features of the earth's surface, since these in the first place have guided the development'. He went on to say that, 'In the latter respect, the distribution of land and water in past times is all-important and the easiest to be traced'. His observations are equally true today. We continue to talk about the same kinds of points relative to paleozoogeography and the thrust of his statement forms the basis for this essay.

The distribution of any organism in time and space can be portrayed as an irregularly shaped polygon (Fig.1) when its distribution is plotted against the axes of time, geography and ecology. A taxon, as defined by a human observer, is said to evolve at a single point in time and space and become extinct at some other point in time and space. Between the two events, however, one is faced with the problem of attempting to reconstruct the shape of the polygon in such a way as to correctly portray the history of growth, dispersal, radiation and ultimately, diminution and extinction. The question I would like to address is whether a reasonable pattern of the paleozoogeographic history of taxa can be constructed when only limited fossil material is available. Under such circumstances, the data points represent checkpoints to at least begin to define the trends of distribution

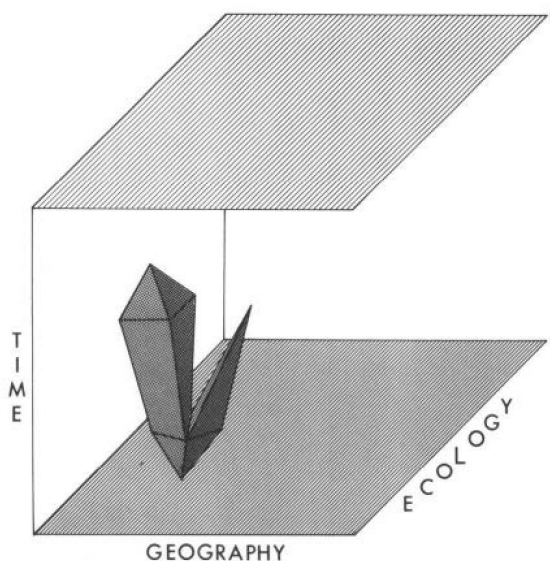


Figure 1. Time-space diagram showing the total distribution in time, space, and ecological setting during the evolution, radiation, and extinction of a hypothetical taxon.

within the continuum. The only test for the adequacy of the system is to compare distributional patterns derived from limited data with established patterns of dispersal based on more frequently collected organisms. I contend that, at least in the case of some of the Cenozoic and late Mesozoic decapods of the southern hemisphere, adequate information is available to recognize some important new dispersal routes, even in the absence of large collections. The conclusion is significant because decapods are almost invariably rare elements in fossil assemblages. If it were always the case that large numbers of individuals, from numerous localities, were essential to analyses of paleobiogeography, little or nothing could be learned about the distributional patterns of decapods.

Description of the paleobiogeography of any group of animals presupposes that one has an adequate understanding of the geographic setting during the time intervals under consideration; that enough data exist to demonstrate time equivalence from one area to another; that the group of organisms in question is adequately identified and described so that proper biological relationships can be defined; and, finally, that an adequate sample exists on which biogeographic distribution can be defined. All of these factors must then be cast in the framework of modern biogeographic principles so that a coherent description of ancient distributions can be made. The biogeographic distribution of two groups of fossil and recent decapod crustaceans from the southern hemisphere, the anomuran family Aeglidae and the raninid genus *Lyreidus*, will be examined. Both demonstrate that even though we have relatively small samples, enough information is, in fact, available to draw meaningful conclusions about their biogeographic distribution.

2 CONTEXT OF PALEOBIOGEOGRAPHY

2.1 *Paleobiogeographic models*

Until relatively recently, models of paleobiogeographic distribution of organisms were cast in a rigid framework owing to the accepted attitude that continents maintained a fixed

position throughout most, or all, of geologic time. Thus, significant biological expeditions, such as that sponsored by Princeton University at about the turn of the century (Ortmann 1902b) and devoted to the study of the biology of Patagonia, provided a tremendous data base documenting affiliations of the fauna of southern South America with those of other southern hemisphere continents. They were, however, forced to rely on what today appears to be a rather fanciful interpretation of land bridges uniting distantly separated continental areas. An analysis of refinements in our understanding of changes in continental positions through time, based on plate tectonic theory, now allows extremely detailed paleogeographic maps to be drawn (Fig. 2) which give a clear picture of the relative geographic position of continental land masses throughout most of Phanerozoic time. Several sets of reconstructions of paleo-continental positions are frequently referred to with regard to the Cenozoic and Mesozoic eras (Firstbrook et al. 1979, Scotese 1979, Smith & Briden 1977). Although some details of continental placements differ, the general patterns are in agreement and provide excellent bases for interpretation of paleocurrents. The former two map bases are used herein, essentially interchangeably, depending upon the projection necessary to convey distributional data.

Paleocurrent reconstructions shown in Figure 2, as well as those constructed in all other contemporary works (Schopf 1980) are based on first cause deductions. Their limitations reflect lack of knowledge of paleobathymetry and are subject to the ever-present problem of generalization. On the other hand, global patterns, those necessary to define dispersal routes, would seem to fall well within the limits of usefulness.

Zinsmeister (1982) summarized data on the distribution of circum-Pacific molluscan faunas varying in age from Late Cretaceous to Tertiary and incorporated the seminal work on southern hemispheric biogeography by Flemming (e.g. 1962, 1963, 1967) to propose a pattern of distribution to explain the fossil occurrences. Employing the paleobiogeographic reconstructions and the style of paleocurrent analyses referred to above, Zinsmeister postulated the development of a highly endemic molluscan fauna in the southern circum-Pacific in what he termed the Wedellian Province. This fauna persisted intact until such time as break-up of the southern continents, northward migration of Australia and New Zealand, and development of circum-Antarctic current patterns subjected the organisms to a series of thermal crises that either induced dispersal into favorable habitats elsewhere, or led to extinction. Because Zinsmeister's data base was large and encompassed molluscan species from Australia, New Zealand, Antarctica, and South America, it forms an excellent framework against which decapod distributions can be compared. The timing and significance of the dispersal event has been more strongly defined by the demonstration that 11 genera in five classes of the Mollusca, Echinodermata, and Arthropoda underwent their early development in the Wedellian Province and dispersed northward from the Antarctic in the Neogene (Zinsmeister & Feldmann 1984). At least in the case of the arthropods, the northward dispersal was probably triggered by the final fragmentation of Gondwana near the onset of the Oligocene.

2.2 Geologic age dating and paleotemperature analysis

Until relatively recently, it has been difficult to date accurately geologic occurrences from widely separated areas of the globe and from different paleoecological settings. The development of relatively routine techniques for determining radiometric ages, the addition

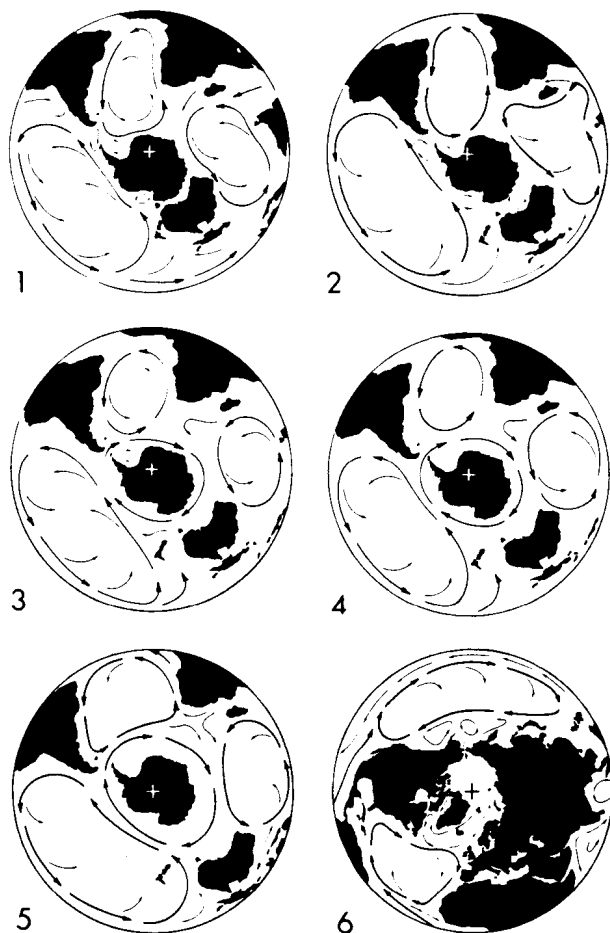


Figure 2. Polar views of paleogeographic maps (from Firstbrook et al. 1979) showing generalized major oceanic current circulation patterns. (1) and (2) 50 MABP and 40 MABP, respectively, showing the circulation of the southern oceans prior to development of the circum-Antarctic current. (3), (4) and (5) 30 MABP, 20 MABP and Recent maps, respectively, showing changes in relative positions of the southern continents subsequent to the development of the circum-Antarctic current system. (6) Recent north polar view showing current circulation pattern analogous to that of the southern polar region prior to northward movement of Australia and New Zealand.

of relatively precise techniques of magnetic stratigraphy and dating, based on the polarity reversal model, and a much improved biostratigraphic correlation, based on the voluminous information provided by the Deep Sea Drilling Project, makes it possible to correlate from one region to another with far greater precision than has previously been possible (see, for example, Hickey et al. 1983). A worthwhile summary of the application of magnetic polarity stratigraphy to the solution of a paleontological problem is given by Opdyke et al. (1979).

These refinements in techniques of correlation have permitted not only the demonstration of age equivalence of faunas in different regions but also have permitted the faunal evidence to be superimposed on data related to paleogeographic changes and other changes in the physical environment. For example, a wealth of information has been accumulating, as a result of the Deep Sea Drilling Project, upon which detailed paleotemperature analyses can be made. Kennett and others (Shackleton & Kennett 1975, Kennett 1978) have conducted a large number of studies using $^{16}\text{O}/^{18}\text{O}$ ratios on foraminiferans from circum-Antarctic deep sea ocean cores and have provided the detailed documentation of changes in sea surface temperature with time (Fig. 3) which can be used to correlate biotic, sedimentational, and paleogeographic events.