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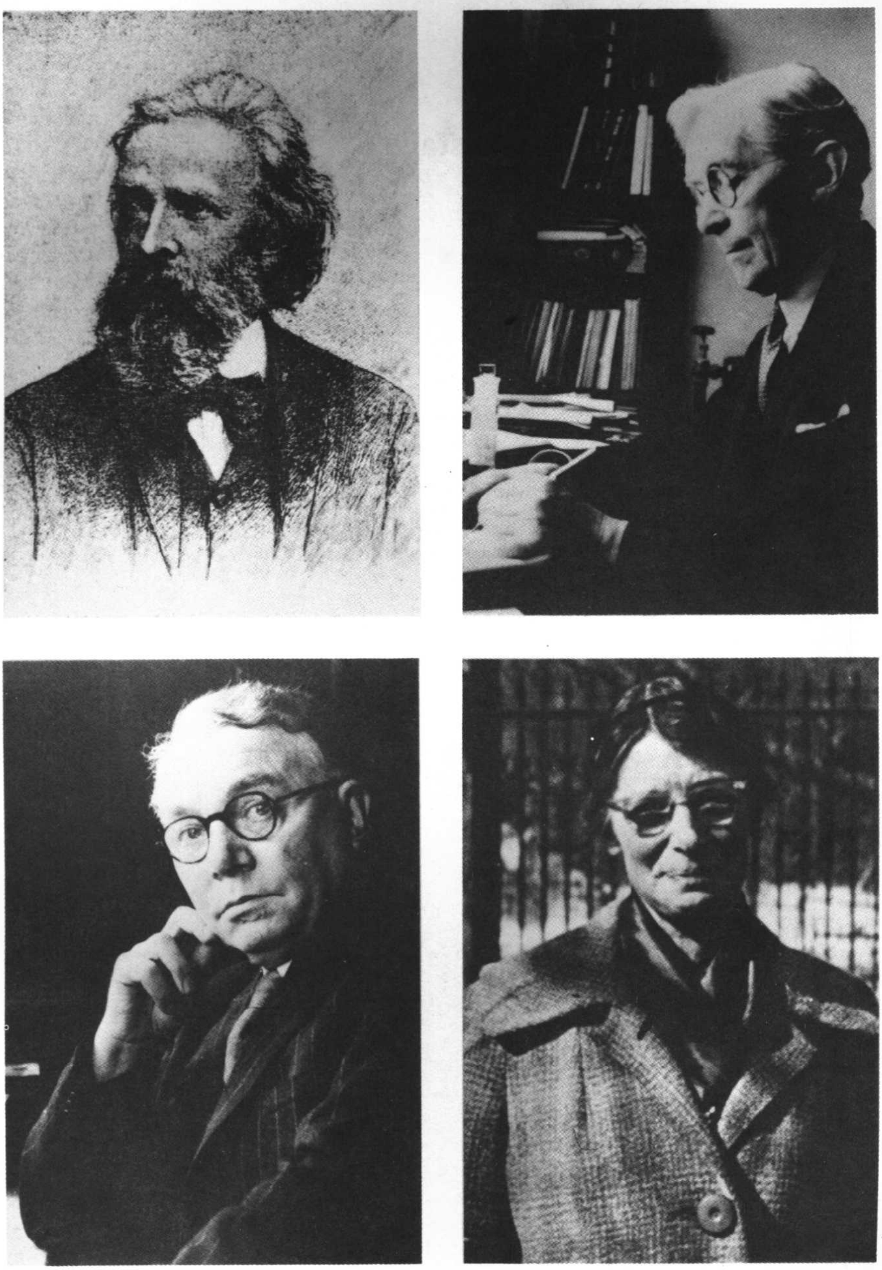

Frontispiece. Above left: Carl Claus (courtesy of J. Sieg, University of Osnabrück, Vechta). Above right: William Thomas Calman (photograph by M. D. Burkenroad). Below left: H. Graham Cannon (courtesy of J. Dalingwater and L. Lockey, University of Manchester). Below right: Sidnie M. Manton (photograph by R. Siewing).

PREFACE

This book was originally undertaken to assuage my own sense of frustration in using the currently available single-volume references on crustacean form and function to obtain an overview of the natural history and evolution of Crustacea. The classic volume in this regard has been W. T. Calman's 1909 treatise *Crustacea*. Despite all that has happened in the field since 1909, that book is still a standard reference, even though quite out of date. Calman provided a remarkably concise synthesis of what was known about crustacean biology up to that time, and so effective was he at doing this that he established the framework upon which the discipline has developed even to the present. Another excellent reference is Kukenthal and Krumbach's (1927) *Handbuch der Zoologie*. Aside from being out of date (and in German), this compendium provides rather complete treatment of the groups it covers. However, it is somewhat uneven given the variety of authors for the various chapters. The multi authored *Traité de Zoologie* suffers from this same uneven treatment and, in addition, is not nearly so comprehensive as Calman or the *Handbuch*. Finally, there is the English edition of Kaestner's (1970) *Textbook of Zoology* which, despite its being a single-author work, is quite uneven and incomplete regarding many aspects of anatomy and development, though, in spite of these shortcomings, it frequently serves as a textbook in carcinology courses.

In quite another category is McLaughlin's *Comparative Morphology of Recent Crustacea* (1980). This book is excellent to the task it was designed to do, that is, as a guide or manual on strictly anatomical matters. I have found it useful in offering access to the literature, since it has reference lists for each group it deals with. However, it covers only recent forms and does not deal with fossil groups. It provides a fine glossary of crustacean anatomical terms.

So, given this background, I originally set out to treat all known groups of crustaceans in as even a manner as I could manage, covering basic external and internal anatomy, modes of locomotion, feeding mechanisms, reproductive biology, habitat and biogeographic distributions, embryonic and larval development, fossil record, taxonomy, phylogeny, and evolution—much in the manner of Calman. My object has not been to cover all aspects of crustacean biology, especially those dealing with physiology, histology, and ultrastructure. Other compendia are currently available that do so much more effective a job than I could do. Rather I wished to present an overview of those aspects of crustacean studies that have been useful in elucidating the interrelationships of constituent groups and the evolution of Crustacea as a whole. Some disciplines within the biology of crustaceans serve rather poorly in this regard. For example, several of my chapter reviewers suggested that I cover more subjects like neurophysiology and field biology. Praiseworthy as these suggestions were, the fact remains that little can be gleaned about crustacean evolution from such subjects, not because they cannot potentially make such contributions, but rather because information in such fields to date has not been accumulated and organized in a manner designed to elucidate crustacean relationships. To have produced a book with this kind of information in it would have strained my capacities and simply was not the kind of book I wanted to write.

However, as preparation of this book progressed, I was struck by how much is still to be learned about basic structure and function, natural history, and evolutionary biology of crustaceans! For example, though ostracodes are the most numerous of crustaceans and quite diverse, living in many different habitats and obviously 'munching' on many different things, we know relatively little about their feeding. Certainly our knowledge is not on a par with what we do know about feeding strategies in cladocerans or thoracican barnacles. Or, despite their ready availability the world over and ease of handling in the laboratory, we lack knowledge about the basic biology of some branchiopod groups, like the notostracans and conchostracans, though we have been making significant strides in understanding other branchiopod groups, like the anostracans and cladocerans. Or, in very diverse and successful groups like isopods, amphipods, and decapods, though we eagerly describe numerous new taxa each year, we still don't know enough about the function of structures in these groups to begin to understand their adaptive radiations—for example, there is no agreement on the higher taxonomy of such large groups.

Nor have students of crustaceans been particularly consistent in their view of the science. Carcinologists seem to continue to be so impressed by differences among some taxa, that they have totally disregarded the significance of their similarities, for example, isopods and amphipods, or leptostracans and 'cephalocarids' and branchiopods. Conversely, in other taxa they frequently focus on similarities in order to minimize differences, for example, the natantian decapods, which include such diverse groups as dendrobranchs, euzygids, and eukyphids, or in malacostracans *sensu lato*, which encompass the phyllopodous leptostracans and the stenopodous hoplocaridans and eumalacostracans.

Such shortcomings and inconsistencies are not to be taken as condemnations of carcinology as a whole; rather, they are merely noted in passing as manifestations of what has been a characteristic phenomenon in the history of many disciplines. Carcinologists have got to become more critical in evaluating their work. They must cut to the heart of what has been published in carcinology to date and not accept things merely because they are 'in the literature.' More than in many other animal groups, carcinology has been dominated by certain key ideas, generated by prominent figures of the past, revered for their capacities for synthesis. This has had bad and good effects on the development of the science: bad in that a too rigid adherence to the pronouncements from the past has often stifled the development of fresh approaches to problem areas; good in that well-done synthetic overviews by single individuals can be quite effective toward channeling work along productive lines of enquiry. So for better or worse, carcinology has been strongly influenced by its traditions.

Four people really came to stand out in this regard as I prepared this volume. Carl Claus (1835-1899), the first of these, was one of the most prolific of the nineteenth century carcinologists. His interests extended from copepods to malacostracans; from species descriptions, through studies of development, to pioneering analyses of basic form and function. It was Claus who established the separate status of tanaidaceans from isopods, who allied leptostracans with the malacostracans, and who was among the first to advance a scheme of the phylogenetic relationships among the higher categories of crustaceans.

William T. Calman (1871-1952), perhaps the most preeminent worker in this century, is of course best known for his classic volumes *Crustacea* (1909) and *Life of the Crustacea* (1911). The former was especially crucial for giving basic overviews of all groups and providing us with the higher taxonomy of the crustaceans used up to this time. However, Calman was also a fine taxonomist at lower taxonomic levels; for example, of this, his careful work on both fossil and recent syncarids has never been found wanting in accuracy. His syncarid papers also illustrate another strength of Calman's work, effective combination of both fossil and recent lines of evidence in order to arrive at a complete overview whenever possible.

H. Graham Cannon (1897-1963) was noteworthy for two reasons. He was responsible for a whole series of papers on a wide range of groups from branchiopods through malacostracans that examined limb functional morphology and ontogenetic development. These have recently been found wanting in some respects, especially in regard to some biases induced by his experimental approaches. However, this has only come with the hindsight born of newer techniques; Cannon's works must be judged in the context of their time, of which they were exemplary efforts. In addition, because of his position as professor at the universities of Sheffield and Manchester, Cannon also produced a whole coterie of his own students and influenced others at sister institutions. Around Cannon was centered a British school that worked on problems of arthropod functional morphology and development.

Chief among Cannon's protégés was Sidnie M. Manton (1902-1979). Her range of interests extended beyond the crustaceans to also encompass onychophorans, myriapods, and cheliceriforms. Her controversial conclusions about arthropod polyphyly, based on her exacting studies of locomotory functional morphology and limb development, have in turn influenced a new generation of carcinologists to more critically examine old assumptions about the meaning of structure and function and to reevaluate long-entrenched ideas about crustacean relationships. Manton, along with Cannon, developed the biramous theory of limb evolution that stood in contrast to Borradaile's mixopodial theory—warring concepts that still battle today within the pages of this book.

These people were not always correct in their conclusions, nor were their methods entirely without flaw. Nor were they the only people to make major contributions to crustacean studies. To try and name all of the major contributors would risk leaving some out. However, these four were the people who in large part did provide the major paradigms within which carcinology has developed and who did produce and/or inspire a significant percentage of the corpus of knowledge upon which our current understanding of crustacean evolution is based. However, we should not accept this corpus of knowledge uncritically. Not to question our predecessors and our peers is not to do real science.

Much work remains to be done, as this book should serve to point out. We still lack knowledge on the internal anatomy of groups like spelaeogriphaceans, mictaceans, some aspects of the brachypodans (cephalocarids), amphionidaceans, conchostracans, and tantulocarids. Knowledge of feeding mechanisms is at best incomplete in all groups; and for some we know currently virtually nothing about how they feed, for example, conchostracans and notostracans. Complete data on ontogeny and larval development are extant for only a very few groups. Data on breeding and reproductive biology are scattered in the literature and have never been subjected to coherent analysis and interpretation. And biogeographic analysis in some taxa still awaits the stabilization of taxonomy in those groups.

It was also my hope that this book might serve to standardize the terminology and orthography used in the discipline. For example, thoracopods not modified as maxillipedes are variously referred to in the literature as pereopods, peraeopods, or pereiopods (the last is used herein), or first antennae and first maxillae are also known as antennules and maxillules (preferred here). I also tend to name limbs in the thoracic series by their ordinal numbers as well as by any specialized names they may hold; for example, there is never any doubt about where a first thoracopod is, but one may not readily recognize where something like a pyllopod is located (the first thoracopod of gnathiidean isopods). In addition, my choice of the anglicized versions of formal taxa will probably not please everyone, for example, ostracodes for Ostracoda, or cirripedes for Cirripedia, or peneids for Penaeidae. My researches on matters of orthography have led me to the choices I made, but I realize that whatever choices I could have made would have left some people unhappy.

So while I hope this book will serve as a reference text in crustacean evolutionary biology, I trust it will also serve as a guidebook and to point the way toward productive lines of research. I would feel my efforts well justified if in a few years this book were quite out of date. For that would indicate my vision was not misdirected.

Several years ago it was remarked to me that the day of single-author compendia was over, that no one person could hope to encompass and comprehend all the available knowledge on a subject. In a sense this is true, and certainly among recently published books, edited multi-author volumes are the norm [see, for example, *The Biology of Crustacea* (Academic Press) or *Crustacean Issues* (Balkema)]. Maybe the days of a Libbie Hyman are gone, but there is still much to be gained from one person trying to develop an overview of a subject. Coherence, unity, or pattern can more easily emerge with the overview of a single person in a way not possible with the view of a 'committee.' This was the strength of synthesizers like Claus, Calman, Cannon, and Manton. Their visions helped shape a science. If their work subsequently constrained thought, that was the fault of their exegetes, not of the visionaries.

Of course, mistakes will be made and inaccuracies will creep in. This book is no exception. I am sure these will be brought quickly to my attention. In the end these imperfections in the book are mine alone, but I have tried to mitigate them by seeking reviews of almost all chapters by relevant authorities. Without exception, people have responded generously in this regard. I am immensely indebted to everyone who have given of their valuable time and had input into developing this book. These include Drs. D. T. Anderson, D. Belk, E. L. Bousfield, G. A. Boxshall, D. E. G. Briggs, R. C. Brusca, M. D. Burkenroad, D. L. Felder, B. E. Felgenhauer, A. Fleminger, G. Fryer, L. F. Gardiner, M. J. Grygier, R. R. Hessler, R. F. Maddocks, R. B. Manning, J. Mauchline, P. A. McLaughlin, W. A. Newman, M. L. Reaka, W. D. I. Rolfe, H. K. Schminke, J. Sieg, I. G. Sohn, J. Stock, R. Swain, L. Watling, D. I. Williamson, and G. D. Wilson. The artwork was done by Bryan Burnett, Robert Chandler, and in particular Michael Emerson. The typing of the basic manuscript and various revisions could not have occurred without the yeoman service of Deanne Demere and Marjorie Rea. And nothing at all would have been forthcoming without the insistent encouragement of my wife Joan.

However, I especially want to 'thank' the Crustacea, for being such a compelling, fascinating group that some days I can hardly wait to get to work in the morning to find out more about them. Geoffrey Smith expressed it well of syncarids in *A Naturalist in Tasmania* (Clarendon Press, 1909):

> Goethe somewhere remarks that the most insignificant natural object is, as it were, a window through which we look into infinity. And certainly when I first saw the Mountain Shrimp walking quietly about in its crystal-clear habitations, as if nothing of any great consequence had happened since its ancestors walked in a sea peopled with strange reptiles, by a shore on which none but cold-blooded creatures plashed among the rank forests

of fern-like trees, before ever bird flew or youngling was suckled with milk, time for me was annihilated and the imposing kingdom of man shrunk indeed to a little measure.

San Diego
May 1985

F.R.S.

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WHAT ARE CRUSTACEANS?

Crustacea is an arthropodous phylum of animals whose members can be characterized by possessing a five-segment cephalon with two sets of antennae, a pair of mandibles, and two sets of maxillae; which display a tendency to fuse the segments of the head to form a cephalic shield and to develop from the posterior aspect of the cephalon a posteriorly directed shield over the body (a carapace); which exhibit a tendency to regionalize the body segments into distinct tagmata and to specialize the associated appendages; and which utilize anamorphic development that typically commences with a unique larva or ontogenetic stage termed a nauplius.

Crustaceans have a definite preference for marine conditions. However, there is hardly a habitat type on the planet that does not have crustaceans in it, albeit fresh water and terrestrial crustaceans usually have rather strict requirements associated with their ability to be present. Unlike other arthropodous groups, which exploit essentially one basic body plan in a sense, when you've seen one insect or arachnid, you have seen them all, the crustaceans exhibit a greater degree of diversity in form than that seen in any other animal phylum. There may be more species of insects than any other group in the world and more individual nematodes, but the inherent capacity of crustaceans to tagmatize and specialize body segments and appendages insures that there are more basic kinds within the crustaceans than any other group in the world. For this reason, aside from the features of the head, it is impossible to characterize crustaceans except by noting *tendencies* toward certain conditions or states. There are certain common anatomical themes noted among crustaceans, and as an orientation to the phylum these will be reviewed here.

APPENDAGES Some groups, such as remipedes and many maxillopodans (especially larvae), have a curious set of frontal filaments in the vicinity of the antennules. Frontal filaments are not thought to be true limbs but are rather considered to be singularly developed sensory organs.

The first set of true appendages is the antennules (frequently referred to as first antennae). Until the discovery of the remipede *Speleonectes*, it was generally assumed that only the Malacostraca had multiramous antennules. Thus it would have appeared that, except for malacostracans, crustaceans conformed to the general arthropodan state wherein the primary preoral antenniform appendages are uniramous. However, there may be some basis to postulate that in fact biramous antennules are a diagnostic feature of adult crustaceans. Those forms with biramous antennules are those that have the most primitive body type with either complete lack of trunk tagmosis or at least possession of limbs on all trunk segments. Thus, it would appear that the biramous condition is secondarily lost in various groups (yielding to triramy in hoplocaridans or uniramy in maxillopodans, phyllopodans, and some eumalacostracans). The antennules typically appear as uniramous anlagen in the course of development; so the convergent appearance of uniramous antennules in many groups of crustaceans could be another manifestation of paedomorphosis in the phylum (see Chapter 44). By the same token, however, one could just as easily conceive of multiramous antennules as being convergently developed in different groups of adult crustaceans. Either one of these alternatives possesses interesting issues for phylogeny within the Crustacea (see Chapter 43). Antennular innervation is deutocerebral.

The antennae (also known as second antennae) are primarily postoral in origin. This is made evident in the course of development, where the typical adult preoral condition is arrived at late in ontogeny. The antennae frequently serve a locomotory and sometimes a food-gathering function in the larval stages but rarely function in this regard in adults where they are primarily sensory. The development of these appendages as sensory antennae in crustacean adults would thus seem to be a distinctive feature for the phylum. The antennal innervation is tritocerebral.

The food processing appendages of the crustacean head are the mandibles, maxillules (= first maxillae), and maxillae (= second maxillae). In all of these, the distal elements of the limb are typically reduced to 'palps' while the proximal protopodal elements develop specialized endites to handle the food. In addition, the mouth is usually marked anteriorly by a labrum, or upper lip, and often by posterior elements called paragnaths, or lower lips.

The first trunk appendages are sometimes modified as maxillipedes to assist in food processing as in nectiopodan remipedes, mystacocarids, some copepods, cirripedes, hoplocaridans, and most eumalacostracans. One or several such pairs of maxillipedes may be developed. However, such limb specializations may or may not be accompanied by fusion of the relevant segments to the head. For example, the nectiopodan first trunk segment is fused to the cephalon, but the maxillipede-bearing segment in mystacocarids is free; those eumalacostracans with maxillipedes generally fuse the relevant segments that bear them to the cephalon, but in mysidans the maxillipede bearing segment is actually free. Though classic theory states the primitive cephalon of crustaceans ends with the maxillary segment, one should be aware that in many instances one or more of the trunk segments can fuse to the head and that this fusion occurs sometimes in some otherwise apparently very primitive groups.

The basic crustacean trunk limb (Fig. 1-1) consists of a protopod, to which can be attached one or more branches. Distally these branches are

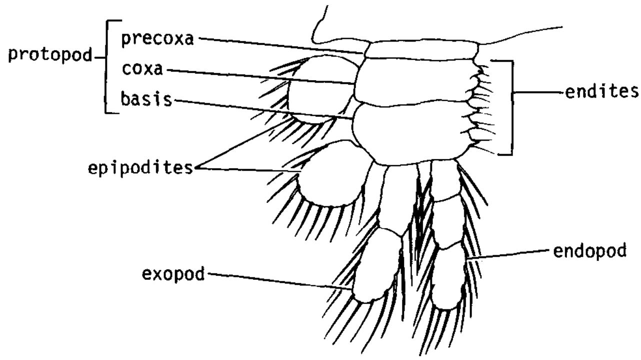

Fig.1-1. Diagrammatic hypothetical crustacean limb illustrating all possible component parts.

termed the exopod (outer branch) and the endopod (inner branch); proximally the protopod may bear lateral exites or epipodites and medial endites. The protopod generally is composed of two segments or joints, the coxa (proximal) and basis (distal). However, Hanson (1925) was among the first to maintain that the protopod is primitively three-segmented, with a proximalmost precoxa. Some groups do in fact clearly possess a precoxa, for example, hoplocaridans. In other taxa the issue is not at all clear, for example, bathynellaceans or branchiurans. The problem is: when is a 'precoxa' an extension of the body wall or true limb joint? Some crustacean groups have no apparent separate protopodal joints whatsoever, such as branchiopods and remipedes. Though much has been made of this issue of protopodal joints in terms of crustacean phylogeny (most of it confusingly so), a greater significance of single segment or multisegment protopods probably lies in relating the morphology of crustacean limb parts to particular functional requirements.

SHIELDS The tendency to develop head and body shields is one of the characteristic phenomena noted in the course of crustacean evolution. The segments of the cephalon are typically fused dorsally into a single shield; only anostracans lack this fusion. This distinctive phenomenon caused Secretan (1980), in an interesting analysis, to treat the formation of the head shield as an integral stage in an evolutionary path which ultimately leads to a complete carapace. Thus she viewed only anostracans as truly lacking a carapace and considered that all other crustaceans possessed a carapace to some greater or lesser degree. This somewhat unusual approach may have some merit; however, its utility is closely tied to an understanding of what the carapace might be.

The body shield, or carapace, can take a variety of forms (see e.g., Secretan, 1964). It need not always arise from the maxillary segment. Boxshall (1983) stated misophrioid copepods have a carapace extension from the