Phylogeny and Evolution of Crustacea

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A Conference on Phylogeny and Evolution of Crustacea was held at the Museum of Comparative Zoology in March, 1962, at the invitation of the Director, Dr. Ernst Mayr. It arose out of a suggestion made by Dr. Martin F. Glaessner, who was visiting the United States as a guest of the American Geological Institute, and was made possible by grant G-22123 from the National Science Foundation. Attendance at the conference was limited to the zoologists and paleontologists listed below, in the hope that free and adequate discussion would take place around the table. Two preliminary reports (*Geotimes*, American Geological Institute, 1962, *Crustaceana*, 1962) have been published. This volume contains the majority of the papers presented, together with references to those presented but published elsewhere. Discussion of these papers occupied more than half the available time, and was recorded. Each participant was furnished with a complete transcription, and invited to condense and emend his contributions where necessary. The discussions given here are compiled from these responses or are our condensations of contributors’ remarks. As printed they total less than half their original length, but we believe we have retained the major points and play of ideas. Where important new material was added subsequently by the speaker, it is indicated. Throughout the volume the sign † precedes the name of a fossil taxon.

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H. B. Whittington
W. D. I. Rolfe
PARTICIPANTS


E. L. Bousfield, National Museum of Canada, Natural History Branch, Ottawa, Ontario, Canada.


H. K. Brooks, Department of Geology, University of Florida, Gainesville, Florida.

Erik Dahl, Department of Anatomy, Zoological Institute, University of Lund, Lund, Sweden.

M. F. Glaessner, Department of Geology, The University of Adelaide, Adelaide, South Australia.

R. U. Gooding, Department of Biology, Boston University, Boston 15, Massachusetts.

Isabella Gordon, British Museum (Natural History), Cromwell Road, London S.W.7, England.

Dora P. Henry, Department of Oceanography, University of Washington, Seattle 5, Washington.


A. G. Humes, Department of Biology, Boston University, Boston 15, Massachusetts.

Otto Kinne, Biologische Anstalt Helgoland, Zentrale Hamburg-Altona, W. Germany.

J. H. Lochhead, Department of Zoology, The University of Vermont, Burlington, Vermont.

Sidnie M. Manton, British Museum (Natural History), Cromwell Road, London S.W.7, England.

Ernst Mayr, Museum of Comparative Zoology, Harvard University, Cambridge 38, Massachusetts.

R. C. Moore, Department of Geology, University of Kansas, Lawrence, Kansas.

W. A. Newman, Department of Zoology, University of California, Berkeley 4, California.


W. D. I. Rolfe, Museum of Comparative Zoology, Harvard University (now at Hunterian Museum, University of Glasgow, Glasgow, Scotland).


Rolf Siewing, Zoologisches Institut und Museum der Universität, Kiel, Germany.

Paul Tasch, Department of Geology, University of Wichita, Wichita 14, Kansas.

T. H. Waterman, Department of Zoology, Yale University, New Haven, Connecticut.

J. H. Welsh, Biological Laboratories, Harvard University, Cambridge 38, Massachusetts.

PARTICIPANTS AND OBSERVERS

OBSERVERS

ISABEL CANET, Museum of Comparative Zoology, Harvard University, Cambridge 38, Massachusetts.

MARY R. DAWSON, representing the National Science Foundation, Washington 25, D.C.

ELISABETH DEICHMANN, Museum of Comparative Zoology, Harvard University, Cambridge 38, Massachusetts.

JOHN S. GARTH, University of Southern California, University Park, Los Angeles 7, California.

RAYMOND B. MANNING, The Marine Laboratory, University of Miami, Miami 49, Florida.

E. L. MILLS, Department of Zoology, Yale University, New Haven, Connecticut.

A. R. ORMISTON, Museum of Comparative Zoology, Harvard University, Cambridge 38, Massachusetts.

HARDING B. OWRE, The Marine Laboratory, University of Miami, Miami 49, Florida.


A. J. PROVENZANO, JR., The Marine Laboratory, University of Miami, Miami 49, Florida.

F. C. SHAW, Museum of Comparative Zoology, Harvard University, Cambridge 38, Massachusetts.
INTRODUCTION

It gives me great pleasure to welcome you on behalf of the Museum of Comparative Zoology, an institution which has a proud tradition in the field of invertebrate zoology. It is our endeavor to continue this tradition, indeed to display even greater activity in this field than was possible in recent years.

The subject matter of this conference—the classification, phylogeny, and evolution of the crustaceans—has made steady advances. This is due, on one hand, to an accumulation of new facts, owing either to a more refined morphological analysis, or to the discovery of new fossils, or even to the discovery of extraordinary new living types such as *Hutchinsoniella*. It must not be overlooked, on the other hand, that some of the advances are due to the emergence of new concepts. All these factors together have caused a revival of research in phylogeny so that phylogenetic studies are once more beginning to be in the center of interest of the evolutionist. In part this has been due to a shift in emphasis. The interest of the earlier evolutionists was almost exclusively in the determination of homologies and the reconstruction of common ancestors. The emphasis throughout was on those characters which various kinds of organisms had in common. The new emphasis that has been added in recent decades is based on the questions: Why do descendants from common ancestors become different? What are the causal factors that are responsible for evolutionary divergence, and what selection pressures and adaptive shifts are involved? Such an approach quite clearly depends on a sound classification if it is not to degenerate into sterile speculation.

Particularly valuable in the development of phylogenetic thinking has been the elimination of a number of formerly dominant misconceptions. I shall single out a few of these unfounded generalizations:

(1) That evolutionary trends always proceed from simple to complex, and that the simple structures or types are always ancestral and the complex ones derived. A consequence of this assumption is the postulate that a morphological series is by necessity a phylogenetic series. You are all familiar with numerous cases in which these assumptions are not true.

(2) That an evolutionary trend in one line must be paralleled by a similar trend in all related lines. Actually, it happens not infrequently that of two related phyletic lines one increases in size or segmentation, while the other one shows a corresponding decrease.

(3) That embryos or larvae pass through a series of stages which reflect or recapitulate phylogeny. Here again we now know that the selection pressure is sometimes stronger on the larval stages than on the phenotypes of the adults. The larvae in such cases are not only more different from each other than are the adults, but also may have more newly acquired structures. To interpret these as ancestral would be misleading.
(4) That new types develop either by saltation or by a harmonious unfolding of an archetype. Actually, we know that the evolutionary rate of different organs and functional complexes can be exceedingly different, and that one key structure is usually far in advance of all others during the morphological reorganization accompanying any major adaptive shift. Mosaic evolution is far more frequent than archetypal evolution.

(5) That there are two sets of characters, phylogenetic characters and adaptive characters, and that by eliminating the unreliable adaptive characters, one is left with a residue of useful phylogenetic characters. It is true that some characters are more plastic than others, but no criteria are known by which such an *a priori* sorting of two such sets of characters would be possible.

The elimination of these misconceptions makes it possible to arrive at sounder generalizations. I shall waste no more of your time with such introductory remarks, but turn the meeting back to your chairman. In concluding, I want to express my warmest wishes for a successful conference.

Ernst Mayr, Director
Museum of Comparative Zoology
CONTENTS

Preface ........................................ iii
Participants and observers ........................................ iv
Introduction—Ernst Mayr ........................................ vii

I. Main evolutionary lines among Recent Crustacea (Figs. 1, 2)—Erik Dahl ............. 1
II. Discussion following Dahl's paper ................................ 17
III. Adaptation, a primary mechanism of evolution (Figs. 3-9)—Otto Kinne ............. 27
IV. On the relationship of Dromiacea, Tymolinae and Raninidae to the Brachyura (Figs. 10-14)—Isabella Gordon ..................................................... 51
V. The pericardial sacs of terrestrial Brachyura (Figs. 15-25)—Dorothy E. Bliss ........ 59
VI. Discussion following papers by Kinne, Gordon, and Bliss ................................. 79
VII. Studies in malacostracan morphology: results and problems (Figs. 26-42)—Rolf Siewing ............................................................. 85
VIII. Discussion following Siewing's paper (Figs. 43, 44) ................................... 105
IX. Jaw mechanisms of Arthropoda with particular reference to the evolution of Crustacea (Figs. 45-61)—S. M. Manton ........................................ 111
X. Discussion following Manton's paper (Fig. 62) .......................................... 141
XI. Evolution of the Branchiopoda (Figs. 63-67)—Paul Tasch ................................ 145
XII. Discussion following papers by Tasch, Brooks, and Rolfe (Fig. 68) .................. 159
XIII. Significance of the Cephalocarida (Figs. 69-78)—Howard L. Sanders ............. 163
XIV. Discussion following Sanders' paper (Fig. 79) ......................................... 177
XV. Discussion of the Peracarida problem (Fig. 80) ......................................... 181
Index ........................................................................ 185

ILLUSTRATIONS

Figure Page
1. Main evolutionary lines in Crustacea ........................................ 14
2. Relations between cohorts of Recent Crustacea ............................. 14
3. Immediate response of oxygen consumption in Artemia .............. 29
4. Under- and overshoot responses of oxygen consumption in Artemia ........ 30
5. Heart activity in Gammarus ................................................... 31
6. Duration of stabilization phase in Homarus .................................. 32
7. Effect of nongenetic thermal adaptation on lethal temperature levels in Homarus .......... 33
10. Thoracic sternites of Tymolus and Cymonomus .............................. 52
11. Intromittent organs of Tymolus and Cymonomus ......................... 53
12. Thoracic sternites of Ranina .................................................. 54
ILLUSTRATIONS

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>13.</td>
<td>Thoracic sternites of Notopoides</td>
<td>55</td>
</tr>
<tr>
<td>14.</td>
<td>Thoracic sternites of Maja</td>
<td>56</td>
</tr>
<tr>
<td>15-19.</td>
<td>Pericardial sacs of land crabs</td>
<td>61</td>
</tr>
<tr>
<td>20, 21.</td>
<td>Ventral aspects of Gecarcinus and Ocypode</td>
<td>63</td>
</tr>
<tr>
<td>22.</td>
<td>Pericardial sac of Gecarcinus</td>
<td>68</td>
</tr>
<tr>
<td>23, 24.</td>
<td>Dorsal views of Gecarcinus</td>
<td>70</td>
</tr>
<tr>
<td>25.</td>
<td>Vertical profile near Bimini</td>
<td>73</td>
</tr>
<tr>
<td>26.</td>
<td>Malacostracan groups</td>
<td>86</td>
</tr>
<tr>
<td>27.</td>
<td>Malacostracan groups and phylogeny</td>
<td>87</td>
</tr>
<tr>
<td>28.</td>
<td>Hypothetical ancestor of Malacostraca</td>
<td>88</td>
</tr>
<tr>
<td>29.</td>
<td>Organization of a Leptostracan</td>
<td>89</td>
</tr>
<tr>
<td>30.</td>
<td>Cross-section of heart of Nebalia</td>
<td>90</td>
</tr>
<tr>
<td>31.</td>
<td>Reconstruction of †Nahecaris</td>
<td>91</td>
</tr>
<tr>
<td>32.</td>
<td>Procephalon of a stomatopod</td>
<td>91</td>
</tr>
<tr>
<td>33.</td>
<td>Blood system of Stomatopoda</td>
<td>92</td>
</tr>
<tr>
<td>34.</td>
<td>Petasma of Squilla</td>
<td>94</td>
</tr>
<tr>
<td>35.</td>
<td>Organization of a stomatopod</td>
<td>94</td>
</tr>
<tr>
<td>36.</td>
<td>Organization of Anaspides</td>
<td>95</td>
</tr>
<tr>
<td>37.</td>
<td>Organization of an isopod and an amphipod</td>
<td>97</td>
</tr>
<tr>
<td>38.</td>
<td>Embryos of amphipod and isopod</td>
<td>98</td>
</tr>
<tr>
<td>39.</td>
<td>Relationships within Peracarida</td>
<td>99</td>
</tr>
<tr>
<td>40.</td>
<td>Comparison of blood systems in Lophogastridea and Decapoda</td>
<td>100</td>
</tr>
<tr>
<td>41.</td>
<td>Organization of a pancaridan</td>
<td>101</td>
</tr>
<tr>
<td>42.</td>
<td>Phylogeny of Malacostraca and relations to other Crustacea</td>
<td>102</td>
</tr>
<tr>
<td>43.</td>
<td>Reconstruction of †Nahecaris</td>
<td>103</td>
</tr>
<tr>
<td>44.</td>
<td>Relations of crustacean groups</td>
<td>107</td>
</tr>
<tr>
<td>45.</td>
<td>Head of Chirocephalus</td>
<td>114</td>
</tr>
<tr>
<td>46.</td>
<td>Diagrams of anostracan mandible, section of Chirocephalus</td>
<td>115</td>
</tr>
<tr>
<td>47.</td>
<td>Transverse sections of Chirocephalus</td>
<td>116</td>
</tr>
<tr>
<td>48.</td>
<td>Transverse sections of Chirocephalus, Hemimysis, and Petrobius</td>
<td>118</td>
</tr>
<tr>
<td>49.</td>
<td>Transverse and sagittal views of arthropods</td>
<td>119</td>
</tr>
<tr>
<td>50.</td>
<td>Mandibles of Anaspides</td>
<td>120</td>
</tr>
<tr>
<td>51.</td>
<td>Lateral view of Anaspides</td>
<td>121</td>
</tr>
<tr>
<td>52.</td>
<td>Sagittal view of Anaspides</td>
<td>123</td>
</tr>
<tr>
<td>53.</td>
<td>Transverse sections of Paranaspiden</td>
<td>124</td>
</tr>
<tr>
<td>54.</td>
<td>Lateral view of Ligia</td>
<td>125</td>
</tr>
<tr>
<td>55.</td>
<td>Sagittal view of Ligia</td>
<td>126</td>
</tr>
<tr>
<td>56.</td>
<td>Posterior view of Ligia, and mandibular cuticle</td>
<td>128</td>
</tr>
<tr>
<td>57.</td>
<td>Mandibles of crayfish and crab</td>
<td>129</td>
</tr>
<tr>
<td>58.</td>
<td>Transverse section of Tachypleus and gnathobase</td>
<td>130</td>
</tr>
<tr>
<td>59.</td>
<td>Sagittal section of Tachypleus and gnathobase</td>
<td>133</td>
</tr>
<tr>
<td>60.</td>
<td>Coxae of Tachypleus</td>
<td>134</td>
</tr>
<tr>
<td>61.</td>
<td>Relations of arthropod jaws</td>
<td>137</td>
</tr>
</tbody>
</table>
ILLUSTRATIONS

Figure Page
62. Limb musculature of Hutchinsoniella ........................................ 142
63. First appearance of branchiopod orders .................................. 146
64. Ribbedness of valve in conchostracans ................................... 148
65. Phylogeny of spined conchostracans ..................................... 149
66. Origin of lea lid rib .................................................................. 150
67. Relationships between branchiopod orders ............................ 155
68. Phylogeny and classification of Eumalacostraca ....................... 161
69. Ventral view of Hutchinsoniella .............................................. 163
70. Mode of naupliar development .............................................. 165
71. Branchiopod nauplii ................................................................. 166
72. Nonbranchiopod nauplii ......................................................... 167
73. Stage 4 nauplius of Hutchinsoniella ......................................... 168
74. Development of limbs of Penaeus ............................................ 169
75. Relationships of trunk limbs ................................................ 170
76. Trunk limbs of Hutchinsoniella ............................................... 172
77. Relationships of crustacean first maxilla ................................. 173
78. Phylogeny of Branchiopoda and Malacostraca ....................... 174
79. Relationships within Crustacea ................................................ 178
80. Relations of Peracarida ............................................................ 182

Table
1. Compound eyes in Crustacea ................................................... 10
2. Surface area of pericardial sacs .............................................. 64
3. Means and standard errors, surface areas ................................ 65
4. Values for t and P, surface areas ........................................... 66
5. Classification of branchiopods ................................................... 145
I. INTRODUCTION
During the last fifty years the tendency, on the whole, has been to split the Crustacea into a growing number of taxonomic units of high and equal rank. In 1909 Calman recognized five groups at the subclass level, namely, Branchiopoda, Ostracoda, Copepoda, Cirripedia, and Malacostraca. More recently two further groups have been discovered, which were given the same rank, namely, the Mystacocarida in 1943 and the Cephalocarida in 1955. At the same time, however, doubts have arisen concerning some of the groups recognized by Calman. Thus, the Branchiopoda, as a result of investigations in the first place by Linder (1941, 1945) and Preuss (1951), have often been regarded as representing two separate subclasses, the Anostraca and the Phyllopoda. Similarly the Branchiura are now generally placed near the Copepoda as a separate subclass. It has also been suggested that the Ascothoracica should be taken out of the Cirripedia. This, however, has found no general acceptance and there seem to exist strong arguments against it.

Even without accepting the separation of the Ascothoracica from the Cirripedia we had, nevertheless, in 1955, nine crustacean subclasses, namely: Anostraca, Phyllopoda, Cephalocarida, Ostracoda, Mystacocarida, Copepoda, Branchiura, Cirripedia, and Malacostraca. It is quite obvious that some of these units have a greater mutual affinity than others and some years ago the present writer (Dahl, 1956b) tried to express the recognition of this fact in the form of a tentative new system. This system comprised four units at the highest level (then regarded as subclasses), two of which were new:

- **Subclass Gnathostraca** (comprising the groups Anostraca, Phyllopoda, and Cephalocarida)
- **Subclass Maxillopoda** (comprising the groups Mystacocarida, Copepoda, Branchiura, and Cirripedia)
- **Subclass Ostracoda**
- **Subclass Malacostraca**

As far as I am aware no serious criticism has been advanced against the general principles underlying this system, but some recent writers suggested changes and improvements. Thus, Sanders (1957) and
Birshtein (1960) both removed the Cephalocarida from the Gnathostomata and restored it to subclass rank. Siewing (1960), on the other hand, retained the Cephalocarida within the Gnathostomata and advanced arguments in favour of including the Ostracoda in the Maxillopoda. Beklemishev (1952) had already taken a step in the same direction by suggesting that the Copepoda, Cirripedia, Branchiura and Ascothoracica might be grouped together in a superorder Copepodoidea.

This brief summary of some recent work brings us up to the present moment. It seems desirable to review, however briefly, the main evidence upon which we can try to build a natural system of the Crustacea, a system recognizing the main evolutionary lines. Considering the enormous crustacean literature it is obvious that only a choice of particularly relevant arguments can be made, and it is equally obvious that this choice will have to be rather subjective. Exoskeletal features have always played the main part in the discussion of crustacean affinities and it is quite clear that they will have to do so also in the future. As some of the evidence is conflicting, however, it seems desirable to draw internal structures also into the discussion, and consequently some internal organs and organ systems will be dealt with at some length, especially those where new evidence has become recently available.

II. EXTERNAL MORPHOLOGY

Carapace

We have been accustomed to regard the carapace as one of the fundamentally crustacean features. The formation of a carapace is often even regarded as one of the initial steps in the evolution of the crustacean organisation (cf., e.g. Siewing, 1960).

It is true that a carapace occurs in widely different groups of Crustacea; on the other hand, a true carapace is missing or is very poorly developed in various groups which for other reasons are generally regarded as more or less primitive, e.g. the Anostraca, the Mystacocarida, the Cephalocarida. Although it is difficult to reach a definite conclusion, it would seem justified to be less categorical on this point and to admit the possibility that although a tendency to develop a carapace is apparently present in the Crustacea, the actual differentiation of this structure may have taken place more or less independently in various crustacean lines. Such a parallel evolution of a carapace in various groups would be quite compatible with the great diversity in its actual shape and structure in different Crustacea.

Head Topography

Tiegs and Manton (1958) called attention to numerous instances of convergent evolution within the Arthropoda and a possible convergence with respect to the development of the carapace, as suggested above, would find many parallels also within the Crustacea. A case in point is the general topography of the head. It can be shown that in connection with changes in the feeding habits of various crustaceans, similar topographical changes have taken place independently in different parts of the system (for details cf. Dahl, 1956a). The failure to understand the functional mechanism underlying such topographical changes has in the past frequently led to misunderstandings of phylogenetic relationships. Thus, to take one drastic example, the rather striking similarity between the organisation of the head
and the mouth parts in certain advanced Peracarida (isopods, terrestrial amphipods), on the one hand, and in certain primitive insects (Thysanura), on the other, has provoked attempts to see in these groups some sort of connecting link between Crustacea and Insecta. In reality the resemblance in general organisation is nothing but convergent adaptation to a mode of life which is in many respects similar.

The Caridoid Facies

The problems concerning the development of the carapace and the changes in head topography bring up the whole question of the caridoid facies in crustacean evolution. The concept of a caridoid facies was introduced by Calman (1909) with reference to the Malacostraca, among which he considered it to represent a primitive type of organisation. The scope of the discussion of the caridoid type was recently extended by Siewing (1960) to include the whole of the Crustacea, since his diagram of a generalized crustacean (Figure 28 herein) reveals a largely caridoid structural plan although at a more primitive level than Calman’s malacostracan.

This brings up the problem whether primitive Crustacea were benthic or pelagic or rather, which is not quite the same thing, whether they were essentially swimming or essentially walking or crawling organisms. In this connection obviously the structure of the abdomen becomes relevant. Many Crustacea in which we find features generally considered primitive (e.g. many Anostraca, the Mystacocarida, the Cephalocarida, and, among the Malacostraca, the Stomatopoda) have a comparatively spacious abdomen containing a considerable part of the internal organs, especially the gonads. The heart, when present in such forms, extends through the greater part of the body including the abdomen. Of the groups mentioned, the Stomatopoda, the Mystacocarida, and the Cephalocarida are benthic non-swimming organisms, while the Anostraca are swimmers of a comparatively low degree of effectiveness and without any adaptations typical of pelagic Crustacea.

The Mystacocarida are known to have so many features in common with copepods that they must obviously be fairly closely related to them, although their organisation on the whole is at a considerably more primitive level. Without anticipating the concluding discussions, it seems justified to refer the two groups to the Maxillopoda. In both the Maxillopoda and the Malacostraca we meet highly adapted pelagic forms. Among the latter we find the caridoid type exemplified by lophogastrids, euphausians, penaeid and other prawns. Among the Maxillopoda we have calanoid and cyclopoid copepods. It is a characteristic feature of the abdomen in all these typically pelagic forms that it is highly specialized to facilitate locomotion by means of pleopods and/or extremely rapid snapping movements which fling its owner in jumps through the water. In connection with these adaptations the abdomen has become much more muscular and as a rule also narrower. The internal space becomes completely filled up with muscles pierced by the narrow intestinal canal and innervated by the ventral nerve chain. Other organ systems have, figuratively speaking, been crowded out of the abdomen and pushed forward into the thorax. The gonopores which in the forms with a spacious abdomen lie near the anterior end of the gonads come in the pelagic forms mentioned instead to lie be-
hind the gonads. It is in this connection a highly suggestive fact that in the pelagic copepods mentioned the gonoducts commence at the anterior end of the gonad and then run backward towards the gonopores.

The considerations summarized above must on no account be understood as an attempt to derive the various groups mentioned directly from each other, e.g. the lophogastrids, etc. from the stomatopods or the pelagic copepods from the Mystacocarida. They are only meant to illustrate changes taking place under the assumption that a "benthic" type of organisation with a spacious abdomen is being transformed into a "pelagic" type of organisation.

It is highly interesting that circumstances permit us to pursue the same line of thought one step further, for, obviously, pelagic types of both Malacostraca and Maxillopoda have given rise to benthic forms. Siewing in his important malacostracan paper of 1956 has summarized old and new evidence clearly showing that the more advanced types of peracaridan Malacostraca, notably isopods and amphipods, have been derived from an ancestor more or less at the mysid, i.e. a caridoid, level of organisation. Similarly the mainly benthic harpacticoid copepods will in all probability have to be derived from pelagic types (Lang, 1948). Despite the fact that in these various types of benthic Crustacea the abdominal musculature has become comparatively much less voluminous, the gonads still retain the thoracic position typical of the pelagic forms. It is interesting to note, though, that in isopods, doubtless as an adaptation to the respiratory activity of the pleopods, the heart has become secondarily located in the abdomen.

The consideration of the changes in the external and, to some extent, also in the internal morphology of the crustacean abdomen rather tends to throw doubts upon the caridoid facies as the primitive morphological pattern in crustacean evolution.

Manton (1953), after studying the locomotion of the Malacostraca, concluded that they could hardly have been derived from caridoid ancestors and we thus have independent evidence from two different sources pointing the same way.

It is quite clear that the arguments advanced here are not conclusive in themselves. But attention should certainly be paid to the possibilities advanced. This is one of the points where further paleontological evidence is sorely needed.

The Appendages

In another contribution to the present volume, H. L. Sanders deals with the functional and evolutionary differentiation of crustacean appendages and therefore little will be said here about these matters.

It seems probable that the primitive crustacean limb was concerned with both locomotion and feeding, and that a transport of food particles took place in a forward direction along the ventral side. As pointed out by various contributors to the present discussions, this need not necessarily have taken the form of a filtering mechanism. A transport of fairly large particles is in no way contradicted by the facts known about Recent Crustacea. If the suggestion concerning the mainly benthic mode of life of the primitive Crustacea, dealt with in the previous section, is correct, such a transport of fairly large particles becomes even more likely. This makes an early evolution of powerful biting or triturating mouth parts quite compatible with the assumption that the
appendages behind the mouth parts were at the same time essentially uniform and primitive. We know from such forms as phyllopods, anostracans and cephalocardi-ans that such a series will often show only a gradient of development, the posterior pairs of legs being as a rule less complete and differentiated than the anterior ones. This phenomenon in its turn is probably to be understood as a regular aspect of metamerism, a tendency towards a more and more incomplete segment formation in the posterior part of a long series, resulting even in the complete absence of appendages in the posterior part of a many-segmented animal, as e.g. in the Notostraca.

Tagmosis

The natural subdivision of the crustacean body into three tagmata, head, thorax, and abdomen, has become almost an axiom. However, the delimitation of the abdomen from the thorax is often quite arbitrary, e.g. in the Notostraca and also in the Mystacocarida and Cephalocarida where not even the position of the gonoporal apertures provide any real guidance. Difficulties of this kind have been fully appreciated by various previous writers (cf., e.g. Calman, 1909, p. 6).

In the light of the views on crustacean metamerism expressed in the previous section, this problem tends to lose much of its importance; nevertheless, it merits some further attention.

The delimitation of the head region from the thorax generally offers no great difficulty, not surprisingly since this limit is the result of an early functional differentiation. The final phases in the handling of the food call for a differentiation of the anterior appendages which is obviously favoured by a process of cephaliza-

If, nevertheless, we regard it as a cephalic segment instead of including it in the thorax this is an entirely arbitrary action designed to facilitate comparisons with other forms but without any direct justification in biological fact.

In the posterior part of the Crustacea a similar argument applies with even greater force. If we regard the gradual dwindling of appendages and of internal segment differentiation as a simple developmental principle in multi-segmented forms, the terms thorax and abdomen in such forms cannot be applied in a strict sense and, more important still, the need for their application vanishes. They acquire a meaning only when some sort of functional adaptation has brought about a differentiation of various regions which is the case, for example, in the Malacostraca and the Copepoda. Then it may be very convenient to distinguish between head, thorax, and abdomen, as has also been done in previous discussions in the present paper. But it must be kept in mind that the region called thorax in the copepods corresponds metamerically only to part of the region designated by the same name in the Malacostraca.

Much of the confusion prevailing at this point is due to the unfortunate habit of trying to find a common denominator for superficially similar phenomena in various arthropod groups, notably for such occurring in insects and in crustaceans. If we could rid ourselves of this inheritance
from early discussions on arthropod inter-relationships it would mean a great step towards clearer thinking. It must be realized that in many Crustacea there is really little more justification for a sub-
division of the body into thorax and ab-
domen than e.g. in chilopods.

Summing up the arguments presented above it is tempting to say that typical tagmosis is a feature not of the primitive but of the specialized crustacean.

Primitive Crustacean Organisation

It is not my intention here to attempt anything like a detailed reconstruction of the ancestral crustacean, for such a recon-
struction would have to be rather conjectural. I feel compelled, however, at this stage to present my views on some features which, in my opinion, were probably present already in the most primitive Crustacea. The arguments upon which these views are founded are contained in the discussion above and in my papers (1956a and b).

I have come to regard the primitive crustacean as an animal with a fairly high number of segments, probably benthic or at least not truly pelagic, with the cephalic appendages placed ventrally and more differentiated than the posterior ones, with the mouth opening directed more or less posteriorly, with the appendages of the body largely uniform and becoming smaller and less differentiated posteriorly and concerned with both locomotion and feeding, and without a clear separation between thorax and abdomen. It will be seen immediately that this conjectural ancestor differs in many respects from some of the other hypothetical primitive forms found in crustacean literature, and also from the one most recently presented by Siewing (1960). It is also evident that this primitive crustacean has many features in common with the Recent Cephalocarida and also with phyllopods and anostracans but that it stands somewhat further apart from the Malacostraca than does Siewing's primitive form.

Siewing arrived at his interpretation of the early crustacean partly as a result of an assumption that the so-called †Pseudocrustacea constitute an early step in the crustacean direction. It seems doubtful that we have the right to make such an assumption, for the few indications we have of the possible crustacean nature of a few pseudocrustacean species suggest that these species may have been fairly advanced Crustacea (cf. Linder, 1945, and discus-
sions in the present volume).

It is not my intention here to make any detailed comparison between the two hypo-
thetical ancestors mentioned above, for such a discussion would have to lie mostly outside the realm of known facts. It seems, however, not impossible to reconcile the views expressed in the two alternatives. As I see no need to find a place for the †Pseudocrustacea in the early stages of crustacean phylogeny, the ancestral Crusta-
cea, in my opinion, will probably have been less differentiated than in Siewing's alter-
native. I would prefer to regard the latter as an early malacostracan rather than an early crustacean, and I see no great difficulty in deriving a form essentially similar to the one described by Siewing from a still more primitive one with the features indicated above.

I think that in this connection attention should be drawn to one crucial point, namely the problems inherent in the recogni-
tion of primitiveness. The problem of crustacean ancestry, as it stands at present, illustrates very well how difficult it is to distinguish between "Primitivmerkmale," in the sense of Remane (1956), and other
morphological features. In order to make such a distinction one must have an extremely complete record of the evolutionary processes involved, a record which is only rarely available and certainly not in this case. Otherwise, the recognition of “Primitive merkmal” also turns into a rather arbitrary process and the concept, however useful in itself, becomes a potential danger to objective reasoning.

III. INTERNAL MORPHOLOGY

Some General Remarks

It is only natural that in animals so highly differentiated with respect to external morphology as Crustacea, internal features will have to play a comparatively subordinate part in phylogenetic discussions. Undoubtedly, however, a critical reconsideration of evidence drawn from this field may turn out to be very fruitful, as demonstrated e.g. by Siewing’s important work on Malacostraca (1956). Some further examples of recent results with a phylogenetic bearing will be given below. The scope of the discussion will, however, have to be rather limited and in the first place the digestive tract and the nervous system and sense organs will be dealt with. Only a few instances referring to other organ systems will be briefly quoted. I hope, however, that this will be sufficient to show that the field is far from exhausted and that both a study of evidence contained in previous literature and new investigations may turn out to be very fruitful.

Digestive Tract

As shown by Siewing (1956), the highly complicated masticatory and filtering mechanism of the stomodaeum in the Malacostraca provides highly valuable evidence concerning relationships within that group. Unfortunately, however, this advanced differentiation of the stomodaeum is a typical malacostracan feature, the stomodaeum of other groups generally forming a single tube of varying length. An exception to this rule, however, is found in certain ostracods which have triturating devices, partly of a complicated nature, in the stomodaeum. A detailed similarity with corresponding organs in the Malacostraca does not seem to exist and most probably we have here another case of convergence.

The midgut and its digestive appendages, on the other hand, show some interesting features permitting comparisons between most of the major crustacean groups.

In anostracans and in nontostracan and conchostracan phyllopods the fusion of the stomodaeum to the midgut rudiment occurs well behind the anterior end of the latter (Dahl, 1956a). At a comparatively early larval stage this anterior part of the midgut grows forward into a pair of diverticula which in the Notostraca end by forming a more or less complicated anterior network of tubes, the walls of which consist of an epithelium rich in glandular cells and with a well developed brush-border.

Only in the Cephalocarida a somewhat similar arrangement is found, for there the anterior end of the midgut in the adult is provided with a pair of short unbranched glandular diverticula, the ontogeny of which is as yet unknown. However, they do not extend nearly as far forwards into the head as in the Anostraca and phyllopods mentioned. In other Crustacea no corresponding structures are found in this region.

In this connection something should perhaps be said of the so-called anterior dorsal caecum (Siewing, 1956), which is to be found in some Malacostraca. It may be paired or unpaired and projects anteriorly from the dorsal part of the midgut above
the wall of the stomodaeal stomach. A good deal of confusion apparently prevails concerning the function and derivation of this caecum, but as far as I dare conclude from an investigation now in progress the explanation of its nature appears to be simple enough. Evidence from Nebalia, mysids, and amphipods shows quite clearly that, when present, this dorsal caecum represents the anterior growth zone of the midgut. Its wall consists of extremely densely packed undifferentiated cells and generally shows rather intense mitotic activity. In the border area between the caecum and the midgut proper the transformation of these undifferentiated cells into typical cells of the midgut epithelium is constantly in progress. In isopods, which possess no endodermal midgut in the ordinary sense, no dorsal caecum occurs, nor is it found in such amphipods (e.g. Hyperia) which have interstitial growth of the midgut epithelium. The posterior midgut caecum just in front of the junction between midgut and proctodaeum, when present, seems to constitute a corresponding growth zone; this at least is the case in various amphipods.

It seems reasonable to assume that the formation of the anterior and posterior dorsal caeca is the result of a process similar to the one just mentioned in the case of Anostraca and certain phyllopods, namely a junction of the stomodaeum (or proctodaeum) to the subterminal part of the midgut. It is interesting to note, however, that even if there possibly exists a similar mode of derivation of these caeca in the Malacostraca, on the one hand, and the phyllopods and anostracans, on the other, the malacostracan diverticula assume no digestive function.

In the Malacostraca, instead, the ventrally attached hepato-pancreatic caeca are concerned with digestion and absorption. As is well known, they show a varying degree of complication in different malacostracan groups.

In free-living copepods and in the Mystacocarida no digestive gut diverticula occur. This may be an adaptation to the small body size. Most of the species in question also lack a circulatory system. However, in some parasitic copepods, as also in the Branchiura and the Cirripedia, lateral glandular diverticula of the midgut occur. Such lateral diverticula are also present in some ostracods. This should be noted because it gives another at least possible argument in favour of the view that the Ostracoda may after all have maxillopodan affinities.

In summing up, the evidence available from the digestive tract points to affinities between the Anostraca and Phyllopoda and also between maxillopodan groups. The Cephalocarida in this respect approach the Anostraca while the ostracods are nearer to the Maxilopoda. The Malacostraca stand well apart.

Nervous System and Sense Organs

The general morphology of the crustacean nervous system is very well known. Although in its fundamental plan it is rather conservative, it is also highly adaptable and shows many rather striking modifications, often appearing independently in the different groups. A good example of this is the shortening of the ventral ganglion chain including a fusion of the segmental ganglia which is found e.g. in ostracods, copepods, and crabs. Purely adaptive structural parallels of this type can of course have no phylogenetic meaning. Conversely, a ventral nerve chain of the primitive step-ladder type may be retained
in very advanced forms, e.g. many of the higher Malacostraca.

It will also have to be remembered that the development of the brain is closely connected with functional emphasis on various sense organs, a fact well exemplified by Hanström (1928). This means, for instance, that in a visually orientated form the brain may at first inspection appear to be widely different from the one in a blind form with chemical orientation. This despite the fact that no differences of phylogenetic interest occur. The present writer (Dahl, 1956a) has pointed out various instances of convergent modifications in general brain topography connected with changes in the mode of feeding and the ensuing dislocation of the mouth parts and mouth opening.

On the whole, it seems rather difficult to base phylogenetic and systematic considerations of the larger crustacean groups on the general structure of the nervous system. However, some of the cerebrally innervated organs, i.e. sense organs and incretory organs, appear to offer more interesting possibilities from a comparative point of view.

Evidence is now available which seems to give a definite answer to the old question about the derivation and comparative anatomy of the crustacean frontal organs. Already in 1957, I found definite proof that the dorsal (paired) frontal organs are not homologous with the sensory pore X-organ, both these organs being simultaneously present in Decapoda Natantia. In *Leander adpersus* I also found that the frontal organ in question was closely connected with the nauplius eye. One of my collaborators, Mr. R. Elofsson (in MS), after comprehensive studies on *Pandalus*, has been able to show definitely that both the dorsal and ventral frontal organs are simply parts of the nauplius eye itself. The same has also been shown to be the case in all other decapods examined. It may truly be said that this provides no new positive proof about relationships between different Crustacea, but, on the other hand, it rids us of a good deal of confusion and some false homologies.

Also, with respect to the sensory pore X-organ, a good deal of new evidence is available. Moreover, this evidence is of considerable comparative interest. The X-organ appears to be a conservative organ. Thanks to investigations by Hanström and others, its structure in decapods and some other Malacostraca is well known. In the course of the last year I obtained definite proof that the so-called cephalic statocyst of amphipods and isopods is nothing but a very typical X-organ of the same structure as that found in mysids and with exactly the same innervation. There, in fact, we get rid of a whole sense organ appearing suddenly in the middle of the Malacostraca and innervated from the protocerebrum. Such an organ would have been, to say the least, a most unexpected innovation. We have now throughout the Malacostraca a sensory pore X-organ of essentially the same structure. It is interesting to note that something of the kind apparently also exists in the copepods. The structure which, in the light of the knowledge then prevailing, I described in 1953 as a dorsal frontal organ in *Harpacticus* has on second inspection turned out to be a sensory pore X-organ of rather typical structure, and the same organ has also been found in *Calanus* connected with the frontal processes, which thus become probably homologous with the eye stalk papilla in Malacostraca. In fact, this structure has already
been described by Carlisle and Pitman (1961) in *Calanus* although the homologies of the organ have not been completely clear till now. In *Balanus* larvae one of my collaborators, Mr. T. Kauri (1962, and verbal information), has shown that the frontal appendage and the structures below it are probably an X-organ of the same type. That would mean that the frontal appendage of the *Balanus* larva is also homologous with the eye papilla of the Malacostraca, and it would also reveal the presence of a sensory pore X-organ in two widely different groups of the Malacostraca. The resemblance between the Malacostraca and the Maxillopoda in this respect becomes all the more interesting because attempts to find corresponding organs in the Anostraca and in the Phyllopoda have hitherto failed. In the posterior part of the eye chamber in *Triops* there lies a group of neurosecretory cells previously wrongly interpreted as a dorsal frontal organ (cf. Dahl, 1958). Proof is still lacking that this is an X-organ and in any case its structure is widely different from that of the sensory pore X-organ in malacostracans and Maxillopoda. Neither has it hitherto been possible to find an X-organ in the Anostraca. The highly aberrant head of the Cephalocarida has not yet been examined in this respect.

Despite a striking general similarity, the compound eyes of the Crustacea show much variation in detail (Table 1). Differences between crustacean groups are to be found in the ommata but they are more profound in the optic ganglia. On the other hand, conditions within the major groups are fairly uniform. This applies in the first place to the Anostraca and Phyllopoda, on the one hand, and the Malacostraca, on the other. As seen in the Table, there are 4 or 5 Semper’s cells and 5 retinular cells with up to 3 accessory retinular cells in the eyes of the Anostraca and the Phyllopoda. In the malacostracan ommata there are 2 to 4 Semper’s cells and generally 7 retinular cells plus 1 accessory retinular cell.

The eyes of amphipods and isopods

**TABLE 1**

**Compound Eyes in Crustacea**

<table>
<thead>
<tr>
<th></th>
<th>Semper’s cells</th>
<th>Retinular cells</th>
<th>Centres</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anostraca</td>
<td>4</td>
<td>5 + 1</td>
<td>L — M</td>
</tr>
<tr>
<td>Notostraca</td>
<td>4</td>
<td>5 + 3</td>
<td>L — M</td>
</tr>
<tr>
<td>Conchostraca + Cladocera</td>
<td>5</td>
<td>5</td>
<td>L — M</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>2</td>
<td>6 - 7</td>
<td>L — M</td>
</tr>
<tr>
<td>Thoracica</td>
<td>3</td>
<td>6</td>
<td>— M</td>
</tr>
<tr>
<td>Branchiura</td>
<td>4</td>
<td>4 + 1</td>
<td>?L — M</td>
</tr>
<tr>
<td>Leptostraca</td>
<td>4</td>
<td>7</td>
<td>L × Me × Mi</td>
</tr>
<tr>
<td>Stomatopoda</td>
<td>4</td>
<td>7 + 1</td>
<td>L × Me × Mi</td>
</tr>
<tr>
<td>Syncarida</td>
<td>2</td>
<td>7</td>
<td>L × Me × Mi</td>
</tr>
<tr>
<td>Euphausiacea</td>
<td>2 + 2</td>
<td>7</td>
<td>L × Me × Mi</td>
</tr>
<tr>
<td>Decapoda</td>
<td>4</td>
<td>7 + 1</td>
<td>L × Me × Mi</td>
</tr>
<tr>
<td>Mysidacea</td>
<td>2 + 2</td>
<td>7</td>
<td>L × Me × Mi</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>2</td>
<td>5</td>
<td>L × Me × Mi</td>
</tr>
<tr>
<td>Isopoda</td>
<td>2 + 2</td>
<td>8 - 17</td>
<td>L × Me × Mi</td>
</tr>
</tbody>
</table>

L, lamina ganglionaris; M, medulla; Me, medulla externa; Mi, medulla interna; ×, chiasma.
are aberrant in this respect with 5 and up to 17 retinular cells, respectively. The differences in the optic ganglia, however, are more far-reaching. As is well known, the Anostraca and Phyllopoda have only a lamina and one medulla without any chiasma between them. The Malacostraca, on the other hand, have a lamina and two medullae with chiasma. It seems to have been generally and tacitly accepted that the malacostracan condition has been derived from the anostracan and phyllopodan one. However, there exists no evidence whatever, either paleontological or morphological, that any such development has taken place. Obviously the malacostracan eye must have developed from simpler types of compound eyes, but there is nothing to tell us whether the ancestral forms had eyes of the anostracan type, or developed along different lines.

Indications of such a possibility are in fact to be found in the eyes of the Maxillopoda. Unfortunately, only a few of the Recent Maxillopoda have compound eyes available for comparison and a discussion of these problems has to be based only on the Branchiura and on the juvenile stages of the Cirripedia Thoracica. In these eyes we find 4 and 3 Semper’s cells, respectively, while the Branchiura have 4 plus 1 retinular cells, and the Cirripedia 6 retinular cells. Again, however, the optic ganglia are of greater interest. In both types the lamina ganglionaris is very poorly developed, and it is indeed doubtful whether a typical lamina occurs at all. In the Branchiura there are in fact a number of cell nuclei in the interior of the eye, but they are not arranged as a typical lamina and it has not been possible to trace the detailed fibre arrangement. Detailed knowledge of the single medulla of the cirripede larva is not available; it has turned out to be a difficult object for this kind of study. Unpublished investigations by Mr. N. Madsen (verbal communications) have shown that the structure of the medulla in Argulus is highly complicated and shows an arrangement of fibres which might indicate a functional splitting into two parts. No definite proof of the existence of any chiasma has, however, come forth, and the general structure of the medulla is rather unlike that found in Malacostraca.

The finer structure of the compound eye found in some ostracods is comparatively poorly known and this applies especially to the most interesting part in this connection, the optic ganglia.

As is seen from this brief summary the evidence now available shows that we have two well defined and rather different types of compound eyes, one in the Branchiopoda and one in the Malacostraca. Further, there are indications to show that in the Maxillopoda we meet a third type of eye differing from both the others.

Finally, the nauplius eye of anostracans and phyllopods is similar both with respect to general structure and to the highly complicated mode of development. They seem to differ profoundly from the nauplius eyes of most other crustacean groups, at least from those of the Malacostraca and the Maxillopoda.

Other Organ Systems

My personal knowledge of other organ systems is too superficial to permit a critical evaluation. Undoubtedly, however, useful information could be obtained in various cases, as shown e.g. by Siewing, 1956, and Mayrat, 1959, with respect to the circulatory system of Malacostraca. With respect to the vascular system we have also another interesting difference between the Anostraca and the Phyllopoda, on the one
hand, and other Crustacea, on the other hand, in that heart function in the two former groups is myogenic while among other Crustacea it is nervously controlled (Krijgsman, 1952; Lagerspetz, 1962). There are also indications that valuable information would be gained from a comparative study of the finer structure of the excretory organs, of vitellogenesis, etc.

IV. CONCLUSIONS

The Main Crustacean Groups

It is interesting to note that the brief summaries of external and internal morphological evidence of crustacean relationships which were made above, give, on the whole, an impression of mutual corroboration. The view that the main groups previously distinguished are natural units is strengthened by this new evidence.

One is repeatedly struck by the great degree of similarity in anostracan and phyllopod organisation in various organ systems. I find it very difficult to accept the conclusions drawn by Preuss (1951), according to which the two groups have very little in common. The general structure of the mouth parts, the close similarity between the metanauplius larvae which are different from those of all other Crustacea (cf. Sanders, present volume), the structure of the alimentary canal, the compound and nauplius eyes, and the mode of function of the heart, all seem to point to a fairly close relationship.

In my tentative systems of 1956 I referred the Anostraca and Phyllopoda together with the Cephalocarida to a new group of higher rank, the Gnathostraca. This seemed justified from the point of view of the evidence then available. The later results obtained by Sanders and particularly those reported in the present volume have, however, convinced me that the Cephalocarida are more suitably regarded as a separate group retaining many features of ancestral crustacean forms, but, on the other hand, with various highly advanced adaptations, especially in head morphology, due to the peculiar mode of life.

If the Cephalocarida are removed, however, the justification for the concept Gnathostraca disappears and we can again group the Anostraca and the Phyllopoda together under the time-honored name Branchiopoda.

The new evidence now available seems, on the other hand, to strengthen the validity of the concept Maxillopoda. To the evidence recorded by Dahl (1956b), Birshstein (1960), and Siewing (1960) can be added the general similarity with respect to the alimentary canal and possibly also the X-organ of some of the forms concerned. A grouping together of the Mystacocarida, the Copepoda, the Branchiura, and the Cirripedia under the heading Maxillopoda thus appears justified. The Ostracoda remain difficult. Some indications of possible affinities to the Maxillipoda exist but they are rather uncertain and the possible relations to the Cephalocarida can in any case not be very close. The Ostracoda are in my opinion better retained as a separate group of rather doubtful affinities.

The Malacostraca also constitute a well defined group although with some indication of affinities with the Maxillipoda and possibly also the Cephalocarida.

As an outcome of these discussions, the Class Crustacea could be subdivided into five main groups, as shown on page 13.

In my tentative system of 1956, the main subunits below the class level were called subclasses, and the next category orders. As pointed out to me by Dr. I.
Gordon, the arrangement then suggested caused difficulties, especially with respect to the Malacostraca. Further, it is clear that if the group Maxillipoda is given subclass rank, the rank of the Cirripedia will have to be lower, and that will again upset the well arranged system within that group. I am indebted to Professor E. Mayr for the suggestion that the highest units should be called cohorts and placed at the level between class and subclass. This suggestion has been followed here.

In this way the Ostracoda and Malacostraca, not to mention the Cephalocarida, have no subunits at the subclass level, but this appears to be a lesser evil than the upsetting of longstanding systems. It has to be left to the specialists on the respective groups finally to decide whether any of the lower units now recognized should be elevated to subclass rank. Considering the high degree of mutual independence of the groups now recognized as subclasses, doubts arise, however, whether this would not upset the scale of values expressed in the system.

**Evolutionary Lines**

In the case of some of the crustacean groups, especially the Malacostraca, but also the Branchiopoda and the Cirripedia Thoracica, so much morphological and/or paleontological evidence is available that the systematics within the groups can be said to approach at least partly a natural system built on the main evolutionary lines.

Numerous attempts have also been made to construct phyletogenetic trees demonstrating the evolution of the Crustacea as a whole. Unfortunately, however, the most important features of these phylogenetic trees have to be conjectural, for at present we possess no actual evidence demonstrating any case of a group at subclass or higher level being derived from another group. We have reasons to believe that e.g. the Mystacocarida and the Copepoda have been derived from common ancestors which already showed many maxillipodan features, but we have no evidence whatsoever to show how and at which level of organisation the lines separated. Similarly, it is reasonable to assume that the Malacostraca and the Maxillipoda are closer to each other phylogenetically than either is to the Branchiopoda. Also, evidence is forthcoming which makes it probable that the Cephalocarida are at least in many respects fairly close to ancestral crustacean groups.
types. But any attempt to derive any one of these groups from the other must be based on guesswork.

A reasonable degree of conjecture must inevitably play a certain part in practically all phylogenetic considerations, and especially on such dealing with the groups of higher rank, for evidence is rarely, if ever, complete. Nevertheless, it seems important to make a clear distinction between what is fact and what is conjecture in phylogeny. This seems the only way to lessen the influence of preconceived ideas, an influence felt only too often in discussions of this kind.

Figures 1 and 2 have been constructed in order to demonstrate the present writer's view on the main evolutionary lines among the Crustacea. The horizontal line cutting across Figure 1 represents the present limit...
of actual knowledge, the area below is open to speculation, and the dotted lines there indicate my own opinion of the main direction in which some evolutionary lines may have gone. Admittedly this diagram is a very poor substitute for a phylogenetic tree. It may be regarded as a retrograde step, but also as a step towards increased realism.

ACKNOWLEDGEMENTS

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REFERENCES


II

Discussion Following Dahl’s Paper

HESSLER: My studies of crustacean abdominal musculature agree with Dahl’s ideas on the primitiveness of the caridoid facies. Syncarids, mysids, euphausiids and decapods (Daniel) all possess a complicated, basically “caridoid” abdominal musculature. The non-mysid peracarids, on the other hand, have a simple abdominal musculature in which a few straight fibers run from segment to segment. Assuming the mysids are primitive, this is a secondary reduction.

In the abdomen of stomatopods the dorsal longitudinal muscles are of the caridoid type. The ventral muscles are a pair of relatively small, spiral bundles in which the fibers make a complete revolution every three segments, attaching in every segment: essentially the form of the ventral caridoid musculature. This suggests that the stomatopods reflect the precursor condition to the caridoid musculature. Siewing has suggested that the stomatopods branched off from the main malacostracan line prior to the appearance of the caridoid facies. Dahl’s findings on the position of the gonads coincide with the conclusions derived from musculature: in higher peracarids the abdominal muscles are secondarily reduced; in the stomatopods their simple development is primary.

The stomatopodan condition is probably derived from that of a leptostracan-like precursor where muscles go straight from segment to segment without a spiral. Such is the condition found in cephalocarids and branchiopods. Thus it seems possible to derive the caridoid musculature from an early entomostracan condition.

GLAESNNER: We heard that the primitive forms are filter-feeders with the mouth curved backwards. How does that fit in, if we look back to a possible origin of the crustaceans? Does not this condition have to be secondary in the ultimate origin of the Crustacea as such?

DAHL: The ancestors of Crustacea may have had a terminal mouth, but at the crustacean level we must suppose that appendages have been drawn into the feeding mechanism. I can’t see how they could have fed after they acquired an exoskeleton, without the use of appendages. We have to assume, on the crustacean level, that filter-feeding, or at least feeding by means of food transported along the ventral side is primitive.

MANTON: We have little evidence of the derivations of the various types of crustacean filter-feeding. If glandular secretions are used in food collection, the labrum is turned backwards, as in many branchiopods. If the collection is more mechanical, by brush setae, etc., as in mysids and copepods, there is no need for the labrum to be turned so far backwards. Is the presence of spiral muscles associated with the capability of an “escape”
or other sudden movement, such as the flapping of the abdomen under the thorax? Such muscles also occur in *Petrobius*, an expert jumper.

**HESSLER:** MacDonald (1927, J. Mar. Biol. Assoc. Plymouth, 14:753-794) says that *Meganyciphanes* does not flex its abdomen as an escape reaction.

**MANNING:** I have observed Recent stomatopods, and they do not flap the abdomen. Their swimming mechanism uses the pleopods or they move along with their walking legs. The loose articulation of the abdomen enables them to turn around in their burrow, but they don’t use it as an escape reaction in the same sense that the shrimps do.

**HESSLER:** When you disturb the water in front of stomatopods, they turn around almost instantaneously. The motion does involve flexure of the abdomen.

**MANNING:** But they don’t move backward in the same sense that a lobster would, with a rapid tail flap first. They roll themselves and turn and retreat perhaps.

**HESSLER:** Perhaps this is an intermediate stage.

**LOCHHEAD:** Getting back to the role of filter-feeding in the origin of crustaceans, it is worth noting that the notostracan, *Triops*, can feed on small particles, despite a complete lack of filter setae. Even in the absence of mud, *Triops* can capture small numbers of 3 μ flagellates and can live on round algae 15-80 μ in diameter. Movements of the limbs produce a current which flows forward under the labrum, where the food organisms are secured. *Triops* does not always feed in this way, but the fact that it can do so suggests how filter-feeding may have originated.

**TASCH:** Lochhead’s observations on feeding in the natostracan *Triops* can be supplemented by fossil evidence. Trusheim found indications that Triassic *Triops* (identical with living forms) indulged in cannibalism. †*Lepidocaris* from the Devonian Rhynie Chert had its anterior appendages modified for a special type of feeding—possibly detrital feeding. We should envisage a variety of possible modes of feeding in some branchiopods—surely for some known from the geologic past.

**DAHL:** In the mysids the mouth is not directed backwards to the same extent as in the branchiopods; still there is a marked difference from those malacostracans which feed on large pieces of food directly below or in front of the mouth parts. And as Manton has shown, there is a clear correlation between head topography and mode of feeding in the Anaspidacea. *Paranaspidides* is much more of a filter-feeder than *Anaspides* and has a larger labrum and the *atrium oris* directed more backwards. On the other hand, the semiterrestrial *Koonunga* is almost prognathous.

**SANDERS:** Concerning the primitive filter-feeding habit in the Crustacea, the evidence from the Cephalocarida indicates that filter-feeding may have been preceded by a detritus-feeding habit, and the type of detritus-feeding we are referring to is probably secondarily derived from a filter-feeding habit. Cephalocarids may have the primary detritus-feeding habit since all the components needed for branchiopod filter-feeding are present. The limbs are similar. There is a well developed endopodite which is not present in the more generalized branchiopods. There are endites; the proximal one is completely unmodified which, as Cannon postulated, must have been the ancestral condition. There are anterior and posterior setae on the protopod and endopod which catch relatively large masses of detritus that are put in suspension by the
naupliar-like or sweep-net movement of the second antenna and the endopods of the trunk limbs. The detritus is first caught by the posterior setae during the anterior or suctional phase and then pushed back into the median chamber by the interdigitating anterior setae. At this point the detritus is drawn dorsally and moved by the spines of the proximal endites to the head region.

MAYR: What is believed about where the crustaceans join any other branch of the arthropods?

WHITTINGTON: I prefer to keep the trilobites entirely separate from Crustacea. The lines of descent of crustacean groups may go back and join within some limit that we know in the fossil record, but before that, the trilobites had separated. Feeding with the mouth facing back is an old and general habit.

MOORE: I would like to ask about trilobitomorphs other than the trilobites.

ROLFE: As Tiegs and Manton (1958, Biol. Rev., 33:292) pointed out, we don’t know how many of them have genuinely trilobitan limbs. The “pseudocrustacean” †Canadaspis [= †Hymenocaris] from the Burgess Shale was asserted by Raymond (1920, Mem. Conn. Acad. Arts Sci., 7:113) to have trilobitan limbs. Of 202 specimens in the Museum of Comparative Zoology, only a few have thoracopods which show anything of their segmentation. Up to eight segments can be counted in the limb, the eighth segment bears four terminal claws, and a large proximal flap is present which is presumably pre-epipodial. This basal lamella is not filamentous as it is in the trilobitan limb. Simply from the number of segments in the limb and the presence of a basal (branchial?) structure it could be a normal crustacean limb minus exopod. But until the United States National Museum specimens have been critically re-studied, it seems worthless to speculate on some of these. Tiegs and Manton’s idea of the “Pseudocrustacea” being mosaic forms is most intriguing, but unfortunately my preliminary study of the limbs of †Canadaspis does not seem to verify it for this genus at least. (A. Simonetta has recently published a restudy of †Marrella, 1962, Monitore Zoologico Italiano, 69(3-4):172-185).

MANTON: Before we build theories as to whether an animal was a trilobite or a crustacean relative we should, I agree, have good evidence of the nature of the outer ramus of the limb.

SANDERS: Would the paleontologists care to speculate on the actual validity of the so-called trilobite limb, since apparently it is known from so few specimens. There may have been differential preservation resulting in only a small fraction of the entire spectrum of limb variation being available to us.

WHITTINGTON: You may be right. What we really know about trilobite limbs is based upon Störmer’s sections, and they show one type of limb in the Ordovician. We do know a somewhat similar limb, not so well, in the Devonian. Then we have the Burgess Shale forms in the Cambrian. It is a reasonable assumption that they were like this, but the evidence is slim.

PALMER: In olenellids and agnostids we know nothing of the limbs, and these are two major trilobite groups.

BROOKS: Störmer brought out the most significant point here in recognizing the amandibulates and the mandibulates among the arthropods. Trilobites, lacking a mandible, are obviously distinct phylogenetically. How are we going to explain the mandible as a biting structure in the
Crustacea by saying that they were primitively filter-feeders?

HESSLER: The mystacocarid mandible is a trilobitan limb except that its basal endite is an elongate gnathobase and there are fewer segments on the endopod. These are not great differences.

MANTON: Fine-food feeders require a mandible mainly for rubbing and squeezing, but not for biting. I do not think that biting is a primitive attribute of the Arthropoda (see p. 111). A crustacean mandible performing rolling, squeezing and grinding movements suits small-food feeding whether this food is derived from the bottom or from suspension.

SANDERS: Certainly the mandible, at least primitively, was more than merely a biting or masticating structure. In adult copepods and mystacocarids, and in the nauplii of a large number of groups, the mandible is used to collect food particles. It can also transport particles or, in the case of the larval cephalocarids, detritus to the region of the atrium oris. In other words, the mandible primitively is a generalized limb doing a number of functions. The elaboration we usually see is further modification or simplification, primarily for mastication.

DAHL: What does the formation of an exoskeleton carry with it in the form of change of ecology? If we assume for the sake of argument an annelid ancestor, it has a highly flexible head, it can turn anywhere to pick up food, crawl on or through the bottom, feeding all the time. If you reach a crustacean stage with a firm exoskeleton, that flexibility tends to be lost, and that must inevitably affect the feeding methods.

GLAESNNER: The late pre-Cambrian annelid †Spriggina has a head which resembles that of the annelid Tomopteris. The latter has a head consisting of several fused segments. To what extent that would affect the position of the mouth and the feeding habits I do not know, because the living tomopterids are secondarily adapted to a pelagic mode of life. The fossil that resembles them is not so adapted and that does not necessarily rule out the relationship. The head could develop a strongly sclerotised integument. We have to decide whether that would go with an anterior position of the mouth, and at what stage it would lead to that downward curvature which is one of the key points when we compare annelids and arthropods. We should keep the background of possible annelid-arthropod relationships in mind when we talk about Crustacea. The latter have inherited their segmentation from somewhere, say from an annelid, and the question is what happens to that segmentation subsequently in connection with changes in locomotion, respiration, etc. That inherited segmentation is one of the problems that is being overcome in a variety of ways: either by concentration and formation of a cephalothorax, or by retention and development of a uniform segmentation which leads to a different mode of locomotion. The Stomatopoda overcome the problem by shifting more of their organization into the abdomen, whereas others concentrate it in the anterior portion of their body. What of the development of the crustacean limb from the ancestral locomotive limb, not the feeding limb? Is that a new development, or is it another shift in position of a pre-existing, pre-crustacean feature?

DAHL: I find it hard, at the primitive crustacean level, to distinguish between a locomotory limb and a feeding limb. The one almost postulates the other.

MANTON: At a primitive level many
functions are done by every limb including the mandible: feeding, locomotion, respiration, etc. Lochhead's point, that *Triops* is capable of feeding on minute particles for unlimited periods of time, without special structures to facilitate this process, is of importance in all considerations of crustacean feeding and speculations as to how the trilobites fed.

MOORE: Do the Onychophora fit into the picture?

MANTON: A good argument can be advanced for supposing that present-day Onychophora are not degenerate or secondarily simplified. Functional considerations can account for their soft body wall, unstriated muscle, connective tissue skeleton, limited scute formation, undifferentiated gaitts, etc. The Onychophora are so similar in superficial appearance to †*Ayshleaia* as to suggest a common derivation, but this must be very far removed from that of Crustacea. The Onychophora are associated with the Myriapoda and Hexapoda on embryological and comparative anatomical grounds. One can see no common basis in either the type of limb or the type of jaw present in the Crustacea and in the Onychophora-Myriapoda-Hexapoda series. Thus a study of the Onychophora does not help with problems of crustacean evolution.

WHITTINGTON: What sort of adaptation, mode of feeding or of locomotion makes a crustacean? You've been saying that possibly the early ones lived on the bottom. So did the trilobites, and the Onychophora. What is the essential difference? How could it be in the environment, if this was presumably somewhat similar? What was the feature that led to the evolution of Crustacea?

MANTON: Work on myriapods has shown how evolution has taken place in association with divergent habits which have been established in the same type of environment. Mandibles, locomotory limbs, and differing trunk characters which are diagnostic of large groups (classes and orders), have evolved in association with these habits. This is a quite different type of evolutionary advance from adaptation to particular niches which occurs in the adaptive radiations of classes and orders, usually taking place at a later evolutionary stage.

WHITTINGTON: Annelids can undulate the body in the horizontal plane, but trilobites cannot. Is this a different habit in the same environment?

MANTON: The great difference between annelid and arthropod surface locomotion (not burrowing) is the predominant use of trunk muscles as well as parapodial muscles in the former, and extrinsic and intrinsic limb muscles but not trunk muscles in the latter, for providing the locomotory force. Body undulations caused by trunk musculature are usually a disadvantage, and in the arthropod are controlled up to a point by various means. The biramous legs of trilobites and of Crustacea have probably evolved quite independently from those of †*Ayshleaia*.

SANDERS: Regarding the trilobite limb and mode of feeding, one tends to think in terms of a filter-feeding current system. Manton feels that one of the difficulties of such a scheme is that the enditic or gnathic spines did not meet along the midline, so that it is difficult to imagine how the food was passed forward. However, the trilobites may have fed in a manner similar to the Cephalocarida utilizing large masses of detritus, or may have been predaceous like Limulus. In such a case, there would be no necessity for the limbs to meet along the midline
since the food could be carried forward from limb to limb as long as the food mass was large enough.

LOCHHEAD: Emphasis is often put on the need for particular setae or other structures to transport or push the food forwards to the mouth under the labrum. In a great many cases the current alone will do this. If you watch a captive filter-feeding anostracan or cladoceran and concentrate on individual particles that are being sucked along in the feeding current, you'll see that a great many particles get all the way to the mouth and in under the labrum, without ever touching any setae at all. The setae are there as a sort of insurance for the ones that go astray. A large percentage of particles will reach the mouth without any help from special structures to push them there, simply because there is a backwash current that will take them up under the labrum.

WATERMAN: The visual organs of crustaceans are of particular interest to me and it is notable that among the apparently primitive crustacean groups a remarkable variety of different eye types occur, often quite distinct from the highly developed compound eye of the decapods (Waterman, 1961, "Physiology of Crustacea," 2:1-64.) Considering the crustaceans alone, one might conclude from such evidence that evolutionary exploration of various kinds of visual organ ultimately led to standardization in one particular type in the most highly evolved forms of the class. Yet the compound eyes of pterygote insects show remarkable structural similarities with those of decapod crustaceans.

This parallelism is marked both in gross and microscopic anatomy not only in the structure of the retina but also in that of the eye's dioptric apparatus which is almost identical. It is true that corneagenous cells present in crustacean eyes are absent in the tracheate compound eye and that certain aspects of the screening pigment differ but otherwise the cell-for-cell detail is astonishingly close. Thus a one-to-one correspondence may be seen in the relations and structure of the more peripheral retinula with its typical 7 + 1 pattern of neurosensory cells, the rhabdom made up of radial microtubules perpendicular to the optic axis, the basilar membrane and strands of primary visual axons as well as the more central three successive optic ganglia (lamina ganglionaris, medulla externa and medulla interna) separated by the external and internal chiasmata. One major neurological difference, which appears as a notable exception, is the medulla terminalis of stalk-eyed crustaceans absent in insects and in sessile-eyed crustaceans, too. This ganglionic mass is believed to have been derived from part of the protocerebrum and to have migrated peripherally in connection with the evolution of movable eyestalks (Hanström, 1928, "Vergleichende Anatomie des Nervensystems der wirbellosen Tiere." 628 pp. Springer, Berlin.)

In view of these extensive similarities, Dr. Manton's remark that the hexapod-myriapod line of arthropod evolution, on the basis of a wide variety of evidence, does not seem to be close to the crustacean line raises some interesting points. If indeed the closely similar compound eyes of the higher insects and higher crustaceans arose independently in a strong evolutionary convergence, one is forced to draw rather drastic physiological conclusions, namely that each of the numerous parallel details in these two kinds of eyes must represent some functional component without which a highly efficient eye of this kind cannot operate.

Thus one should then ask what it is operationally that requires the presence of
7 retinular cells plus 1 basal or eccentric cell in each ommatidium. Perhaps color perception or sensitivity to the plane of polarized light is dependent on the clustering of retinal cells in this specific way. Hypotheses of these sorts have been proposed (Hanström, 1927, Z. vergleich. Physiol., 6:566-597; Autrum and Stumpf, 1950, Z. Naturforsch., 5b:116-122.) but no direct evidence of their validity is yet available. Similarly the physiologist should demand an explanation for the presence of three optic ganglia separated by two chiasmata in these optic tracts. We do know that extensive processing of optic information takes place in these regions in decapods (Wiersma, Waterman and Bush, 1961, Science, 134: 1435 (Abst.); Waterman and Wiersma, 1963, J. Cell. Comp. Physiol., 61:1-17) but cannot yet tie together structure and function effectively.

These unanswered questions raise still another challenging problem. This relates to the existence, or not, of evolutionary alternatives in the development of certain functions. Certain biological processes seem to be the unique solution available to animals for effecting a particular task. Thus all animals known use the carotenoid retinene (or the very closely related retinene2) as the chromophore of their visual pigments. No exceptions are known although cephalopods, insects, crustaceans and many vertebrates have been studied in this regard. Furthermore, these visual pigments, whose individual characteristics are endowed by the opsin moiety of the whole molecule, are invariably located either in submicroscopic lamellae (vertebrates) or in submicroscopic oriented fine tubules (arthropods and cephalopods) (Fernandez-Moran, 1959, Rev. Mod. Physics, 31:319-330.)

Such monotonous regularity in animal groups which cannot conceivably be considered closely related in terms of their eye evolution suggests some strikingly stringent functional requirements and limitations. Yet it is equally clear that at certain levels the evolution of the eye as a whole has been enormously affected by natural selection, as witness the many differences between camera eyes, compound eyes and ocelli as well as their extensive variations. The attempt to distinguish a priori between these two types of biological characteristics is a challenging and important point which has received little attention.

DAHL: This is one of the most challenging problems which the student of arthropod anatomy meets. I am struck by the great structural differences in the eyes of various Crustacea. Still more so if you regard the arthropods as a whole, finding what you regard as the final product with almost identical eyes. In the branchiopods Hanström showed that the types of ganglion cells and interpart connections there are much simpler than in decapods and insects. It seems to be the same in the eyes of Maxillopoda, which also have much simpler pathways. It is hard to conceive how one of these eye types could have been derived from the other ones at that high level. In the embryology of Notostraca, there is, more or less in the middle portion of the head, a large proliferation area of undifferentiated cells which migrate out to form the optic apparatus of the compound eye. Also, there is one strip of cells wandering in to constitute the lamina ganglionaris, and another strip of cells going to form part of the ganglion layer of the medulla, while other parts of the ganglion cells forming the medulla come from the brain. At the same time elements of this proliferation zone wander into the vast nauplius eye complex. So whatever the final function of these
cells may be, they come from a quite different area of the head from that in the Malacostraca, where the rudiment of the optic ganglia forms a proportionately much larger portion of the optic apparatus. This is a further challenge to the correlation of structure and function.

TASCH: Is there a development which Waterman attributes to natural selection and another development outside of natural selection that is the unique solution?

WATERMAN: Not correctly so since I believe natural selection to be the molding force in both types of biological characteristics I was referring to. In the case of the carotenoid part of visual pigments, however, natural selection has nearly zero scope for action since in all known cases the molecular pattern of this component is essentially the same. Therefore, if vision is going to be present, apparently either retinene$_1$ or retinene$_2$ must participate. On the other hand the form, shape, size, color, dioptrics and other such details of eyes obviously can be varied enormously under natural selection and have in fact undergone fascinating changes of all sorts as already mentioned. In some cases there may be only one way of doing something biologically; in other cases there may be several or many alternatives.

TASCH: I am always afraid of the type of formulation which speaks of unique solutions, out of random selection.

WATERMAN: I agree with your distrust if you mean that lack of evidence is a dangerous substitute for negative evidence. However, it seems fair to say that the nature of the universe and of the physics and chemistry which underlie living systems surely put definite restrictions on what may or may not take place in evolution whatever the mechanism of the latter. This thesis was elegantly developed many years ago by L. J. Henderson in “The Fitness of the Environment” (1913).

TASCH: Or you can speak of natural selection amongst compounds.

MAYR: I think there are three or four things we might distinguish. One is that certain basic enzymes are so important for life that they start almost simultaneously with life. So if they are now widespread both in animals and plants, it is simply that they were so essential that living organisms could not have gotten very far without them. There have been enzyme studies in microorganisms which have revealed the enormously wide distribution of certain enzymes. However, sharing such an enzyme or metabolic pathway cannot be used as proof of common descent because, in the case of the chemistry of certain metabolic phenomena, it seems that only one solution is possible. To find the same macromolecule in different organisms does not necessarily prove their origin from a common ancestor who also possessed such a molecule. The case of hemoglobin is a good illustration for the polyphyletic origin of a complex molecule, as pointed out by Waterman. Hemoglobin, apparently, transfers oxygen more efficiently than any other respiratory pigment, and whenever there was strong selection pressure in favor of efficient oxygen transfer, hemoglobin was “invented.” This has happened at least three times, independently, in the animal kingdom.

Cilia, and many components of cell structure, pose the question whether there is only one possible solution or whether the existing similarities are due to extreme phylogenetic age. Electron-microscopy pictures of the mitochondria of animals and plants, for instance, look very much the same to me. The peculiar lamellar structure is presumably the key component of
DISCUSSION

25
discussions. Most likely, we have here a combination of a unique solution and great phylogenetic age. We now come to the fourth and most difficult example. All these things up to now were simple things, in one case macromolecules, in the other case, very simple structures. But when we get to something as complex and yet as similar as the compound eye of the decapods and the insects, it puts one’s faith in natural selection to a severe test, and that in two separate ways. The first is the assumption that the compound eye is the only truly superior eye that an arthropod can have; the second one is that natural selection could have put together all of these pieces in such a way that independently the same kind of eye emerged, and yet, this is what the phylogeny at first sight seems to suggest. A possible solution to this puzzle is as follows:

Evolutionary changes do not happen as the early Mendelians thought by a gene turning up that creates a new character. This atomistic thinking has been completely refuted. There is a total genotype, and it is highly “integrated,” co-adapted, “cohesive,” and it has certain potentialities. One can assume that the potentialities that produced this type of eye go back to the common ancestors of the decapods and the insects. It wasn’t until a particular selection pressure set in that demanded an eye that was better than the eyes of some of the lower crustaceans or primitive relatives of the insects, that this similar compound eye emerged. It emerged because the two lines possessed the same genetic potential, a potential which responded in an analogous manner to a similar selection pressure. This is rank speculation, but we have a puzzling situation, and we have to propose an explanatory model.

DAHL: The anostracans and phyllopods have an eye consisting of generally five plus one retinular cells, a lamina and a medulla without a chiasma between and few connections, and on the other hand, the decapod eye with seven plus one retinular cells, two chiasmata and various synapses in the pathway. Can one expect any functional differences, with respect to image formation, or color vision, or analysis of polarized light, etc?

WATERMAN: This raises an interesting point about arthropod organization in general. As a whole arthropods seem to be most economically organized on a cellular basis. Thus the central nervous system, motor efferents and the sense organs themselves contain far fewer neurons than do the comparable elements of vertebrates. In Daphnia for example there are only 22 ommatidia (and hence perhaps 150 sensory cells) in its fused median eye. Yet these creatures are very strongly sensitive to polarized light, differentiate colors and show good evasive action if you try to catch them. Even in decapods there are only a few tens-of-thousands of retinular cells involved in the eye, yet our studies on visual information transfer in these systems (Waterman and Wiersma, 1963, J. Cell. Comp. Physiol., 61:1-17) indicate that the functional performance is closely similar to that found in the frog (Maturana, Lettvin, McCulloch and Pitts, 1960, J. Gen. Physiol., 43(6), supp. 2:129-175). In crustaceans there are movement receptor units, intensity receptors and novelty receptors that respond only to sudden changes in the visual field and not to general illumination or other sustained aspects of the potential stimulus.

DAHL: I follow Tiegs and Manton’s view that the compound eyes have been formed independently in various arthropods. It is hard to explain the derivation
of the various arthropod groups without assuming that. If you don’t assume that you encounter other convergences, which are equally difficult. It is not due to pure chance that we have compound eyes at these rather different levels of cellular organization.

MAYR: There is an amusing parallel with the phylogeny of the mammals. It is not many years ago that perhaps more than half of the people writing on the subject said they couldn’t possibly see how the mammalian middle ear and the jaw mechanism could have ever evolved from the reptilian one—it was an impossibility. Now, it is firmly established that on the basis of a basic potentiality for it, this shift has happened independently at least five times, and quite likely seven times. It is evident that the reptilian ancestors of the mammals had the basic potentiality in their genotype that permitted parallel evolutionary changes in several independent lines. This is that basic potentiality I was talking about as having independently given rise to the compound eye both in the arthropod and in the insect line.

WATERMAN: Dr. Mayr suggests that some basic genetic potentiality of a major group like the arthropods might remain un-expressed until some of its component taxa had evolved into quite distinct lines, like crustaceans and insects. Such an idea seems difficult to correlate with the observed emergence of typical compound eyes only in the most highly developed members of these two classes. In other words as their over-all organization drifts further and further apart, we find an important complex sensory system developing a high degree of convergence.
Adaptation is a universal phenomenon, characteristic of all living things. Like all great concepts, the concept of adaptation is basically a simple one, stating “that any living thing is somehow fitted to live where it does in fact live” (Simpson et al., 1957, p. 13). In its broadest sense adaptation refers to all alterations of living things which favor survival. Adaptation is therefore essentially an ecological concept—a concept of compensation for changes that occur in the nonliving and living environment of a given species. And there is no environment—nonliving or living—that does not change with time. Mentioning time emphasizes at once that adaptation is also an evolutionary concept, referring to gradual changes in organisms during the course of phylogeny, changes that increase the chances of survival, that make for increased fitness.

Darwin himself has proposed that evolution could be accounted for completely on this basis. Stanier et al. (1957) state that “in nature, genetic adaptation is the principal mechanism of evolution” (p. 410), and Simpson emphasizes that... “the origin of adaptation... is the prime problem of evolutionary biology” (1958, p. 521). As a primary mechanism of evolution, adaptation is based on genetic variation and subsequent natural selection; it is—as Mayr (1960) has put it—“a compromise between conflicting selection pressures” (p. 497).

Now that the statement contained in the title of the present paper has been documented and justified, let me restrict its ambitious sounding scope. I propose to set here before you a brief outline of our present knowledge of nongenetic and genetic adaptation in Crustacea to temperature, salinity and to life on land. I shall attempt to illustrate some general trends on the basis of a few subjectively selected examples from literature, with emphasis on the intact, whole organism and on “ecological” conditions.

But first let us clarify some terms and concepts that are often used in different ways. The term “adaptation” is taken here to mean adjustments of living systems to one or more factors of their natural environment, which result ultimately in an increase in their capacity to com-
pete, i.e. to survive and reproduce. Such adjustments are ecologically “advantageous” in an objective sense, and on this basis, distinguishable from mere responses. Adaptations may be effective continuously, or during certain periods only; they may be different in different life cycle stages, e.g. in nauplius, cypris and adult of the barnacle Balanus, which exhibit a series of different adaptations, a phenomenon known as serial adaptation.

Not all functions or structures of a phenotype are necessarily adaptive. An effort was made therefore to exclude papers reporting mere responses. A clear-cut separation between response and adaptation, however, proved to be difficult or even impossible in many cases. Assessment of the adaptive value of an adjustment requires more knowledge of the ecology and phylogeny of a species than is frequently available.

For detailed analysis, distinction is necessary between nongenetic adaptation involving nongenetic changes in the response mechanism, also known as acclimation or acclimatization, and genetic adaptation involving genetic changes in the response mechanism. Adjustments known as “sensory adaptation,” for example, accommodation of eyes to different intensities of light, do not generally produce actual changes in the response mechanism per se; such rather simple and fast adjustments represent a special case and are excluded here.

Nongenetic adaptations as such are not passed on to the next generation; however, the ability to adapt and the mechanisms involved are evolutionary products. In this sense then, nongenetic and genetic adaptations represent different aspects of the same basic phenomenon, even though they operate at different levels. In practice, these two kinds of adaptation can be distinguished on the basis of breeding experiments and performance tests under different environmental conditions.

Both nongenetic and genetic adaptation may be expressed at a functional level, e.g. in changes of rates and efficiencies of metabolism or in changes of behavior, and at a structural level, e.g. in changes concerning the architecture of cells, organs or the whole organism. Most of our present knowledge on adaptation in Crustacea is based on results obtained on macroscopic forms, especially decapods. There is great need for information on smaller forms such as branchiopods, ostracods, copepods and cirripeds. Some nongenetic and genetic adaptations in Crustacea are universal among animals—for example, functional adaptations to temperature such as shiftings of lethal limits, changes in activity or in metabolic rates; others appear principally to be related to specific crustacean features, such as their primarily aquatic way of life, respiration through gills, urine formation in antennal or maxillary glands, exoskeleton and body shape.

Species names have been used in accordance with *The Physiology of Crustacea* (T. H. Waterman, ed., Academic Press, New York, 1960/61) regardless of the names originally employed by authors of cited articles.

**Nongenetic Adaptation**

Let us first consider the nongenetic type of adaptation. *The ability to acclimatize* appears to be greatest in species that encounter extensive alterations in their natural nonliving or living environment. While it is usually necessary for a qualified analysis to begin with studies of acclimation to single factors such as temperature, salinity, light or social and behavioral as-
pects, it should be kept in mind that an organism acclimates to its total environment rather than to single factors.

The capacity for acclimation depends on—besides genotype and environment—physiological condition and age of the individual and may vary at different life cycle stages. In general, the capacity seems to reach its maximum during early ontogenetic development, that is, in eggs or early postnatal stages, and to decrease with increasing age of the individual. Nongenetic adaptations that have been acquired during the most sensitive phase of a life cycle or that are the results of repeated reinforcements, may be transferred to the next generation or even through several life cycles by nongenetic transmission (examples in Prosser, 1958). It is necessary in such cases to distinguish between individual nongenetic adaptation (without nongenetic transmission) and superindividual nongenetic adaptation (with nongenetic transmission). No critically analysed cases of superindividual nongenetic adaptation among Crustacea have, however, come to my attention.

In the time course of nongenetic adaptation, three successive phases may be distinguished: (i) immediate responses, beginning seconds or minutes after change of environment and involving increased fluctuation of performance, i.e., over- and undershoots and shock behavior; (ii) stabilization, beginning minutes or hours after the change and leading to progressively increasing constancy of performance, thereby gradually approaching a steady level; (iii) new steady state, beginning hours, days or weeks after the change, i.e. after completion of the most effective adjustments.

Immediate responses to sudden changes in temperature or salinity may involve fluctuations in the overall activity, changes in behavior and over- or undershoots of metabolic rates (examples in Kinne, 1963). Of particular interest here are the over- and undershoot responses observed in Cyclops strenuus by Scherbakoff (1935), in Neomysis integer, Hemimysis lamornae, Diaptomus gracilis, Artemia salina and developing eggs of Astacus pallipes by Grainger (1956), and in Daphnia magna and Simocephalus vetulus by Meijering (1960). A typical example is the oxygen consumption of the brine shrimp, Artemia salina (Grainger, 1958) (Figs. 3, 4). Oxygen consumption of Artemia overshoots upon changing the water temperature from 10°C to 30°C (Fig. 3). This

Fig. 3. Immediate response of oxygen consumption in the brine shrimp, Artemia salina, following a sudden increase in temperature. The four shrimps used in this experiment had previously been kept at 10°C for several weeks (After Grainger, 1958).

metabolic overshoot response ends largely after 30 minutes and completely after 1 hour. Oxygen consumption remains then fairly constant for the next 8 hours and thereafter decreases to what may be considered the final new level. The period between 2 hours and 26 hours (Fig. 3) seems to indicate the phase of stabilization, and the period beginning after 26 hours, the commencement of the new
steady state. Metabolic over- and under-shoots occur even in *Artemia salina* anesthetized with ether and lying motionless in the respiratory chamber (Fig. 4). The only motor activity in the anesthetized individuals was the beating of their hearts and occasional slight twitches of their intestines. This interesting result indicates that the immediate responses observed are not simply due to changes in locomotory activity but based on actual rate changes of basal metabolism.

Sudden changes of rather constant temperatures may also occur under natural conditions, and the immediate responses reported above may therefore be considered a normal first step in the acclimation process. Our present knowledge on this subject is meager and does not allow further generalizations. A more normal situation is doubtless gradually changing temperatures. These may cause fluctuations of rates around the steady state curve (obtained after acclimation to various constant temperatures) with the tendency of overshooting that curve under conditions of slowly rising temperatures and of under-shooting it at slowly declining temperatures (Fig. 5).

The term *phase of stabilization* constitutes at present not much more than a brief description of the period between the highly unstable immediate response and the rather stable new steady state. The duration of the phase of stabilization varies in different species and for different processes. Within a given species it depends on age, physiological condition, temperature and the severity of the stress employed. In general, speed of acclimation seems to be proportional to metabolic rate. McLeese (1956) has transferred the marine lobster *Homarus americanus* from 14.5° to 23.0°C and shown that thermal acclimation was practically completed in about 22 days (Fig. 6); substantial acclimation to low salinity had occurred within one week. Schwabe (1933) exposed the

![Fig. 4. Under- and overshoot responses of oxygen consumption, following abrupt temperature changes, in anesthetized, motionless *Artemia salina*. Two of the nine individuals died during this experiment (After Grainger, 1958).](image-url)
Fig. 5. Typical immediate responses of heart activity to slowly rising temperatures in two 16 mm long *Gammarus duebeni* males. A, steady state curve. Male 1 had been kept at 6-7°C for 14 days and was then exposed to temperatures rising to 23.0°C within 3½ hrs; male 2 had been kept at 14°C for 14 days and was then exposed to temperatures rising to 26.1°C within 2 hrs. All points represent averages of 10 counts. 10‰ salinity. (Modified from Kinne, 1952.)

Freshwater living *Astacus astacus* into blood isosmotic water of 15‰ salinity and found that blood osmoconcentration reached a new steady state after 12 days, and O₂ consumption after 20 to 30 days; the crab *Potamon* acclimated to new salinity levels in about 12 days (Driihon-Courtois, 1934). Shorter periods were found in the freshwater isopod *Asellus aquaticus* and the Australian mangrove crab *Heloccius cordiformis*. According to Edmonds (1935), *Heloccius* transferred into 25‰ sea water, reached a new steady state of its blood osmoconcentration after about 12 hours; this period, however, is longer after transfer into more extreme salinities. From these and other references, it may be concluded that the phase of stabilization may last anywhere from a few hours to several weeks.

The new steady state relative to the original steady state has been dealt with in innumerable papers, particularly with reference to lethal limits of temperature.

2 The symbol ‰ expresses salinity in parts per thousand.
Fig. 6. Duration of phase of stabilization in the lobster Homarus americanus. Given is the gain in average survival time of groups of 6-10 lobsters which had been kept at 14.5°C; the groups were transferred to an acclimation temperature of 23.0°C for periods ranging from 1 to 31 days and then tested at 30°C. Thermal acclimation is practically complete after about 22 days (After McLeese, 1956).

and salinity and metabolic rate. In most cases, acclimation to low intensities of temperature or salinity tends to shift the lower lethal limit downward, and acclimation to high intensities tends to shift the upper lethal limit upward; examples are: Armadillidium, Porcellio, Oniscus, Ligia (Edney, 1951a, b; 1960), Gammarus (Kinne, 1953a), Streptocephalus (Moore, 1955), Homarus (McLeese, 1956) (Fig. 7), Artemia (Grainger, 1958). Matutani (1960), however, reports a case of inverse compensation for the marine copepod, Tigriopus japonicus: while 30°C-acclimated Tigriopus exhibit a higher heat resistance than 20°C-acclimated ones, acclimation temperatures below 20°C (10°; 5°C) cause progressively increasing heat resistance.

Metabolic acclimations to temperature may result in characteristic quantitative differences between the original and the new steady state which have been described and classified by Precht (e.g. 1949, 1958) and later, in a modified version by Prosser (1958). Precht distinguishes between compensations (types 1 to 3), no compensation (type 4), and "inverse" compensation (type 5); type 3 represents the normal case, namely, partial compensation; type 1 represents over-compensation, and type 2, perfect compensation resulting in constant rate functions. Metabolic acclimations have been demonstrated in many
crustaceans, including *Daphnia* (Precht, 1949), *Gammarus* (Kinne, 1952, 1953a, b; Krog, 1954), *Pachygrapsus* (Roberts, 1957a, b), *Balanus* (Barnes and Barnes, 1958) and *Uca* (Vernberg, 1959a, b, c).

Acclimation to different temperatures may also involve changes in behavior (orientation, migration, territorialism) and in the quantity of physiologically important substances as well as in body size and structure. In *Eriocheir sinensis* kept in fresh water, for example, acclimation to 1°C to 3°C results in a marked decrease of free proline concentration in the intracellular pool of amino acids in muscles, relative to individuals kept at 15°C (Duchâteau and Florkin, 1955) and in *Daphnia* kept at a constant O₂ pressure, temperature increase augments the synthesis of hemoglobin (Florkin, 1960). In various species, different levels of temperature cause functional and structural color changes which may have adaptive value. Structural or morphological color changes involve actual changes in the amount of pigment per pigment cell or changes in number of chromatophores per unit area (e.g. Brown, 1934). Changes in body shape are documented by the well known phenomenon of cyclomorphosis in Cladocera (Wesenberg-Lund, e.g. 1900; Ostwald, 1904; Woltereck, e.g. 1913; Brooks, 1946, 1947, 1957; Lieder, 1951) and Copepoda (Margalef, 1955). Species from small bodies of water in high temperate latitudes, such as *Daphnia cucullata* and *Daphnia retrocurva*,

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**Fig. 7.** The effect of nongenetic thermal adaptation on the lethal levels of temperature in *Homarus americanus*. Numerous lobsters were exposed to various test temperatures after acclimation to 5°, 15° or 25°C. The curved lines are drawn through points representing per cent mortality at the respective test temperatures after 48 hours; the temperature that would cause 50% mortality is indicated by dotted lines and arrows. 30% salinity; 6.4 mg O₂/l (After McLeese, 1956).
exhibit spectacular variations of helmet, head crest and spines, particularly if the parthenogenetic young develop at high temperatures of at least 18° to 20°C. These structural modifications per se, however, do not seem to have adaptive value. They seem to be incidental expressions of a functional acclimation to the overall seasonal conditions, especially to high temperature and increased water turbulence. Water temperature and turbulence affect relative growth presumably through an increase in metabolic rate (Brooks, 1957; see also Hrbáček, 1959).

Metabolic acclimation to different levels of salinity leads to new steady states which may be (1) unaffected, i.e. identical with the original state, (2) higher in subnormal salinities and/or lower in supranormal salinities, and (3) higher both in sub- and supranormal salinities. An unaffected, constant respiratory rate has been reported in *Eriocheir sinensis* after acclimation to fresh water, 15‰ or 32‰ (Schwabe, 1933; Krogh, 1939). Examples for the second case—higher metabolic rates in subnormal salinities and/or lower metabolic rates in supranormal salinities—include most species tested, e.g. *Carcinus maenas*, *Eriphia spinifrons* (Schlieper, 1929; Schwabe, 1933), *Gammarus locusta* (Schlieper, 1929), *Pagurus longicarpus* (Maloeuf, 1938), *Uca* spp. (Gross, 1957a), *Hemigrapsus oregonensis* (Dehnel, 1960), *Astacus astacus* (Schwabe, 1933), *Potamon edulis* (Rafiý, 1934) and *Gammarus duebenii* (Kinne, 1952). Examples for the third case—higher metabolic rate in both sub- and supranormal salinities—include: *Ocypode quadrala* (Flemister and Flemister, 1951), *Palaemonetes varians* (Lofts, 1956) and *Metapenaeus monoceros* (Rao, 1958).

As has already been pointed out, organisms acclimate to their total environ-

ment rather than to single factors. Studies concerned with acclimation to factor combinations and with acclimation in the natural habitat are therefore of great importance. A critical, detailed analysis of such studies is, however, difficult for three reasons: (1) the situation is extremely complex; (2) sufficient information on environmental and biological history of habitat and organisms is mostly not available and difficult to obtain; (3) nongenetic and genetic components of an adaptation cannot readily be distinguished and assessed. It is evident though, from literature, that quality and quantity of a given acclimation to one environmental factor depend not only on the physiological condition of the individual involved and its genetic background, but also on other environmental factors. The capacity and rate of an acclimation to salinity, for example, may be different at different levels of ambient temperature or oxygen tension. In other words, the efficiency and perfection of a given acclimation may be different at different levels of other simultaneous acclimations. Harmony or disharmony between concomitant acclimations may therefore well be a fundamental way of increasing or decreasing the total capacity for nongenetic adaptation in complex environments.

**GENETIC ADAPTATION**

Evidence for genetic adaptation to temperature, salinity and life on land comes largely from crustaceans living in different latitudes, in sea or fresh water or in aquatic or terrestrial habitats. An attempt to attribute a given adaptation to a single ecological master factor like temperature or salinity is therefore difficult, certainly more so than in the case of nongenetic adaptations which are documented largely on an experimental basis.
In Crustacea, genetic adaptation to temperature is much less pronounced than to salinity or to life on land. Scholander and his collaborators (1953) and others have established that metabolism of arctic crustaceans is much higher at a given temperature than that of their tropical counterparts. These adjustments may be considered a genetic adaptation of basal metabolism to life at low temperatures, since locomotory activity appears to be similar in both groups and since metabolism in isolated tissues shows parallel adjustments. Such adaptations result often in considerable differences in temperature optima (Wingfield, 1939), and lower and upper limiting temperatures (Krog, 1954; Takeda, 1954; Spoor, 1955; Southward, 1958) and may consist of a genetic as well as a nongenetic component.

A variety of interesting genetic adaptations to salinity have made it possible for numerous crustaceans to leave their oceanic home and to establish themselves in a wide range of salinity conditions such as brackish water, fresh water and brine, and even to conquer land. The adjustments known so far are largely of an osmotic nature involving changes in (1) quantity and quality of active absorption and excretion of salt and water, (2) surface permeability to salt and water, (3) osmoconcentration and ionic composition of body fluids, (4) tissue tolerance to fluctuations of osmoconcentration and ionic composition of blood, (5) salt and water storage in tissues, and (6) behavior.

In an attempt to classify different degrees of genetic adaptation to salinity, four major groups may be distinguished: (1) Polystenohaline inhabitants of the ocean with its rather constant salinity, (2) euryhaline inhabitants of coastal, estuarine or brine habitats characterized by reduced, fluctuating or extreme salinity, (3) oligohaline inhabitants of fresh water and (4) holohaline inhabitants of sea water, brackish water and fresh water.

(1) Polystenohaline species are osmoconformers with ion and volume regulation but little or no osmoregulation; examples are: Maja verrucosa, Hyas araneus, Cancer antennarius, Emerita, Callianassa, Upo- gebia, Speocarcinus, Lophopanopeus, Pagurus and Palmurus (e.g. Duval, 1925; Schlieper, 1929; Schwabe, 1933; Robert- son, 1949, 1960; Gross, 1957a) and presumably most other oceanic Crustacea. Osmoconformers swell rapidly in diluted sea water and gain salts in concentrated sea water. Their blood osmoconcentration is isosmotic to the surrounding medium \( \Delta = -1.9^\circ \text{C} \) and conforms readily to any salinity changes (Krog, 1939).

(2) Euryhaline species have developed a reduced permeability of gills and carapace to water and salt as well as improved mechanisms for differential absorption and excretion of ions; examples are: Carcinus maenas (e.g. Duval, 1925; Schlieper, 1929; Nagel, 1934), Rhithropanopeus harrisi (Kinne and Rotthauwe, 1952), various species of Gammarus (e.g. Widmann, 1935; Beadle and Cragg, 1940a; Kinne, 1952; Wernitz in Prosser and Brown, 1961), Palaemonetes, Palaemon, Penaeus, Metapenaeus (Panikkar, 1939, 1940a, b, 1941a, 1950), Crangon (Broekema, 1941), Artemia (Crogan, 1958b), Uca, Pachygrap- sus (Jones, 1941; Prosser et al., 1955; Gross, 1955, 1957a; Green et al., 1959), Ocypode (Flemister and Flemister, 1951), Hemigrapsus (Gross, 1955), Helocicus, Leptograpsus (Dakin and Edmonds, 1931; Edmonds, 1935) and Birgus (e.g. Gross, 1955, 1957a). On the basis of their osmo- regulative performance, these euryhaline species can be subdivided into two groups:
the hyperosmotic regulators which are hyperosmotic in diluted sea water but more or less isosmotic in higher salinities (e.g. *Carcinus*, *Rhithropanopeus*, *Gammarus* (Fig. 8) and the hyper-hypo-osmotic regulators which are hyperosmotic in diluted sea water as well as hypoosmotic in higher salinities (e.g. most shore shrimps, brine shrimps and semi-terrestrial and terrestrial crabs) (Fig. 8). Hyporegulation is always correlated with hyperregulation suggesting that hyper-hypo-regulation is indicative of

Fig. 8. Blood osmoconcentration as function of salinity (fresh water to double strength sea water) in euryhaline Crustacea. Hyperosmotic regulators: amphipod *Gammarus* (from Kinne, 1952), and brachyure *Rhithropanopeus* (Kinne and Rotthauwe, 1952); both had been acclimated to the respective salinities for several weeks at temperatures between 20° and 21°C. Hyper-hypoosmotic regulators: land crab *Uca* (Jones, 1941), shore shrimp *Crangon* (Flügel, 1959), and brine shrimp *Artemia* (Croghan, 1958b); all three had been acclimated to the respective salinities for at least 2 days, *Uca* at 17°-18°C, *Crangon* at 15°C and *Artemia* at 18-24°C. Blood osmoconcentration may change significantly with temperature.
an advanced stage of genetic adaptation to fluctuating or extreme salinities. Hyper-hypo-regulation is found also in sea water-inhabiting insects and represents presumably the most elaborate genetic adaptation to osmotic stress within the invertebrates.

(3) Oligohaline species inhabit fresh water and are characterized by a well developed hyperosmotic regulation meeting the osmotic requirements for life in very dilute media. Usually their osmoregulatory mechanism collapses in salinities above 5 to 10‰; examples are: Potamon (Schlieper and Herrmann, 1930; Shaw, 1959), Palae-monetes antennarius (Parry, 1957), Gam-marus pulex, Gammarus lacustris (Lockwood, 1961) and presumably most other freshwater living crustaceans (Fig. 9).

Fig. 9. Blood osmoconcentration as function of salinity in oligohaline Crustacea; Potamon (from Duval, 1925; Schlieper and Herrmann, 1930), Astacus (Herrmann, 1931; Beadle, 1943), Gammarus (Beadle and Cragg, 1940a), Daphnia (Fritzsche, 1917), and in the holoeuryhaline crab Eriocheir (Scholles, 1933). Details on acclimation period and temperature are mostly not available.
Genetic adaptations to life in fresh water include: very low surface permeability to water and salt, active salt absorption by gills, reduction of normal osmoconcentration of body fluids, salt reabsorption, water expulsion and accumulation of food and salt in the egg, making the species more independent of the medium during its most critical stage. Gaining the ability of perfect hyperregulation apparently goes hand in hand with losing the ability to adjust to increasing salinities.

(4) Holoerythaline species are rare and poorly investigated. They inhabit sea-, brackish- and fresh water, migrating as individuals from one medium to the other, or establishing populations in all three media. The best investigated example is the crab *Eriocheir sinensis* (Scholles, 1933; Schwabe, 1933; Schlieper, 1935; Krog, 1954) (Fig. 9); another example is its close Indian relative, *Varuna littlerata* (Panikkar, 1950). Adaptation to life in the whole salinity range from fresh water to sea water includes genetic and nongenetic plasticity, exceedingly low surface permeability to water and salt, highly advanced absorption and excretion of salt against steep gradients, and high tissue tolerance to fluctuations in blood osmoconcentration.

The mechanism of hyperosmotic regulation appears to be primarily based on an antagonism between loss of salt from external surfaces and antennary glands, and active salt uptake from the medium. In *Gammarus duebeni*, *G. locusta* and *G. obtusatus* changes in blood osmoconcentration are due to salt movements rather than to water movements (Beadle and Cragg, 1940a). *G. duebeni* is capable of reducing salt loss under conditions of hypoosmotic stress (Shaw and Sutcliffe, 1961). In salinities below 50% sea water, such reduction is accomplished by producing urine which is hypoosmotic to the blood but hyperosmotic to the external medium (Lockwood, 1961) and possibly also by changes in surface permeability (Shaw and Sutcliffe, 1961; Lockwood, 1961). As the salinity is decreased below 50% sea water, *G. duebeni* increases the rate of urine flow (until in fresh water it reaches the equivalent of 70% total body water/day) and decreases its urine concentration. Such adjustments may be achieved within 2 hours, a fact that appears to be important in view of rapid salinity fluctuations to which *G. duebeni* is often exposed in its natural habitat. Blood-hypoosmotic urine is presumably also produced by *G. sad-dachi* and *G. salinus* when they are in dilute media (Lockwood, 1961). In the shore crab *Carcinus maenas*, genetic adaptation to life in reduced salinities includes reduced surface permeability to water and salt, high tissue tolerance to lowered osmoconcentration of body fluids and active salt absorption from the external medium (probably by gills). The most important osmoregulatory organ seems to be the gill. In sea water and brackish water the antennal glands produce urine which is approximately blood-isosmotic; they play no significant part in osmoregulation. Urine output increases with decreasing salinity, and it is assumed that the gills replace such progressive salt loss by a reciprocal increase in active salt absorption (Nagel, 1934).

The mechanism of hypoosmotic regulation is not yet sufficiently investigated to generalize. The most thoroughly analyzed species is the brine shrimp, *Artemia salina*, an anostracan which exhibits pronounced genetic adaptation to life in high salinities (Croghan, 1958a-e). *Artemia* swallows its medium continuously and takes up water from the gut lumen. The osmotic
pressure of the gut fluid is appreciably higher than that of the blood but in more concentrated media is considerably below that of the medium. Regulation occurs in gills (salt balance) and gut (water balance). The ionic ratios of the hemolymph are relatively constant, and very different from those of the medium. Changes in hemolymph osmoconcentration that may occur as salinity is varied, are due more to net movements of NaCl than to water movements. The low osmoconcentration of body fluids, the type of ionic regulation and the low internal Mg concentration resemble conditions found in freshwater animals and have been interpreted as evidence for the freshwater ancestry of brine living forms (e.g. Robertson, 1960). Artemia shows an appreciable degree of permeability, especially in the gut epithelium. It can actively excrete (first 10 pairs of gills) and absorb (probably first 10 pairs of gills and gut) NaCl. The gut has apparently become adapted as a mechanism for active uptake of water, controlling water balance and preventing dehydration in hyperosmotic media (Croghan, 1958b, c, d). These mechanisms are similar to those employed by marine teleosts. Palaemonetes varians and Palaemon longirostris produce rather large amounts of blood-isosmotic urine over a wide range of salinities (Panikkar, 1939; Parry, 1955, 1957); there must consequently be an intensive absorption of salt, particularly in rather diluted media. Pachygrapsus crassipes produces slightly blood-hypoosmotic urine when in a diluted medium, and blood-isosmotic urine when in hyperosmotic sea water (Prosser et al., 1955). By immersing Pachygrapsus crassipes in different salinities containing varying concentrations of Mg, it was shown that the urine Mg concentrations are not a direct function of Mg influx, but rather of water influx. Furthermore, it could be demonstrated that the muscle tissue of P. crassipes swells if the crab is immersed in dilute sea water and shrinks if it is immersed in concentrated sea water. The volume changes of muscles take place at the expense of the blood space; the crab does not change weight (Gross and Marshall, 1960). In Uca pugnax and Uca pugilator kept in 100% and 175% sea water, urine osmotic and electrolyte concentrations are significantly blood-hyperosmotic. The chief sites of entrance of water and salt are the stomach and the gills, and the chief sites of regulation are the antennal glands and the gills with some regulation by the stomach and possibly the midgut gland (Green et al., 1959). Ocypode quadrata reabsorbs water in its antennal glands when in air or in blood-hyperosmotic salinities. It excretes water in its antennal glands and may also excrete chloride when in hypoosmotic salinities. The gill membrane is assumed to function in the reverse way (Flemister and Flemister, 1951). Reabsorption of water in antennal glands has also been demonstrated in the land crab Gecarcinus lateralis (Flemister, 1958). The antennal glands play little or no osmoregulative role in Palaemonetes, Palaemon and Pachygrapsus but may assist in ionic regulation (Pachygrapsus). In the semiterrestrial Uca, however, and in the quite terrestrial Ocypode and Gecarcinus, antennal glands have become progressively capable of reabsorbing water and of excreting salt against the gradient—capabilities that are clearly effective in osmoregulation and that must be considered adaptations to life on land.

Behavioral mechanisms of hypoosmotic regulation have been reported for the land crab Pachygrapsus crassipes which selects suitable salinities if given a choice (Gross,
1957b), for Coenobita perlatus, which varies the frequency with which it visits water of different salinities as well as the time spent in or outside of such waters (Gross and Holland, 1960) and for Birgus latro, which can moisten its respiratory membranes with the help of its appendages and drink water even from small sources (Gross, 1955).

In semiterrestrial and terrestrial crabs it has been suggested that the primary importance of hypoosmotic regulation is an adaptation to evaporation from the branchial chamber, and that regulation against branchial fluids reaching extremely high concentrations by evaporation would prevent the blood from attaining critical osmotic pressure (Jones, 1941). This hypothesis was later rejected, mainly on the grounds that the salt contained in the small volume of branchial fluid (Pachygrapsus) is insufficient to effect a harmful rise in osmoconcentration of body fluids even if it were completely absorbed (Gross, 1955). The fact remains, however, that semiterrestrial crabs may be subjected to extreme osmotic conditions, i.e. rain and extensive evaporation, and that they may have to enter water of deviating salinity even if only for short periods. Hyperregulation then seems to be of adaptive value in conditions of heavy rainfall or other contact with fresh water or water of reduced salinity, and hyporegulation seems to be of adaptive value in meeting osmotic stress endured during submersion in water of high salinity (such submersion also presents a respiratory problem) or during periods of prolonged desiccation, and they may aid in water conservation. In air, gills must be kept moist to facilitate respiration (Krogh, 1919); consequently, they lose water. Excessive water loss from evaporation leads to significantly increased blood osmoconcentration (Jones, 1941; Parry, 1953). Hyporegulation could conceivably be of advantage here in two ways: (1) in facilitating active salt excretion against the gradient and thus compensating to some extent for the increase in osmoconcentration of body fluids, (2) in maintaining a high salinity on the moist gill surface which would lead to a somewhat decreased vapour pressure and hence reduce the rate of evaporation.

With respect to the osmoregulatory mechanism employed by oligohaline species, two groups may be distinguished: the first group produces a more or less blood-isosmotic urine, e.g. Potamon edulis (Schlieper and Herrmann, 1930), Potamon niloticus (Shaw, 1959), Palaemonetes antennarius (Parry, 1957); the second group produces a blood-hypoosmotic urine, e.g. members of the family Astacidae in which the urine has usually only about 10% of the blood osmoconcentration (Robertson, 1960), Gammarus pulex, G. lacustris (Lockwood, 1961) and presumably numerous other freshwater living crustaceans.

The river crab Potamon appears to be rather poorly adapted to life in fresh water: it has a high blood osmoconcentration ($\Delta = -1.1^\circ \text{C}$ to $-1.2^\circ \text{C}$ in $P. edulis$); it is more permeable to water and salts than many other freshwater organisms, and it produces urine, which is practically blood-isosmotic. However, if compared to Carcinus or Eriocheir, it shows an all-around reduction in surface permeability, both to water and salts. Potamon produces only small amounts of urine and actively absorbs sodium and potassium from the external medium (Schlieper and Herrmann, 1930; Shaw, 1959). The shrimp Palaemonetes antennarius has a lower blood osmoconcentration ($\Delta = -0.75^\circ \text{C}$) than Potamon, but loses large amounts of salt via
an almost blood-isosmotic urine ($\Delta = -0.67^\circ$C), which is produced at the rate of about 2% body weight/hr (Parry, 1957). *Palaemonetes antennarius* is not particularly well adapted to its freshwater environment. Not only does it have to use energy in order to compensate for considerable salt losses via diffusion and excretion, but it appears in addition to be limited by a "threshold" Na-concentration in the medium which effectively stops the uptake mechanism below a finite Na-concentration. This "threshold" lies between 0.125 $\mu$m Na/l and 0.183 $\mu$m Na/l. Similar thresholds may exist for other monovalent ions and may attribute to the prawn's discontinuous geographic distribution. The potential difference across the body wall is negative with respect to the inside of the prawn, implying that Cl$^-$ is taken up actively, and Na$^+$ follows passively. Divalent ions may be equally important, since they can seriously affect the permeability of the prawn's surface. A low concentration of Ca$^{++}$ in the medium would, for example, tend to increase cuticle permeability, which in turn would increase urine flow and salt loss, thus forcing the prawn to increase the rate of active salt uptake (Parry, 1961a).

Within the second group, the Astacidae, blood osmoconcentration varies between $\Delta = -0.6^\circ$ and $-0.8^\circ$C (Robertson, 1960). In an external medium of $\Delta = -0.018^\circ$C, the crayfish *Astacus astacus* maintains a blood osmoconcentration $\Delta = -0.81^\circ$C and excretes a very dilute urine of $\Delta = -0.09^\circ$C. In fresh water its urine output amounts to 4% of its body weight per 24 hours (Herrmann, 1931) or to 0.175% body weight/hr (Scholles, 1933). Urine output decreases with increasing salinity, approaching zero in a blood-isosmotic medium (Scholles, 1933). *Procambarus clarkii* compensates for osmotic water inflow in fresh water by excreting blood-hypoosmotic urine at the rate of 5.2% of its body weight per 24 hours (Lienemann, 1938). Under none of the conditions offered in experiments has a crayfish been observed to excrete a completely salt-free urine. A 50 gram crayfish loses 600 mM of Cl$^-$ daily (Prosser and Brown, 1961).

Very low blood osmoconcentrations are found in smaller forms such as *Gammarus pulex* and *Asellus* sp., which have $\Delta$'s of $-0.4^\circ$ to $-0.6^\circ$C (Beadle and Cragg, 1940a; Parry, 1953), and *Daphnia magna* with a $\Delta$ of $-0.2^\circ$ to $-0.3^\circ$C (Fritzsche, 1917). *Gammarus pulex* lacks the capacity to vary its urine concentration (which is present in *G. duebeni*); consequently, in solutions more concentrated than 20 to 30 mM/l, its urine becomes hypoosmotic not only to the blood but also to the medium (Lockwood, 1961). Its main regulatory mechanisms seem to be active ion uptake and differential surface permeability. *Asellus aquatics* is fairly permeable to salt and water, and maintenance of its internal concentration against a gradient of approximately 100:1 must result primarily from replacement of ions from the medium at the same rate as they are lost from the body by diffusion and in urine. Continued maintenance of blood osmoconcentration during 8 days of starvation shows that NaCl loss can, if necessary, be replaced solely by active uptake from the medium, i.e., independent of the food supply (Lockwood, 1959). The freshwater living branchiopod *Triops cancriformis* maintains its blood osmoconcentration by (1) relative surface impermeability, and (2) salt uptake from food. Its osmoregulation breaks down in slightly blood-hypersomotic media (Parry, 1961b). Salt uptake from food has also been demonstrated or sug-
gested in other freshwater crustaceans, e.g. Branchipus (Krogh, 1939) and Chirotecephalus (Panikkar, 1941b).

Beadle and Cragg (1940a,b) have suggested that adaptation to life in fresh water has proceeded by two main stages: (a) Maintenance of a high blood osmoconcentration (as in Potamon) associated with a large blood/tissue Cl gradient; at this early stage sudden increase in salinity can still be tolerated. (b) Evolution of renal salt-reabsorption and lowering of both blood osmoconcentration and blood/tissue Cl gradient to levels more easily maintained (as in Gammarus pulex and most other freshwater species); at this advanced stage higher salinities are lethal. Pearse and Gunter (1957) consider the most essential requirement for permanent establishment in fresh water to be the accumulation of food and salt in the egg, making the species in its most critical stage relatively independent of the medium (see also Pearse, 1950). Once the transition from the sea to fresh water has been achieved, it is seldom reversed. Gaining the ability of perfect hyperosmoregulation apparently goes hand in hand with losing the ability to adjust to changing or increased salinities (e.g. Adolph, 1925).

The main osmotic problems facing an organism migrating into fresh water from the sea or from brackish water are: continuous inflow of water which has to be expelled; paucity of ions which have to be actively absorbed from a very dilute medium and from food; increased variability of the ionic composition of the medium, and of its temperature and chemistry. Adaptations in crustaceans to life in fresh water that have been demonstrated or suggested, include very low differential surface permeability to water and salt, active salt absorption by the gills, reduction of normal osmoconcentration of body fluids, salt reabsorption and water expulsion. More information on extrarenal routes of water expulsion as well as on the regulatory capacities of gills, intestinal tract and antennal (maxillary) glands is urgently needed.

Calculations concerning the thermodynamic work performed in osmotic regulation suggest that the reduction of normal osmoconcentration of body fluids is the principal means of easing osmotic stress in crustaceans migrating into brackish and fresh water, and that production of a hypoosmotic urine affords little advantage to the organism until a salinity well below 17% is reached; in freshwater animals, however, hypoosmotic urine may reduce osmotic work by 80 to 90% (Potts, 1954). These considerations have been criticized by Shaw (1959), pointing out that Potts' calculations are based on the assumption that the outer surfaces are semipermeable, which is not true for several species including Potamon niloticus and Eriocheir sinensis (the latter was used by Potts as an example to illustrate his arguments). According to Shaw (1959) reduced differential surface permeability to water and salts is of greater importance than reduced osmoconcentration of blood or urine. If, on the other hand, reduction in permeability is restricted largely to salts and the animal remains relatively permeable to water, as in Astacus, then the production of a dilute urine or the further reduction in normal blood osmoconcentration would have adaptive value (Shaw, 1959).

Little is known about the mechanism employed by holeuryhaline species. In Eriocheir sinensis blood osmoconcentration was found to be high \( \Delta = -1.1^\circ \text{C} \) to \(-1.2^\circ \text{C} \) in individuals exposed to fresh water, and urine output low (3 to 5 ml/day
in a 60 gram individual). The urine is isosmotic or slightly hyperosmotic to the blood both in fresh water and sea water (Scholles, 1933; Schlieper, 1935), and chloride and ammonia losses are the same whether the excretory pores are open or closed. Metabolic rate remains practically constant in fresh water and sea water (Schwabe, 1933). Salt (NaCl) is actively absorbed from very dilute media by the gills (Schwabe, 1933; Koch, 1954). The existence of a K pump separate from the Na absorbing mechanism has been indicated, suggesting the presence of a similar mechanism as has been reported for larvae of insects, i.e. Chironomus and Aedes (Koch and Evans, 1956a), and various aspects of ionic exchange have been studied (Koch and Evans, 1956b, c). Eriocheir resembles the river crab Potamon in (a) maintaining a high blood osmocentration in fresh water, (b) actively absorbing sodium and potassium, and (c) excreting small amounts of more or less blood-isosmotic urine.

Structural genetic adaptations to salinity have been reported by several authors; however, only a few cases have been worked out in some detail. Most reports refer to size or structure of regulatory organs such as gills, gut and antennal glands. Pearse (1929a, b), for example, has shown that the gills of some estuarine or freshwater crabs are reduced in number or size, leading to a decrease of total area through which exchange diffusion with the diluted medium occurs. And Schwabe (1933) has demonstrated that the nephridial canals are longer in the freshwater living Gammarus pulex than in the brackish-marine Gammarus locusta; these canals have been shown by Peters (1935) to be more highly differentiated in the freshwater Astacus astacus than in the marine Homarus gammarus.

Genetic adaptations to life on land are well documented. The major route of land immigration appears to have been, and still is, from the sea via the littoral zone. Thus terrestrial Crustacea are mostly closer related to marine species than to estuarine or freshwater ones (Vandel, 1943). In spite of a variety of functional and structural adaptations to life on land, crustaceans have “never quite made it,” and are—compared to insects—rather poorly equipped for life on dry land. Even the most successful terrestrial representatives, the isopods, cannot fully exploit the ecological opportunities offered by the terrestrial habitat and must avoid completely terrestrial conditions. In order to be able to occupy their present niches on land, crustaceans did not have to change very much; all successful immigrants were to some extent pre-adapted. The most important pre-adaptations to land life are: (1) the hard exoskeleton, (2) jointed, strong extremities, (3) internal or quasi-internal fertilization, (4) the carapace-covered gill chambers of crabs, and (5) the egg protecting brood pouches of isopods and amphipods.

Our present knowledge on terrestrial adaptations in Crustacea has recently been competently reviewed by Edney (1960). Edney comes to the conclusion that remarkably few profound changes have resulted from assuming the terrestrial way of life, and that even in land isopods, all devices for land life were present in the aquatic ancestor, or if not, are to some degree makeshift. Thus there is no effective protection against surface evaporation (no wax layer in epicuticle); respiration is still accomplished by gills, which have been only slightly modified, and the pseudotracheae are but short bunches of tubes;
the eggs are by no means cleidoic and must be carried by the parent; excretion is still predominantly ammonotelic; osmotic changes are tolerated rather than controlled; and high ambient temperatures are suffered only at the expense of increased transpiration.

Vandel (1943; 1954) has arranged the families of land isopods on the basis of their fitness for survival in dry air in the following order: Ligiidae, Trichoniscidae, Oniscidae, Porcellionidae, Armadillidiidae. As a first approximation, this order seems also to be indicative of the increasing degree of morphological specialization to increasingly drier habitats. We may summarize the most obvious functional genetic adaptations to life on land as follows: (1) increased tolerance to extreme temperature, (2) reduced evaporation, (3) collection of water from small sources and absorption of water against a gradient, (4) active salt secretion, (5) reduction of the total nitrogen excreted per unit weight, and possibly a general suppression of nitrogen metabolism, (6) reduction of total osmoccentration of body fluids, (7) development or improvement of behavioral devices: for selection of suitable microhabitats, for feeding, for controlling extreme body temperature by exposure to conditions which cause different rates of evaporation (humidity, wind), and for orientation, sensory perception, walking and mating.

Let us now finally consider a few structural adaptations to terrestrial life. Bliss (1956) has shown that in Geecrinus lateralis the pericardial sacs are adapted for water absorption, and premolt swelling can occur only when these organs are in contact with a moist substrate. Verhoeff (1917; 1920) demonstrated a series of water conducting channels in Oniscus and other advanced land isopods, which run along externally on both sides of the body from head to uropods, with cross channels on the pereion. This capillary system can pick up water from the substrate via the apposed uropods and conduct it to the respiratory surfaces on the pleopods. If no free water is available, regurgitated fluid may be conducted from the mouth to the pleopods to keep the respiratory surfaces moist (Edney, 1960). Some shore and land isopods are able to roll themselves into balls, e.g. Sphaeroma, Armadillidium and Tolypeutes. Such rolling protects the softer, appendage-carrying subsurface from potential enemies and may also reduce water loss in dry habitats; it is often accompanied by a relocation of eggs from the external brood pouch into internal brood sacs (Hansen, 1905; Kinne, 1954).

The gill has undergone several modifications in terrestrial species: (1) it has received additional support by sclerotization and ridges (van Raben, 1934); (2) its functional surfaces have been reduced (Ayers, 1938; Gray, 1953; Pearse, 1929a, b, 1950); and (3) its external surfaces are continuously moistened. Uca and Ocypode have special respiratory openings between their third and fourth legs (Edney, 1960). Land isopods use the same structures for respiration as their aquatic ancestors, the pleopods. These show, however, definite adaptations to air breathing in more terrestrial species (Modlinger, 1931): the semiterrestrial Ligiidae and Trichoniscidae have still unmodified pleopods; Oniscidae have the exopodites of their pleopods hollowed out below; Porcellionidae and Armadillidiidae possess hollow tuft-like invaginations known as pseudotracheae which facilitate respiration in air of reduced humidity.

The most profound respiratory adap-
tations to land life are the vascular tufts and the vascularization of gill chamber walls in *Ocypode*, *Coenobita* and *Birgus* (Harms, 1932; van Raben, 1934). Both are developments *de novo*.

With respect to the topic of this conference—Evolution of Crustacea—the facts and brief considerations that I have presented here demonstrate two things:

1. They illustrate important relationships between environmental factors and organismic functions and structures, which promise to provide useful tools in an attempt to analyse and understand the forces at work and the biological mechanisms involved in evolutionary processes.

2. They show that our present knowledge of nongenetic and genetic adaptations to temperature, salinity and to life on land cannot explain the substantial macroevolutionary differences of crustacean body plans which we witness today.

Macroevolutionary changes are presumably based on adaptations to conditions that were effective before the first crustaceans began to leave their oceanic home. They may represent adaptations, for example, to the different feeding habits of hunters and lurers, substrate- and filter feeders and to differences in modes of locomotion and habits in pelagic, benthic, sessile, vagile, epizoic and endopsammic forms (e.g. Kaestner, 1959). Some macroevolutionary differences in structure may turn out to be based on random variations with more or less neutral adaptive value, or to be incidental by-products of primarily functional adaptations.

It will certainly be a long and difficult task to bring to light the complex and manifold relationships between environment and organism in such a large and heterogeneous group as the Crustacea.

And it is to be hoped that the modern studies of nongenetic and genetic adaptation—both at the functional and at the structural level—will produce useful, complementary means for opening up additional avenues for a new, comprehensive and dynamic approach to an old, fundamental problem of biology, the problem of evolution.

**SUMMARY**

A brief review is presented of our present knowledge of nongenetic and genetic adaptation in Crustacea (mostly macro-crustaceans) to temperature, salinity and life on land. Some of the adaptations reported are universal among animals, for example, functional adaptations to temperature involving shiftings of lethal limits, changes in activity or in metabolic rates. Other adaptations appear to be related to specific crustacean features, i.e. their primarily aquatic way of life, respiration through gills, urine formation in antennal or maxillary glands, exoskeleton and body shape—for example, the different mechanisms involved in osmoregulation, respiratory adaptations and adaptations to life on land. Important relations are illustrated, between environment and function or structure, which promise to provide useful tools in an attempt to analyse and understand the forces at work and the biological mechanisms involved in evolutionary processes. Macroevolutionary differences in structure cannot be explained on the basis of the outlined adaptations to temperature, salinity and land life. They are assumed to be based on differences in feeding, respiration and locomotion, to represent incidental by-products of primarily functional adaptations, or random variations with rather neutral adaptive value.
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KINNE: ADAPTATION


IV

On the Relationship of Dromiacea, Tymolinae and Raninidae to the Brachyura

By

Isabella Gordon

British Museum (Natural History), London

In 1950 I described in some detail the spermathecae of females belonging to species of the families Dromiidae and Thelxiopidae (= Homolidae), and showed how the male intromittent organs were adapted to suit these two kinds of spermathecae. I did not at that time discuss the relationship of the Dromiacea to the brachyuran crabs, because it was my intention to continue the study of other crab-like forms that are often referred to the Brachyura. This work, however, was delayed, partly because of other commitments, partly for lack of certain essential material. As mentioned by Balss (1957, p. 1616), I found in the Raninidae a special kind of unpaired female spermathecal opening or pit, quite different from the paired ones of Dromiidae or Thelxiopidae. Quite recently I obtained some material of the so-called Tymolinae which enabled me to examine the sternal furrows in the female, structures that are absent in females of the supposedly related subfamily Dorippinae. I hope ere long to publish a detailed account of these spermathecae; here I can only deal with some of them briefly.

TYMOLINAE

In Figure 10A the thoracic sternum of a female of Tymolus japonicus Stimpson is represented, tilted so that the almost vertical posterior sternites are seen. In true ventral aspect, most of the sternum behind the ridges (r) on sternites 5 is not visible. In the tilted position, however, the sternal furrows are obvious; they resemble rather closely those of the family Dromiidae. But the large spermatophores, or spermatophoral masses, visible through the thin sternal wall, are situated near the spermathecal openings (Fig. 10A, j, o and s). As in Dromia, these sternal furrows in the female are just the 7/8 sutures carried forwards and anteriorly modified; the papillae on which the spermathecal openings are placed are situated on a level with the sockets for peraeopods 2 and thus well in front of the genital openings on the coxae of peraeopods 3. In this tilted position, the coxae of peraeopods 4 and 5 are also visible (Fig. 10A, p4 and p5). I have been able to confirm the presence of very similar sternal furrows in the now fragmentary female syntype of Xeinostoma cuchear Stebbing. In the genus...
Fig. 10. A. *Tymolus japonicus* Stimpson, ♀ from Manazuru, Japan; thoracic sternites tilted to show the almost vertical posterior ones and the sternal furrow (f) ending distally in the spermathecal opening (o). B. *Cynomonus granulatus* Norman, left thoracic sternites of ♀, slightly tilted, to show oval area (o) at the spermathecal opening. Abbreviations: 1-8, thoracic sternites; g, genital opening on coxa of peraeopod 3; r, ridge on sternite 5; p1-p5, coxae of peraeopods 1 to 5; s2, socket for peraeopod 2; s, indicates position of the spermatophore.

*Cynomonus*, on the other hand, the thoracic sternum is bent much less abruptly than in *Tymolus* and the large oval areas that indicate the spermathecal openings are visible in ventral aspect. In Figure 10B, however, the specimen is tilted so that sternites 7 and 8 are seen more completely. Here the 6/7 suture runs across the full width of the thorax; thus the 7/8 suture is shorter than in *Tymolus*, ending opposite the coxa of peraeopod 3, but still in front of the genital opening on that coxa. Only the distal half of the 7/8 suture forms the spermatheca, the position of which is indicated by a distinct bulge on sternite 8; the sutural margin of sternite 8 overlaps that of sternite 7, as shown in Figure 10B. The spindle shaped area (o) presumably belongs to sternite 7 and the entrance to the spermatheca is along its posterior edge. The position of the relatively small spermatophoral mass is indicated by a broken line (s, Fig. 10B). This type of spermatheca is reminiscent of that found in the Thelxiopidae.

There seem to be, within the so-called Tymoliniae, two different kinds of spermathecae. When the intromittent organs of the male are examined (Figs. 11A and 11B), they differ chiefly as regards the apex of pleopod 2. In *Cynomonus* and in *Tymolus* there is a large penial projection on the coxa of peraeopod 5; the terminal segment of pleopod 1 (= the endopod) is a hollow, folded, leaf-like structure; pleopod 2 is large in both. But the apex of the last segment (= the endopod) resembles a hypodermic needle in *Tymolus* (2a, Fig. 11A); in *Cynomonus* it is like the sole of a boot (apex of 2, Fig. 11B). In *Tymolus* only the needle-like tip of
pleopod 2 probably enters the small opening of the female spermatheca and the seminal fluid is probably poured into the spermathecal sac. In *Cymonomus*, pleopod 2 probably acts as a sort of piston, the "sole" pushing aside the spindle-like flap to place a spermatophore in the spermathecal pocket. At least that is how I interpret these structures. This fits nicely with Ihle’s subdivision of the “Tymolinae” into two tribes *Cyclodorippae* and *Cymonomae* (Ihle, 1916, p. 154). Since *Cyclodorippe* is a synonym of *Tymolus* the tribe should be called Tymolae.

**RANINIDAE**

In the Raninidae the thoracic sternites are specially modified, presumably in connection with their burrowing habits. Figure 12A represents the thoracic sternites of a very immature female of *Ranina ranina* (L.), carapace length 63 mm. Owing to the fact that the sternum bends abruptly upwards, at an angle of nearly 90°, in the region of the genital or sixth somite, the posterior part is foreshortened. Sternites 8 are not visible because the last pair of pereaeopods are dorsal and somewhat anterior to pereaeopods 4. The separate figure of sternites 7, at the same scale, gives a better idea of their length although the portion behind the articulation of pereaeopods 4 is still foreshortened. Even at this immature stage sternites 7 can be distinguished from those of a male because of the median depression in the anterior half, which indicates an incipient spermathecal opening. In the adult female this single spermathecal pit is very conspicuous (Fig. 12B). It is situated in the anterior half of sternites 7 behind the small genital openings on the coxae of pereaeopods 3.

The single spermathecal opening is even more conspicuous in the much smaller species *Notopoides latus* Henderson (Fig.
Fig. 12. *Ranina ranina* (L.), ♀. A. Thoracic sternum of a very immature specimen (carapace length = 63 mm.). B. Thoracic sternites 7 and 8 of an adult (carapace length = 138 mm.), to show the large spermathecal opening (so). Abbreviations: 1-8, thoracic sternites 1 to 8; c4, c5, coxae of pereaeopods 4 and 5; p2-p4, sockets for pereaeopods 2 to 4; g, genital opening on third coxa.

On dissection, I found that the spermathecal pit leads obliquely backwards and inwards to a spermathecal pocket (s) enclosed in part of the endophragmal skeleton. The endophragmal system of a raninid differs strikingly from that of a typical brachyuran crab such as *Maja squinado* (Herbst)—compare Figures 13B and 14B. One of the peculiarities of *Notopoides* is the very high median apodeme arising from the median suture of sternites 6 and 7, respectively. In a male of *Notopoides* the apodeme arising from sternites 7 is similar to that arising from sternites 6 (see Bourne, 1922, pl. 4, fig. 9 of *Ranina*); in the female, however, part of apodeme 7m is modified to form the spermathecal pocket and the passage leading to it (s, so, Fig. 13B). The male intromittent organs are also modified in a special way, pleopods 1 being fused basally and the free portions being relatively slender and closely apposed so that both can enter the single spermathecal opening.
Fig. 13. *Notopoides latus* Henderson, ♀ syntype. A. Posterior almost vertical portion of thoracic sternum, to show the large spermathecal opening (so) on sternites 7. B. Posterior part of endophragmal system of same, in median aspect. Abbreviations: g, genital opening of coxa on pereopod 3; p4, p5, sockets for pereopods 4 and 5; 5m-7m, median apodeme from sternites 5 to 7; s, spermathecal pocket.

**BRACHYURA**

*Maja squinado* (Herbst): This common spider-crab may be taken as an example of a typical brachyuran crab. The endophragmal system has been described and figured by Drach (1939, pp. 369-373). The thoracic sternites of the female are much broader than those of the male and all are visible in ventral aspect (Fig. 14A). The genital opening is sternal, situated on sternite 6 just behind the 5/6 suture line. The posterior part of the endophragmal system of the same female is represented in median aspect in Figure 14B. The *sella turcica* or turkish saddle (ts) with its wing-like extension (w), and the way in which the five posterior endopleurites above and the four posterior endosternites below (4/5-7/8) are all conjoined, give great strength to the whole. The vagina lies in the space between endosternites 5/6 and 6/7 but it and its spermathecal portion (s) are quite free, not incorporated in any part of the endoskeleton.

**DISCUSSION**

The division of one family Dorippidae into "Dorippidae sternitremente" (Dorippinae) and "Dorippidae peditremen" (Tymolinae) has always seemed odd to me. Because, if the Decapoda are taken as a whole,¹ all the Natantia and many of the Reptantia are "peditremen" (with genital opening coxal in the female). It is only in the Brachyura

¹ The classification in Balss (1957) may be taken as the latest, though Balss was ultra conservative in places.
that a few families and subfamilies are "peditremen," all the rest being "sternitremen," with the female genital opening sternal. The "peditremen" forms among the Brachyura are the Dromiacea, the Raninidae and the Tymolinae, and, as I have shown, it is these that possess various kinds of spermathecae in the formation of which the endophragmal system is involved. To me it seems logical to exclude all these from the true Brachyura, restricting the term to the vast majority of crabs with the female genital openings sternal (the "Decapoda sternitremen"). In 1922 Bourne made a careful study of various raninids and separated them from the Oxystomata, placing them in the new superfamily Gymnopleura. Previous workers like Boas, and Milne Edwards and Bouvier also thought the raninids were not related to the Oxystomata. The discovery of a special, unpaired spermathecal pit leading to a spermathecal pocket in the endophragmal system, together with the specialisation of the male pleopods, fully supports Bourne's conclusion and justifies the term Gymnopleura. I do not know why Bourne missed the conspicuous spermathecal pit, but the abdomen and the pleopods have to be turned right back in order to see it. He happened to dissect a male Ranina for the endophragmal system (Bourne, 1922, pl. 4, fig. 9).

Certainly the so-called Tymolinae with sternal furrows and coxal genital pores should not be placed in the same family as the dorippids without sternal furrows and with the genital openings of the female sternal. The tymolids should at least be placed in a separate family, Tymolidae;

Fig. 14. Maja squinado (Herbst), ♀. A. Right thoracic sternites 1 to 8, with genital opening (g) on sixth sternite. B. Posterior part of endophragmal system of same, in median aspect. Abbreviations: 4/5-7/8, endosternites 4 to 7 arising from the sutures between the sternites indicated; s, spermathecal part of vagina; ts, sella turcica; w, wing of sella turcica.
their true place in the classification is with or near the Dromiacea. All the females of Tymolidae that I have examined have been in poor condition and the endophragmal system is either poorly or not at all calcified, at least in the region of the spermathecae. The internal structure of the spermathecae has been studied as far as the imperfect condition of the material allowed, and will be described more fully elsewhere. If the “Tymolinae” are given family rank, then Ihle’s two tribes become the subfamilies Tymolinae and Cymonominae. If the term Brachyura is restricted to the eminently successful “Decapoda sternitremen” and the Dromiacea, Gymnopleura and Tymolidae placed where they belong in the “Decapoda peditremen,” the term Anomura will probably have to be abandoned. At present it is in Monod’s words simply a “rag bag” into which is thrown an assortment of superfamilies and families that do not fit in anywhere else. Our knowledge of the endophragmal system of the Decapoda is still fragmentary and imperfect. Drach (1950) has pointed out that it is present in the Decapoda Natantia, contrary to what is generally supposed. He also thinks that the Eryonidea should be excluded from the Palinura because their endophragmal system proves to be of a different kind, much more primitive. He also says that the homolids (Thelxiopidae), homolodromiids and “certain raninids” differ as regards endophragmal system from the rest of the Brachyura. Much work has still to be done before we can arrive at a satisfactory classification of the Decapoda.

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V

The Pericardial Sacs of Terrestrial Brachyura

By

Dorothy E. Bliss

The American Museum of Natural History
New York, N.Y.
and
The Albert Einstein College of Medicine
New York, N.Y.

INTRODUCTION

Associated with the evolution of terrestrial life in brachyuran crustaceans are striking modifications in their physiology and morphology, particularly of their respiratory organs. Due to greater curvature, the branchial chambers grow more capacious. They become either partially or completely filled with air. Vascular channels appear in the membrane that lines the branchial chambers, with branchial tufts arising from the membrane in some forms. The vascularized membrane and tufts may serve as respiratory structures. Gills become fewer in number and reduced in volume and surface area, these modifications being possible because of the greater amount of oxygen per unit volume in air compared with that in sea water. With less surface then available for respiratory exchange, the loss of water through the gills is reduced.

No single species necessarily displays all the modifications just enumerated. The ghost crab, Ocypode quadrata (Ocypodi-
the degree of activity characteristic of each animal affects such results. An active marine crab like the blue crab, *Callinectes sapidus*, maintains a higher basal metabolic rate than does a sluggish marine form like the spider crab *Libinia*, and may have a rate comparable to that of an intertidal form like *Panopeus*—but nevertheless not as high as that of the active terrestrial crab *Ocyopode quadrata* (Vernberg, 1956).

These and various other features of terrestrial crabs have been reviewed by Pearse (1929a, 1929b), Edney (1960), and Wolvekamp and Waterman (1960). Detailed studies on the osmotic concentrations of the blood in terrestrial crabs have been made by Pearse (1934), Jones (1941), Gross (1955), Flemister (1958), Green *et al.* (1959), Gross and Holland (1960), and Dehnel (1962). One adaptive feature of land crabs that seems not to have been investigated, however, is the greater development of the pericardial sacs. A discussion of these important organs follows.

**GROSS ANATOMY**

The first published account of the pericardial sacs to come to the attention of the writer is that of Milne-Edwards (1834) who noted in decapod crustaceans the existence of a spongy, whitish organ extending on both sides of the body from the posterior portion of the branchial cavity to the beginning of the abdomen. Milne-Edwards described the organs as enveloped in a fold of the tegumentary membrane and resting on the flanks (thoracic epimera).

Cuénot (1891) appears to have been next to study the pericardial sacs. In *Maja* and *Carcinus* he remarked particularly on the relationship of these organs to the heart, which they partially surround, and on the adherence of their internal border to the overlying pericardial membrane and to the adjacent calcified endoskeletal wall. He also noted that they contract sharply if pricked with a needle, that they contain whitish, pulpy material, and that their external border is free. He emphasized that the pericardial sacs are external in the same way as are the gills, that is, both types of organs are bathed by the external medium. Subsequently, Cuénot (1893) reported pericardial sacs to be present in all brachyurans and, in reduced form, in Palinurids, galatheids, and some pagurids. He noted their absence from other macrurans, including crayfish.

In a classic monograph on *Cancer*, Pearson (1908) pictured and described the pericardial sacs, which he termed "pericardial pouches." He found each sac to be covered with a cuticle that constitutes an extension of the chitinous wall of the branchial chamber and to have a cavity continuous with the pericardial sinus. The cavity, he said, is broken up by connective tissue cells and muscle fibers.

The pericardial sacs of three species of terrestrial crabs appear in Figures 15-17, those of two species of marine crabs in Figures 18, 19. In the marine form *Callinectes sapidus* Rathbun (Fig. 19), the pericardial sacs are narrow, elongate, and pouch-like. They lie on the flanks (thoracic epimera) just posterior to the tips of the gills, which barely overlap them. In *Cancer borealis* Stimpson, also a marine crab (Fig. 18), the gross structure of the pericardial sacs and their relationship to other organs differ little from *Callinectes sapidus*. In *Cancer borealis* the pericardial sacs are likewise narrow, attenuated, and pouch-like; they
Figs. 15-19. Figs. 15-17, pericardial sacs of land crabs: 15. Geocarcinus lateralis. 16. Caridoma guanhumi. 17. Ocypode quadrata. Figs. 18, 19, pericardial sacs of marine crabs. 18. Cancer borealis. 19. Callinectes sapidus. Only male crabs are shown. Abbreviations: A, heart; E, posterior extension of the pericardial sac; F, flanc; G, gill; L, flap (anterior prolongation of the first abdominal segment); M, folded arthrodial membrane; O, stomach; P, pericardial sac; S, external tuft of setae; V, vas deferens. In all cases the midgut gland has been removed, as have also the mastigobranch of the first maxilliped and a portion of the gills on the right side.
too lie on the flanks and are overlapped only slightly by the gills.

In the terrestrial crab *Ocypode quadrata* (Fabricius) (Fig. 17) an outward extension of the pericardial sacs has occurred, with the result that the lateral tip lies far out on each flanc. The tip, nevertheless, is pointed rather than broad and there is little overlap of the pericardial sacs by the gills.

The same sort of lateral extension of the pericardial sacs occurs in *Cardisoma guanhumi* Latreille (Fig. 16). However, the lateral tip, although still attenuated, has penetrated farther into the branchial chambers. Furthermore, a new feature is apparent in *Cardisoma guanhumi*. There has occurred a posteroverentral extension of each pericardial sac towards the ventral surface of the abdomen. The tip of each extension bears setae which lie close to the many external setae that border the abdomen.

The most extensive modifications of the pericardial sacs have occurred in *Gecarcinus lateralis* (Fréminville) (Fig. 15). Laterally the pericardial sacs not only extend far out on the flanks and well into the branchial chambers but each lateral extension terminates in a broad expanded lobe. As a result the gills overlap the pericardial sacs extensively.

Posterovertrally in *Gecarcinus lateralis*, as in *Cardisoma guanhumi*, an extension of the pericardial sacs has taken place. The tip of each posterovertral extension is fringed with setae which lie in close proximity to an external group of setae situated on the lateral edges of the first three abdominal segments (Figs. 15, 20).

Perhaps the most striking modification in *Gecarcinus lateralis* is the extensive development of the arthrodistal membrane that links thorax and abdomen. In this crab the membrane is both sturdy and voluminous. It stretches in folds across the medial region between the two pericardial sacs and over the sacs themselves (Fig. 15). It is firmly attached to the movable chitinous flap that constitutes an anterior prolongation of the first abdominal segment. In effect the membrane forms an extensible chitinous bag within which the pericardial sacs lie protected. As the pericardial sacs swell during premolt water uptake in *Gecarcinus lateralis*, the arthrodistal membrane unfolds and the “bag” expands enormously (Fig. 24).

Reference to Figures 15-19 leaves little doubt that the pericardial sacs of the three terrestrial species of crabs are larger than those of the two marine species. Furthermore, the pericardial sacs of *Gecarcinus lateralis* seem to be more extensively developed than are these organs in *Cardisoma guanhumi* and *Ocypode quadrata*. Yet it is rather unsatisfactory to base conclusions on gross observation alone when quantitative data can be obtained. Therefore, the surface area of the pericardial sacs in the five species of crabs was determined with a Compensating Polar Planimeter (Keuffel and Esser Co., number 4236). Results appear in Tables 2-4. Because *Cancer borealis* was not always available, the surface area of the pericardial sacs of *Cancer irroratus* Say also was determined. Morphologically the two species are similar.

It was not always possible to obtain and dissect the crabs in the live state, hence some of the data of Table 2 are expressed in terms of fixed weight. In every case the crab was blotted and drained of preservative (70% ethyl alcohol) before it was weighed. For *Gecarcinus lateralis* the ratio of fixed weight to live weight is approximately 0.9.
All data of Table 2 concern pericardial sacs that either have been taken from already preserved crabs or have been removed from fresh crabs and then fixed for 24 hours in 70 per cent ethyl alcohol. The amount of shrinkage that a fresh pericardial sac undergoes during fixation varies with species. For 12 specimens of *Gecarcinus lateralis* the fixed pericardial sacs have a mean surface area that is approximately 70 per cent that of the fresh sacs. Yet for two specimens of

![Diagram](image)

**Figs. 20, 21.** 20, ventral aspect of *Gecarcinus lateralis* with portions of the abdomen and the carapace cut away to show the posterior extension (E) of the left pericardial sac, the setae at its tip, and the setae-lined channel (C). One external tuft of setae (S), on the opposite side of the abdomen, also is shown. Abbreviations: N, abdomen; V, vas deferens; D, left first pleopod. 21, ventral aspect of a female specimen of *Ocypode quadrata* showing the external row of setae at the base of the second and third walking legs when the legs have been separated (left arrow), and when the legs are in normal resting position (right arrow).
TABLE 2
THE SURFACE AREA OF FIXED PERICARDIAL SACS

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Carapace Width (cm)</th>
<th>Weight (g.)</th>
<th>Surface Area of Pericardial Sacs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>mm²/cm. carapace width</td>
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<td>58.9</td>
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<td>47.9</td>
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</tr>
<tr>
<td></td>
<td>♂</td>
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<td>52.3</td>
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</tr>
<tr>
<td></td>
<td>♀</td>
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<td>4.31</td>
<td>29.8</td>
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<td></td>
<td>♂</td>
<td>4.16</td>
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<td>173.9</td>
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<td>♂</td>
<td>14.11</td>
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</tr>
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<td>borealis</td>
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</tr>
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<td>190.0</td>
<td>30.9</td>
</tr>
<tr>
<td></td>
<td>♂</td>
<td>11.17</td>
<td>185.0</td>
<td>31.8</td>
</tr>
</tbody>
</table>

1 For G. lateralis, Callinectes sapidus, Cancer borealis, and last 2 specimens of Cancer irratoratus, live weight is given; for C. guanhumi, O. quadrata, and first specimen of Cancer irratoratus, fixed weight is given.
Cancer irroratus, one of Cancer borealis, and eight of Callinectes sapidus, the surface area of the fixed pericardial sacs averaged 83 per cent that of the fresh sacs.

Body weight is a good basis on which to make comparisons of surface area of the pericardial sacs in various species, provided all the species in question have approximately the same mass of exoskeleton. Body weight is not a good basis for making such comparisons if one species has a light, fragile exoskeleton and a second species has a heavy, sturdy one, for the body weight of the second species will include much more inert skeletal material than will the body weight of the first species. Thus in Table 3 the mean surface area per gram body weight as calculated for the pericardial sacs of Gecarcinus lateralis, Cardisoma guanhumi, Callinectes sapidus, and the two species of Cancer decreases in the order given. Yet in the midst of this series lies Ocypode quadrata with what appears to be an aberrantly high value. O. quadrata possesses a very light, fragile exoskeleton, whereas the other five species have firm, heavy shells. In O. quadrata abnormally high values for surface area of the pericardial sacs on a weight basis may be attributed, at least in part, to the fact that the body weight of this crab does not include the weight of considerable inert skeletal matter, whereas the body weights of the other five species do.

For closely related species of comparable body form (e.g. Gecarcinus lateralis and Cardisoma guanhumi) or for different individuals within the same species, carapace width is a good basis for comparison. Thus, in Table 2 the surface area of the pericardial sacs per gram body weight for Cardisoma guanhumi is approximately the same regardless of size, and therefore age, of the individual crab. Yet on the basis of carapace width there is evident an increase in surface area of the pericardial sacs with increasing size of crab. For this species, because of the considerable increase in body weight with age, carapace width is the more valid basis on which to make intraspecific comparisons.

In the case of Gecarcinus lateralis, on the contrary, aging leads to no marked increase in size of claws nor in weight of exoskeleton. Hence body weight and carapace width are equally valid criteria on which to base intraspecific comparisons. With either unit of measurement,

<table>
<thead>
<tr>
<th>TABLE 3</th>
<th>MEANS AND STANDARD ERRORS FOR SURFACE AREA OF FIXED PERICARDIAL SACS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species of crab</td>
<td>Number in Sample</td>
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<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Gecarcinus lateralis</td>
<td>11</td>
</tr>
<tr>
<td>Cardisoma guanhumi</td>
<td>6</td>
</tr>
<tr>
<td>Ocypode quadrata</td>
<td>7</td>
</tr>
<tr>
<td>Callinectes sapidus</td>
<td>9</td>
</tr>
<tr>
<td>Cancer borealis and Cancer irroratus</td>
<td>5</td>
</tr>
</tbody>
</table>

1 Original data on which this table is based appear in Table 2.
G. lateralis shows no consistent variation in surface area of its pericardial sacs with age—or with sex (Table 2).

In individuals of comparable size and with carapace width as a basis for comparison, the surface area of the pericardial sacs in Gecarcinus lateralis is greater than that of the corresponding organs in Cardisoma guanhumi (Table 2). Yet because of the increase in size of pericardial sacs per centimeter carapace width that occurs with age in C. guanhumi, the difference in surface area per centimeter carapace width between the samples of G. lateralis and C. guanhumi is not statistically significant (Table 4). On the basis of body weight there is a statistically significant difference; nevertheless, this must be discounted because of the disproportionate increase in size of the claws and in weight of exoskeleton that occurs in older C. guanhumi.

Therefore, we are forced to base our conclusions regarding these two species on values for individuals of comparable size (Table 2). Then we find that the surface area of the pericardial sacs is greater in Gecarcinus lateralis than in Cardisoma guanhumi.

On the basis of carapace width (which is the more valid for the following comparisons), there is a statistically significant difference in mean surface area of the pericardial sacs between Gecarcinus lateralis and Ocypode quadrata, and also between Cardisoma guanhumi and Ocypode quadrata (Table 4). The existence of a significant difference in the surface area of these organs when Ocypode quadrata is compared with the three marine species

<table>
<thead>
<tr>
<th>TABLE 4</th>
<th>VALUES FOR t AND P FOR MEAN SURFACE AREAS(^2) OF FIXED PERICARDIAL SACS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Per centimeter carapace width</td>
</tr>
<tr>
<td></td>
<td>t</td>
</tr>
<tr>
<td>G. lateralis and C. guanhumi</td>
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</tr>
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<td>G. lateralis and O. quadrata</td>
<td>9.5</td>
</tr>
<tr>
<td>G. lateralis and C. sapidus</td>
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</tr>
<tr>
<td>G. lateralis and C. borealis + C. irroratus</td>
<td>7.8</td>
</tr>
<tr>
<td>C. guanhumi and O. quadrata</td>
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</tr>
<tr>
<td>C. guanhumi and C. sapidus</td>
<td>4.0</td>
</tr>
<tr>
<td>C. guanhumi and C. borealis + C. irroratus</td>
<td>2.4</td>
</tr>
<tr>
<td>O. quadrata and C. sapidus</td>
<td>0.52</td>
</tr>
<tr>
<td>O. quadrata and C. borealis + C. irroratus</td>
<td>0.23</td>
</tr>
<tr>
<td>C. sapidus and C. borealis + C. irroratus</td>
<td>0.89</td>
</tr>
</tbody>
</table>

1 Original data on which this table is based appear in Table 2, means and standard errors in Table 3.
2 A difference in mean surface area is considered significant if P < 0.05, highly significant if P < 0.01.
of crabs is highly questionable. There appears to be a significant difference on the basis of body weight but not on the basis of carapace width. As a matter of fact, neither body weight nor carapace width is a good basis for comparison when *Ocypode quadrata* is being compared with *Callinectes sapidus* and with the two species of *Cancer* because of the great differences in amount of inert skeletal material and in body form. Thus there are no reliable data from which to draw conclusions regarding the surface area of the pericardial sacs in *Ocypode quadrata* as it compares with that of the pericardial sacs in the three marine species of crabs.

In summary we can say: (1) that on the basis of both body weight and carapace width the surface area of the pericardial sacs in the terrestrial species *Gecarcinus lateralis* and *Cardisoma guanhumi* is significantly greater than that of the pericardial sacs in the three marine species *Callinectes sapidus*, *Cancer borealis*, and *Cancer irroratus*; (2) that on the basis of individual values for specimens of comparable size (the best basis for this comparison) the surface area of the pericardial sacs of *Gecarcinus lateralis* is greater than that of the pericardial sacs of *Cardisoma guanhumi*; (3) that on the basis of carapace width (the best basis for this comparison), the surface area of the pericardial sacs in *Gecarcinus lateralis* and *Cardisoma guanhumi* is significantly greater than that of the pericardial sacs in *Ocypode quadrata*; (4) that there exists no valid quantitative basis for comparison of the surface area of the pericardial sacs in *Ocypode quadrata* with that of the pericardial sacs in the three marine species of crabs.

Thus, with the exception of the data for *Ocypode quadrata*, the quantitative results confirm earlier conclusions based on gross morphology, namely: (1) that the pericardial sacs of terrestrial crabs are larger than those of marine crabs; and (2) that of the six species included in this study the one with the largest pericardial sacs is *Gecarcinus lateralis*.

**MICROSCOPIC ANATOMY**

Thus far histological study of the pericardial sacs has been confined to the single species *Gecarcinus lateralis* (Fig. 22). Externally these structures have a soft covering that probably consists of epicuticle and undifferentiated endocuticle (Leo Schatz, personal communication). Just within lies a single layer of epidermal cells. A considerable capacity for expansion is suggested by the many convolutions that are present in the outer layers of the pericardial sacs.

The main mass of a pericardial sac seems to be composed of loose connective tissue similar to the sub-epidermal connective tissue of *Panulirus argus* (Travis, 1955, 1957). Within this loose connective tissue of the pericardial sacs of *Gecarcinus lateralis* are bands of striated muscle fibers oriented in many directions, although primarily transversely.

Much of a pericardial sac appears vacuolar in character. There probably exist both intracellular vacuoles and blood lacunae continuous with the pericardium. In stained sections large amounts of blood, including hemocytes, can be seen scattered throughout the loose reticulum of connective tissue. Also visible, particularly within certain areas of a pericardial sac, are large inclusions of unknown composition. According to Mrs. Mary Weitzman (personal communication), such inclusions are found generally within the connective tissue of *Gecarcinus lateralis*.
Fig. 22. Microscopic structure of a pericardial sac of *Gecarcinus lateralis*. Note the cuticle (C), epidermis (E), vacuolated connective tissue (T), bands of striated muscle fibers (M), hemocytes (H), coagulated blood (B).

Many of the histological details given above agree with the early description of the pericardial sacs of *Maja* and *Carcinus* reported by Cuénot (1891). He described the "glandes lymphatiques pericardiques" as covered by a chitinous cuticle that is secreted by a palisade type of epithelium. According to Cuénot, the organ is filled with a loosely formed meshwork containing numerous bands of striated muscle, most of which are oriented circularly. Cuénot observed the reticulum to contain blood cells and large, clear, rounded vesicles, as well as smaller vesicles bearing refringent material that Cuénot believed to be of an albuminous nature.

In a later paper Cuénot (1893) characterized the connective tissue as composed
of two types of reserve cells, namely, cells of Leydig and proteic cells. These two types of cells, according to Travis (1955, 1957), correspond to the "reserve cells" that she has described in the loose connective tissue of Panulirus argus, as well as to the "lipo-protein cells" described by Sewell (1955) for Carcinus. Travis (1955) has noted that the reserve cells of integumentary tissues resemble those of the midgut gland, which are known to store large quantities of fat.

In summary, we can conceive of the pericardial sacs as two diverticula of the pericardium that possess a marked capacity for expansion and contraction and a considerable potential for storage. Let us now consider possible functions for these organs.

FUNCTIONS

The earliest investigators to study the pericardial sacs were not loathe to suggest a possible function. Thus Milne-Edwards (1834) thought that he could detect a canal running from each sac to the exterior and wondered if these organs could be the site of an excretory product analogous to urine. In 1891 Cuénot felt that the pericardial sacs might serve both for storage of reserve materials and as a site for developing amoebocytes. Two years later, however, he denied any storage or "lymphatic" (hemopoietic) function and suggested that the pericardial sacs may play a mechanical role of unknown sort.

Generally speaking, more recent authors have refrained from assigning a function to the pericardial sacs. Thus Pearson (1908), Borradaile et al. (1935), and Lochhead (1950) have stated that the function of these sacs is unknown. Pyle and Cronin (1950) have not mentioned the pericardial sacs at all. Borradaile et al. (1958) have included the pericardial sacs in figures illustrating the internal anatomy of Carcinus maenas but have not referred to them in the figure legends or text.

Drach (1939), however, has studied the pericardial sacs in relation to molting. He has reported that in the marine crabs Cancer and Maja the "poches pericardiales" are extremely elastic and can undergo rapid changes in volume as the pressure within the hemocoel is altered. He has suggested that the sacs may regulate and limit hydrostatic pressure during molting, by storing water while it is being absorbed. In Cancer and Maja Drach has found the site of water absorption during molting to be the new lining of the digestive tract, which undergoes rapid changes in permeability when the old lining is shed.

Our own studies on the pericardial sacs of Gecarcinus lateralis (Bliss, 1956) have suggested that in this terrestrial crab these structures play an important role in the premolt uptake and retention of water, which after ecdysis is used to expand the new soft exoskeleton before it hardens at its larger dimensions. In Figure 23 appears the posterior portion of an unswollen intermolt specimen of Gecarcinus lateralis. In Figure 24 is another specimen of the same species as it appears one day before ecdysis. The pericardial sacs are so swollen that they bulge far out from under the carapace. During ecdysis, as the old carapace is forced forward and the crab gradually emerges, the pressure exerted by the old shell on the soft body of the crab diminishes and the pericardial sacs begin to decrease in size. By the end of ecdysis they appear once again as in Figure 23.

Our studies (Bliss, 1956, 1962) have indicated that the neuroendocrine system regulating growth and molting also regu-
lates premolt water uptake and retention by the pericardial sacs. Thus light, which acts hypothetically through the medium of the neurosecretory system to inhibit limb regeneration and molting, also inhibits premolt water uptake and retention. Darkness, which acts hypothetically via the neuroendocrine system to favor limb regeneration and molting, also favors premolt water uptake and retention. Crabs from which eyestalks (and therefore sources of the molt-inhibiting hormone) have been removed may show extreme swelling of the pericardial sacs before ecdysis.

It is likely that the pericardial sacs of

Fig. 23. Posterior dorsal view of *Gecarcinus lateralis* during the intermolt period. There is no external evidence of the pericardial sacs, which are unwollen and lie entirely beneath the carapace.

Fig. 24. Posterior dorsal view of *Gecarcinus lateralis* just prior to ecdysis. The pericardial sacs have become so swollen that they protrude from under the carapace. They lie protected within the unfolded arthrodial membrane. Abbreviations: P, pericardial sac; G, gill.
Gecarcinus lateralis are the primary means of water uptake and retention during the intermolt period as well. The water may replace that lost by evaporation (e.g. from the gills). Perhaps the significant alteration that occurs just prior to ecdysis is an increased rate of water uptake and increased retention of water. If so, then a change in membrane permeability, in osmotic pressure of body fluids, or in both may play a role at the time of molt.

In order for the pericardial sacs to take up water, there must be some means whereby water can reach the sacs, which are situated under the carapace partly within and partly posterior to the branchial chambers (see Fig. 15). It has already been noted briefly (Bliss, 1956) that the pericardial sacs of Gecarcinus lateralis swell prior to ecdysis only if the crab is on a moist substratum. No swelling occurs if drinking water is the only type available. The question arises, therefore, as to how a crab gains access to the water in a damp substratum. A possible answer to this question has been suggested by the results of the following experiments.

If a specimen of Gecarcinus lateralis is held ventral side up and distilled water containing the vital dye, neutral red, is placed carefully on the external tufts of setae located on each side of the abdomen (Fig. 20), the fluid disappears with extraordinary speed. This procedure may be repeated several times before the rate of disappearance of the fluid begins to decline. If a few moments are allowed to pass and then drops of fluid again are applied, they vanish rapidly once more.

When a small portion of the exoskeleton that covers the extension of a pericardial sac at the base of the fifth walking leg is cut away, a setae-lined channel, formed by adjoining segments, is revealed (Fig. 20). This channel leads directly from the external tuft of setae to the setae-fringed tip of the pericardial sac. Here a small lacuna, large enough to hold fluid, is located.

Should dye-containing distilled water now be placed drop by drop on the external tuft of setae on the same side as the cutaway, the drops can be seen to run swiftly along the setae-lined channel and to collect in the lacuna at the tip of the pericardial sac. Within the next moment or so, the fluid disappears from the lacuna as if being blotted by absorbent tissue.

One may speculate that this is the normal pathway followed by tiny drops of moisture (e.g. dew, soil water) from the substratum to the pericardial sac. The presence of a lacuna at the tip of the sac may provide a temporary reservoir for fluid when it is present in excess. Recall that distilled water applied to the external tufts of setae disappears at a decreasing rate, and that if a few moments without application of fluid are allowed to pass, the rate rises again. It seems likely that the drops of applied fluid run along the setae-lined channel to the lacuna, where they collect and then are slowly absorbed by the pericardial sac. Once the lacuna is full, no more fluid can be carried there by the setae until the excess is absorbed.

The conduction of water from the external tufts along the setae-lined channels to the lacunae may be due entirely to capillary action. Subsequent absorption of fluid from the lacunae by the pericardial sacs may involve either simple diffusion or ac-

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1 Gross (personal communication) has confirmed in detail our observations that Gecarcinus lateralis takes up fresh water from damp sand. Gross' observations were made entirely on intermolt crabs.
vive uptake. Evidence regarding this process awaits physiological experimentation.

In an effort to obtain some measure of the amount and rate of fluid uptake, application of drops of distilled water was made with a one-milliliter hypodermic syringe and needle. When fluid was thus applied to the external tufts of setae on a crab that had been without food or water for four days, 0.085 milliliters of distilled water were taken up within 32 minutes. Three days later the experiment was repeated on the same crab which in the meantime had had no food or water. Now 0.290 milliliters of distilled water were taken up within 72 minutes. The mean rate of uptake in these two experiments was 0.0034 milliliters (or 3.4 microliters) per minute.

Probably of considerable significance is the observation that drops of sea water, when applied to the external tufts of setae, do not disappear readily. The first few drops vanish, presumably into the lacunae, but subsequent drops remain on the external tufts. It would appear that this mechanism of water uptake does not function if sea water is the only moisture available.  

In Cardisoma guanhumi setae are found around the entire edge of the abdomen, with longer, thicker ones occurring in the area near the extensions of the pericardial sacs. It is likely that in Cardisoma guanhumi water is carried by setae to the pericardial sacs through capillary action, just as postulated above for Gecarcinus lateralis.

Setae occur in Ocypode quadrata on each side of the body at the base of the second and third walking legs. At each of these locations the setae mesh with one another to appear as one tuft (Fig. 21). If, however, the second and third legs on one side are separated, two distinct rows of setae become visible. These lead dorsally to other setae which in turn lead through an orifice in the exoskeleton directly into the branchial chamber, close to the gills and the lateral tip of the pericardial sac. Fluid applied to the external setae at the base of the legs moves with great speed up into the branchial chamber.

Regardless of species, the external tufts of setae occur in areas of the body that make contact with the substratum when the crab is at rest. The ventral surface of Ocypode quadrata is considerably more rounded than is that of Gecarcinus lateralis and Cardisoma guanhumi. When Ocypode quadrata is at rest, not the posterior portion of the abdomen but the portion adjacent to the base of the second and third walking legs is in contact with the substratum. The presence of two large tufts of setae in this area ensures that moisture from the substratum will be conducted into the branchial chambers where it can moisten the gills and the pericardial sacs. The same mode of water uptake from damp sand has been described for Ocypode gaudichaudii by Koepcke and Koepcke (1953).

A final point concerns the relationship of gills, pericardial sacs, and pericardium. Injection experiments by the writer on Gecarcinus lateralis have confirmed the early findings of Cuénot (1891) that the pericardial sacs are continuous with the pericardium. If several tenths of a milliliter of neutral red in sea water are injected into the central portion of one peri-

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2 Gross (personal communication) has observed that when intermolt specimens of Gecarcinus lateralis are maintained on sand moistened with sea water, few survive for even two weeks; furthermore, the gills of these crabs appear extremely dry.
cardial sac, it spreads quickly throughout the sac both towards the heart and towards the gills. After injection into the posterior extension of the pericardial sac, the dye moves rapidly towards the heart. Following such injections, however, no dye is visible in the other sac.

There can be no doubt that blood flows into the pericardial sacs from the pericardium and thence close to the external surfaces of the gills. It is conceivable that diffusion of water (transpiration) from the hemolymph to the cells of the pericardial sacs and thence across the cuticular membrane of the sacs into the branchial chambers can take place. The portion of the pericardial sac that is overlain by the gills has a thin cuticle and numerous blood spaces. Indeed, one may question parenthetically whether this part of the sac may not also serve as a respiratory apparatus.

Edney (1957) has commented that to some extent water can probably pass across the entire cuticle of most arthropods, for no osmotic barrier exists and even a waxy cuticle, such as occurs in insects, spiders, and ticks, is somewhat permeable. No waxlike layer has been demonstrated in the exoskeleton of crustaceans.

If transpiration across the cuticle of the pericardial sac does occur, then this structure may serve to maintain a high relative humidity in the branchial chamber and thus to reduce the rate of evaporation from the gills and the branchial membrane. This effect may be enhanced by the actual contact that exists between some of the gills and the pericardial sacs.

The more terrestrial a crab may be, the more important the functions of the pericardial sacs may become. Therefore, in the next section, we shall consider briefly the distribution of the three species of land crabs on an island in the Bahamas and relate it to the degree of independence that each species shows with respect to an aqueous environment.

THE DISTRIBUTION OF LAND CRABS, WITH REFERENCE TO THE AVAILABILITY OF WATER

The property of the Lerner Marine Laboratory in Bimini, Bahamas, B. W. I., covers an area that is approximately 600 feet by 200 feet and extends across the island of North Bimini from the waters of the Bahama Bank to those of the Florida Straits. A vertical profile along the south-southwesterly boundary of this property appears in Figure 25. On it is indicated the distribution of the three species of land crabs that occur there.

A primary factor governing the distribu-

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3 This section is a brief summary of material that will be presented in detail in a forthcoming paper.

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Fig. 25. Vertical profile along the south-southwesterly boundary of the property of the Lerner Marine Laboratory, Bimini, Bahamas, B. W. I. The distribution of Gecarcinus lateralis, Cardisoma guanhumi, and Ocytpode quadrata on the property is indicated.
tion of these crabs is the availability of water. *Ocypode quadrata* remains on the beaches at either end of the property, where it can run into the ocean frequently, thus moistening its gills and replenishing its body fluids. *Cardisoma guanhumi* is found only in areas of very low elevation. It burrows down to ground water, that is, to the fresh water lens that the natives tap for their drinking water. When this crab is dug out of its burrow, it is taken from wet mud or even from mucky water.

*Gecarcinus lateralis* ranges widely throughout the laboratory property, overlapping *Cardisoma guanhumi* in open areas of sun or light shade. Where there is deep shade and a high population density of *Cardisoma guanhumi*, as in the area marked *Cardisoma* on Figure 25, no *Gecarcinus lateralis* occur.

The burrows of *Gecarcinus lateralis* never descend to ground water and the crab never enters the ocean (except females with spawn—to drop their eggs). The soil out of which *Gecarcinus lateralis* is dug feels powdery dry to the touch and contains only a small percentage of moisture.

Of the three species of land crabs, therefore, *Gecarcinus lateralis* is the only one to which copious supplies of water are not always available. Only during heavy rain showers does this crab become thoroughly wet. Yet particularly during the winter dry season, rains may be very infrequent.

Unpublished experiments by the writer have indicated that in air *Gecarcinus lateralis* is far more resistant to desiccation than is *Ocypode quadrata* and somewhat more resistant than is *Cardisoma guanhumi*. *Gecarcinus lateralis* loses water at a significantly lower rate than does *Ocypode quadrata* and is able to withstand a greater total amount of water loss than can either of the other two species. Accordingly its period of survival in air is longest.

Clearly *Gecarcinus lateralis* has acquired the greatest independence of an aqueous environment. How has this been done?

The answer to this question involves in part a recapitulation of much that has already been discussed in this paper. The gills of *Gecarcinus lateralis*, although numbering 18, have the smallest surface area per gram body weight of any of the crabs considered here and smaller than any species listed by Gray (1957) in his extensive study of marine, intertidal, and terrestrial crabs. The gill lamellae of *Gecarcinus lateralis* are strongly sclerotized and are held apart by ridges that ensure free circulation of air between the lamellae. The branchial chambers are capacious and their epidermal lining is highly vascularized. The pericardial sacs have the largest surface area of any crab so far studied. They penetrate far into the branchial chambers where they may help significantly to keep certain gills moist by contact and where they may also reduce drying of the gills and the branchial membrane by maintaining a high relative humidity. Accordingly, *Gecarcinus lateralis* is assured adequate respiratory exchange without marked danger of desiccation.

Not only have various morphological adaptations served to emancipate *Gecarcinus lateralis* from dependence upon an aqueous environment, but climatic conditions have done so as well. This crab is restricted to maritime locations. For example, North Bimini is an oceanic island where the relative humidity of the atmosphere is very high, averaging 85 per cent for the whole year and varying only slightly from summer to winter. Maritime
air is moist, regardless of season. The air that filters into the burrows of *Gecarcinus lateralis* on this island is laden with moisture.

At its highest point the island of North Bimini is not far above sea level, maximum elevation on the laboratory property being about 20 feet. Ground water lies close by and capillarity serves to raise some of this ground water to upper levels. The relative humidity of the soil atmosphere at the level to which many burrows of *Gecarcinus lateralis* descend, therefore, is high. At night the atmosphere often reaches saturation, with light to heavy dews common in both summer and winter.

Earlier in this paper it was postulated that moisture coming in contact with external tufts of setae on the abdomen of *Gecarcinus lateralis* follows setae-lined channels to lacunae situated at the tip of the pericardial sacs. It was also postulated that either by simple diffusion or by active uptake this water enters the pericardial sacs. Now it is suggested that the principal form of natural water to come in contact with the external tufts and subsequently to be absorbed by the pericardial sacs is dew.

While *Gecarcinus lateralis* rests within its burrow or while it runs outside of its burrow during nocturnal forays for food, dew may form on the body of the crab or on objects with which the external tufts make contact. This dew then may be absorbed by the pericardial sacs. The frequency with which dews occur would make it unnecessary for the crab to depend upon sporadic showers during which to replenish its body fluids.

Thus, through a combination of morphological and physiological adaptations and favorable climatological factors, *Gecarcinus lateralis* has become almost totally independent of an aqueous medium. *Cardisoma guanhumi* and *Ocypode quadrata* possess many of the same adaptive features as does *Gecarcinus lateralis*, but they depend upon them for survival far less. For *Cardisoma guanhumi* and *Ocypode quadrata*, water in quantity must always be available for immersion, and due to the limits of their distribution, it always is. These species regularly immerse themselves in ground water or in the ocean, as the case may be.

*Gecarcinus lateralis* returns to the ocean only to provide its young with the environment that they must have for development. After completing larval development this species remains entirely dependent for its well-being upon the adaptive changes that evolution has wrought to equip it for life in a relatively dry terrestrial environment. Among these changes, not the least important appears to be the greater development of the pericardial sacs.

**SUMMARY**

1. The comparative gross morphology of the pericardial sacs is discussed in three species of terrestrial crabs, *Gecarcinus lateralis*, *Cardisoma guanhumi*, and *Ocypode quadrata*, and in three species of marine crabs, *Callinectes sapidus*, *Cancer borealis*, and *Cancer irroratus*.

2. Determination of the surface area of the pericardial sacs indicates that, in general, terrestrial crabs have larger pericardial sacs than have marine crabs and that *Gecarcinus lateralis* has the largest pericardial sacs of any species studied.

3. Histologically, the pericardial sacs of *Gecarcinus lateralis* are characterized by the presence of a thin covering (epicuticle and probably undifferentiated endo-
cuticle), a single layer of epidermis, considerable vacuolated connective tissue, and numerous bands of striated muscle fibers oriented in many directions. They also contain blood spaces in which hemocytes are numerous. The presence of many convolutions in the outer layers and numerous muscle bands within the sacs suggest a considerable potential for expansion and contraction.

4. For many years the functions of the pericardial sacs were virtually unrecognized. Drach (1939) suggested a probable function for these structures in marine forms, that of regulating hydrostatic pressure within the hemocoel during water uptake at ecdysis. Our own studies have indicated that in the terrestrial crab Gecarcinus lateralis the pericardial sacs take up water from a damp substratum. Just prior to ecdysis water uptake and retention are intensified so that the pericardial sacs may become extremely swollen. At all times these structures may help to maintain a high relative humidity in the branchial chambers and thus to reduce the rate of evaporation of water from the gills.

5. In Gecarcinus lateralis an extension of each pericardial sac posteriorly towards the base of the fifth walking leg where there is a small lacuna may serve as the actual site of water uptake. External setae and a setae-lined channel are believed to conduct minute drops of water (e.g. dew) from the substratum to the lacuna where the water is then absorbed by the pericardial sacs. A somewhat comparable arrangement may exist in Cardisoma guanhumi, but not in Ocypode quadrata, where the external setae are located in a more anterior position. Nevertheless, in the latter they may serve the same function, that of conducting water to the pericardial sacs—and in this case directly to the gills as well.

6. The distribution of the three species of terrestrial crabs is considered in relation to the availability of water. Gecarcinus lateralis is the only one to which plentiful supplies of water are not regularly available. It is also the species most resistant to desiccation. A combination of morphological, physiological, and ecological factors have combined to provide this species with a high degree of independence of an aqueous medium.

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Histological preparations that served as a basis for Figure 22 were made by Miss Kate Gruen. Figures 20-24 were drawn by Miss Maria Wimmer when she was a member of the Department of Graphic Arts at the American Museum of Natural History. Figures 15-19 were modified by the writer from sketches by Miss Wimmer. Topographical data upon which
Figure 25 was based were obtained from the staff of the Lerner Marine Laboratory.

Stimulating discussions regarding the histology and gross anatomy of the pericardial sacs were held with Mrs. Mary Weitzman and Mr. Leo Schatz. Some biological material used in determining the surface area of pericardial sacs was contributed by Mrs. Weitzman. Dr. Warren J. Gross kindly made available certain unpublished observations regarding water uptake in *Gecarcinus lateralis*.

The contributions of all named above are gratefully acknowledged.

**Ayers, John C. 1938.** Relationship of habitat to oxygen consumption by certain estuarine crabs. Ecology 19:523-527, 1 fig.


———. 1934. Freezing points of bloods of certain littoral and estuarine animals. Papers


VI

Discussion Following Papers by Kinne, Gordon and Bliss

WATERMAN: Dr. Kinne has restricted the coverage of adaptation to its ecological aspects in which there are direct interactions between various environmental parameters, such as temperature or salinity, and the organism. Considering the organism as a self-perpetuating steady-state system, there are four other important aspects of adaptation which also deserve to be mentioned: physiological, genetic, developmental and evolutionary (Waterman, 1961, "Physiology of Crustacea"). Also we must keep in mind the adaptive implications in the "fitness of the environment."

These different facets of adaptation show considerable overlap; yet they can be rather easily distinguished on the basis of the time scale over which they are significant. Thus physiological adaptation is mainly concerned with the immediate short-term mechanisms maintaining the steady state whether these deal with sensory functions, nutrition, or the molecular basis of hormone action. The adaptations with which Dr. Kinne was mainly concerned involve time scales of hours, days or weeks which are significant for physiological ecology. Developmental adaptations extend throughout most of a generation; genetic adaptations, at least at the population level, extend through several or many generations while the time scale for evolutionary adaptation is the longest of all.

Although it is a common opinion, perhaps a nearly universal one in the present company, that evolution is the explanation in biology, I would like to propose a different point of view which seems to place the study of evolution in a more reasonable perspective. Since whatever happens in biological systems must be adaptive in order to persist (otherwise it would throw the organism out of its essential steady state), the basic explanation which we are looking for in all kinds of biological phenomena is their adaptiveness. This would seem to be a valid generalization for the whole field regardless of whether we are more specifically interested in evolutionary, embryonic, genetic, ecological or physiological events. Obviously this view is consistent with the central role of natural selection in evolutionary studies.

KINNE: I have tried to define and restrict the often loosely and widely applied term "adaptation" to provide a useful tool for the evolutionist as well as for the physiologist. Waterman's enlarged concept of adaptation is practically identical with biology as a whole, comprising genetics, ecology, embryology (development), evolution, and physiology and appears to be less specific and less useful. How do you distinguish, for example, between genetic and evolutionary adaptation, and between internal and chrono-
logical adaptation? It is certainly true that the so-called internal adaptations (i.e. the functional and structural mechanisms involved on the enzyme-, hormone-, cellular-, and organ-levels) deserve more attention. However, our knowledge concerning the physiological mechanisms of adaptation is rather limited and does not provide an adequate basis for a review that could be integrated with the primarily ecological approach that was chosen here.

GLAESSNER: Adaptation, unless more strictly defined, is not a very useful concept in paleontology. When we discuss things from the point of view of adaptation, we end up relegating evolution to a minor subdivision, or to a general philosophical context, and bringing everything under an enlarged concept of adaptation. We should not consider everything as either an adaptation or not an adaptation. What is not an adaptation is what the Crustacea have inherited from their predecessors. What follows when they come into being and differentiate is their adaptation. In the higher Malacostraca, the division of the body into a cephalothorax and an abdomen, the division of the various organs, and the distribution of locomotory, respiratory, and sensory organs, is inherited, but not acquired by that group as an adaptation. The modifications of that inheritance are the adaptations that we are discussing here. Let us talk more about evolution and restrict the concept of adaptation so that it remains useful.

KINNE: As long as we talk about adaptation in Crustacea, it is correct to say that what the Crustacea have inherited from their phylogenetic predecessors (the characteristics which make the Crustacea a distinct group of animals) is not to be considered an adaptation. I would like to add a word concerning the overemphasis of the structural aspect in evolution. It appears desirable to relate defined structures to functions, e.g. different modes of life, locomotion, and respiration, or to different habits of feeding. Adaptation provides a useful, synthetic concept, emphasizing the relationships between structure and function of a given organism and its environment.

MANTON: A hermit crab, adapted in innumerable ways to the gastropod shell in which it lives, is an example of adaptation related undoubtedly to a particular environmental niche. Another type of evolutionary change, which is not directly imposed by any property of the environment, is much the more important concerning the major steps in evolution, as pointed out by D. M. S. Watson (1949, Proc. Linn. Soc. London, 160 (2): 75-84) for †Plesiosauria. I can only give you comparable examples outside the Crustacea, but the principles probably apply to the Crustacea also.

In the same decaying log today you can find Peripatus, centipedes, millipedes, Symphyla, scorpions and other arachnids, apterygotes, etc. Their taxonomic morphological characters are related to divergent habits, which were probably established at an early terrestrial stage. A hundred or more conspicuous body features recently have been shown to be correlated with these habits: the form of head, trunk and legs; the shape, size and number of scutes, their fusion together or doubling in number; the musculature and endoskeleton, etc. These taxonomic characters suit: the bulldozer burrowing habits of the diplopods; the fast moving predatory habits of the chilopods, with extreme adaptation towards manipulating food in shallow crevices; the gaining of shelter by twisting and turning without pushing of the Sym-
phyla; the amazing powers of body distortion in the Onychophora, by which they gain shelter (again without pushing) through narrow crevices far too small to permit pursuit by predators large enough to harm them, etc. Adaptation to a particular niche leads to the edge of a "precipice" when conditions change. But adaptations which facilitate particular habits of life, which lead to better or easier living in a variety of habitats, result in persistent and far-reaching evolutionary advance. It is not easy to recognise which, among the many things an animal does, represents the habit or habits of real evolutionary importance. Great advances have been made with the Onychophora and Myriapoda along these lines. Comparable work on the aquatic Crustacea may be much more difficult, but it is an approach which should be made.

KINNE: This is certainly an important aspect of adaptation. But was it not mentioned in my paper when I talked about behavioral adaptation?

WATERMAN: I do not quite agree with that interpretation of what Dr. Manton said. My understanding of her comments would be as follows. If a variety of different arthropods were to approach a log of wood, some of these would walk around it, others would push through it, some would wriggle under it, and so on. These forms differ in their behavior when confronted with the same environmental situation. Such differences are clearly of adaptive value since those which conform to the structural and functional needs of the particular organism will confer a selective advantage on it. I think Dr. Manton has made an important point which had previously been neglected, namely that a crucial issue in evolution and adaptation is the initial presence of some particular habit or behavior pattern which emerges from the structural and functional details of the creature's organization.

MOORE: Does what Manton calls habit really mean the behavior that is controlled in terms of what Waterman said?

WATERMAN: For the present discussion we may perhaps consider this behavior as spontaneous. To go into some explanation of its origin would take us too far afield. However, I again emphasize the importance of time scale in speaking of adaptiveness. For example, it seems impossible for me to accept Glaessner's contention that hereditary information which each individual organism receives from its parents is not adaptive. Clearly the individual could not go on living unless it received this information. However, I agree that in the immediate sense to which he was referring it is not adaptive, which illustrates the key position of time scale in such considerations.

Also I object somewhat to Kinne's statement that what we, or other organisms, are now is just the result of evolution. From a strictly operational approach, such as most physiologists, biochemists and biophysicists take, an organism is what it is now because of its immediate relations to itself and to its environment. What it may have been in the remote past or what it may become in the distant future are quite irrelevant from this point of view.

SANDERS: There is a different way of viewing the same problem. Physiologists are most interested in those environments where the physical conditions tend to fluctuate rather widely demanding physiological adaptations. However, when one thinks of the number of species on our globe, only a small fraction lives in such environments.

One might think of two pure types of
communities: (1) the physically controlled, and (2) the non-physically controlled where physical factors such as temperature, salinity, light, etc. vary very little in the course of the year, and have remained essentially unchanged for extensive periods of time. In the predominantly physically controlled community, the number of species is small, and there is marked numerical dominance by few species; in the predominantly non-physically controlled community there are many species with no species markedly abundant. In the physically controlled community the niches are broad, large, and tend to be diffuse. In other words, biological interactions are not well developed—the adaptations are to physical conditions. In the other type of environment the niches are smaller, more circumscribed as a product of biological interactions resulting in biological accommodation. Probably most of the functional adaptations that we have been talking about evolved in the non-physically controlled environment as a response to biological accommodation. Thus the physiologists find the physically controlled environment inherently more interesting while the functional morphologists find that the reverse is true.

WATERMAN: Can you give an extreme example of each of those?

SANDERS: An extreme example of a physically controlled environment would be a hypersaline bay where only three species may be present. The salinity may vary from zero to sixty or even seventy parts per thousand, and there may also be appreciable temperature change. The high Arctic is another example. A tropical rain forest or the deep sea represent relatively stable environments, and in such situations one finds non-physically controlled communities.

WATERMAN: The organism that is living in the deeps at a thousand atmospheres, in the dark and in a place where there is no primary food production is under a very difficult biochemical and physiological stress.

SANDERS: A limitation of food does not necessarily imply a limitation in the variety of animals, but rather a limitation in the number of animals.

WATERMAN: As I understand it you distinguish between the degree of stress and the rate of change of such stress.

SANDERS: If the environment remains constant in time with a stress factor such as high pressure in the deep sea, the animals have made the necessary physiological adaptations a long time ago. From that period on, biological interactions came into play resulting in biological accommodation, and the numerous niches of the non-physically controlled community.

WATERMAN: Does this tie in with the rate of speciation?

SANDERS: I believe so. Most of the centers of evolutionary activity have been in non-physically controlled environments—for example, southern Asia for freshwater fish.

TASCH: I should like to stress the concept of the antiquity of a given adaptation. In the region of the Great Salt Lake, recent cores show that Artemia salina was an inhabitant at least 600,000 years ago. Its adaptation to a hypersaline environment was established by then, and undoubtedly long before that time. Take the matter of ephippial eggs in cladocerans. The oldest known cladoceran fossil is a daphniid ephippium from the Oligocene, 40 million years ago. Ephippial eggs occur in times of stress in the environment. Adaptations of this type are very ancient.

WATERMAN: One of the most im-
important things that paleontologists can do is to tell us in which direction and how fast evolution has in fact moved in its historical course. On the basis of comparative morphology, ethology, physiology, biochemistry, development, and so on, biologists can construct a plausible ladder or tree of evolutionary change. However, none of this comparative evidence can tell us anything certain about the direction or actual rate of change in the proposed phylogeny. This is largely true even for the population geneticists who are directly studying evolutionary mechanisms. However, if the geological record yields relevant data from more than one stratum both direction and rate of evolution can be defined in terms of the history of the sediments in question. Such information seems to me crucial in controlling the speculative nature of phylogenies otherwise obtained.

BOWMAN: To verify what Sanders said, in terms of planktonic animals: in the study of populations of calanoid copepods of the southern coast of the United States we get definite zonation of the number of species into inshore and offshore. Inshore, the number of species is quite limited, but the number of individuals is much greater than offshore where you get more species.

MANTON: Details could be given of habit reversals and their morphological consequences or accompaniments, in which the direction of change is not a matter of speculation, but is quite clear. These habits are not adaptations to environmental niches. For example, there are a few millipedes which have given up their basic habit of burrowing by pushing and show convergent resemblances to centipedes in accomplishments and structure, superimposed upon a basic diplopodan morphology. There is also a centipede (Craterostigmus) which has given up the ability of fast running and its structure is much modified permitting great flexibility of the trunk. In this case I do not know the full nature of the habits associated with these features. They clearly are not adaptations to a particular niche. We now know that there are many arthropodan groups whose basic evolution has not been adaptive to the immediate environment or to Sanders' narrow niches, but to habits which can be employed in various circumstances. There is much too great a readiness at the present time to believe that structure, and the physiological capabilities of that structure, are largely explicable as direct adaptations to the environment, although general adaptations to a terrestrial or an aquatic environment are also important.

WATERMAN: It is also familiar that independent parallel adaptations apparently appear over and over again in different families of the same group.

GLAESSNER: If we work on the basis of the traditional classification, for example, then we are discussing whether the differences between the Raninidae and the Oxy stomata should be given a certain taxonomic rank, a problem in which nature does not give us much guidance. If we assess the differences in the structure of the genital organs, we may be in danger of arriving at a single character classification on the basis of important differences. We have to take into consideration the fossils, no matter how incomplete the record, because we know something of what happened in the past, in this transition from Macrura to Brachyura, and the origin of crabs. We know from the Cretaceous a number of undescribed crabs of this group, including Dorippidae. We have to study the evolution of these systems of functioning organs before we decide what
importance to give them in classification. We have to study evolution, not only on the basis of comparative morphology or of embryology, but also on the basis of paleontology. I do not agree that they should be given different values and that paleontological evidence should be given more value than the others. Certain things Gordon has said appeal to me. For example, that there is a distinction between Macrura, Anomura, and Brachyura was a rather crude approach in the past when little was known about the decapods. "Natantia," "Reptantia" was a purely functional approach to classification, and not the evolutionary one which our system should represent. I diverge somewhat from Gordon's opinion in believing that the peculiar habit of the Dromiacea and Dorippidae (to have used their reduced last pairs of legs or one pair of legs for carrying objects on their backs) is a distinctive pre-adaptation. It is connected with the reorganization of the body in the internal skeleton, from a macruran type with its cylindrical internal skeleton to the conical internal skeleton of the crabs, with a different habit of locomotion and different arrangement of muscles of the branchial chamber and so on. There was not enough space, until this reorganization was completed, for the muscles of the last pairs of legs (which are affected by the loss of the ancestral lobster tail) to be fully developed and remain fully functional. Only when the stage of the Dromiacea and Dorippidae was passed did the organization of this internal skeleton allow the full development of the attachment of the last pairs of legs and of their muscles to come into play again. Nothing was lost completely. In the transitional stages the legs were utilized for other functions, for carrying objects. This was a reasonably successful group, but when the crab habit was fully developed in the later, more advanced forms, then the last pairs of legs could grow to their full size, could be adapted for swimming as in the portunids, and in all sorts of ways, and the balance of the organism was restored in a new way, leading to adaptive radiation.

GARTH: As I listen to various people, I realize that what we are talking about would be called adaptation by Kinne, physiology by Waterman, and probably evolution or phylogeny by Glaessner. I think Gordon and I would include most of it under systematics.
VII

Studies in Malacostracan Morphology: Results and Problems

By

Rolf Siewing

Zoologisches Institut und Museum der Universität, Kiel, Germany

For more than a hundred years there has been discussion of phylogenetic relationships within the Crustacea. But, up to the present we have not succeeded in reconstructing a system reflecting in all respects the natural relationships. There are several reasons for this, including the insufficient paleontological data, the interpretation of which is partially disputed. Nearly always we need to work with Recent material.

The first step in reconstructing the phylogeny is the establishment of natural systematic categories (Fig. 26). This is done by the determination of homologies, using exact criteria, following the method recently elaborated and interpreted by Remane (1956). We can carry out this step in a number of crustacean groups, so that we get a horizontal or a two-dimensional arrangement of the different groups.

The second step consists of a transition into a three-dimensional arrangement. The homologous similarities of the natural groups depend on their common descent. We can thus draw a picture of phylogenetic connections between the systematic groups, and depict them in a schematic phylogenetic tree (Fig. 27). This picture represents the best demonstrable and best explained way of understanding the phylogenetic relations of one group. New investigations and discoveries may lead to the alteration of details.

The third step in morphological science is the reconstruction of the phylogenetic ancestor of the different natural groups (Fig. 28).

It may be suitable first to define several words. "Primitive" means that a structure is simple. But simple and primitive do not necessarily imply a phylogenetic state. Primitiveness or simplicity can also originate secondarily. An early phylogenetic state, "ursprünglich" in German, I have translated as "original." The opposite term is "derived."

With the above point of view, I have investigated different malacostracan groups, and have obtained the following results.

The Malacostraca is the only group of
Fig. 26. Diagram showing the two-dimensional arrangement of natural groups within the Malacostraca derived by the homology-investigation method.
Fig. 27. Diagram showing the three-dimensional arrangement of natural groups within the Malacostraca, with phylogenetic connections.
subclass rank of which we can say with certainty that it represents a natural group; this means that it has a monophyletic descent. Marked by the constant situation of genital openings, the Malacostraca possess moreover a constant number of segments, consisting of six segments in the head, eight in the thorax, and originally seven in the abdomen.

Since the synthesis of Calman (1904), the Malacostraca have been classified into divisions or superorders (Fig. 26), and these have the character of natural groups. There has long been agreement that the Leptostraca must be regarded as the most original Malacostraca. This basic position is proved by the great carapace, which is free of all the thoracic segments; moreover they are original in having a true furca and seven abdominal segments. In a certain sense also the extension of the heart through almost the whole body is original and particularly its invasion into the hind part of the head region (Fig. 29). Nearly all the paired lateral arteries consist of two components, one of which provides for the extremities, the other for the internal organs (Fig. 30). I have found a similar composition in the Anaspidacea, and it is present, more or less clearly, in other Malacostraca. It is interesting to note that similar conditions are also found in some errant polychaetes. Perhaps direct phylogenetic connections exist here. Possibly therefore the bipartite arteries are original. The possession of two pairs of nephridia is also original.

Diagnostic characters of the Leptostraca are the change of legs into phyllopod-like extremities, the structure of the stomach with its gastric mill, the structure of the first antenna and the lack of exopods on the second antenna. Further, the carapace has developed into a bivalved shell, the halves of which can be moved by an adductor muscle. One finds parallels for these characters in other crustaceans.

The differences do not justify a separation of the Leptostraca from the rest of the Malacostraca. Moreover these dif-
Fig. 29. Schematic diagram of the organization of a leptostracan. (Siewing, 1956.) 1.A = antennula; 2.A = antenna; AA = aorta anterior; ADD = adductor; AN = antennal nephridium; AP = aorta posterior; AU = eye; CAR = carapace; DAC = dorsal artery; END = endopodite; EP = epipodite; EX = exopodite; F = furca; GH = brain; H = heart; KM = stomach; MN = maxillary nephridium; OLG = artery of labrum; OT = ostia; OV = ovary; PK = podial branch of a paired segmental lateral artery; R = rostrum; RLG = artery of rostrum; VK = visceral branch of segmental artery.
Fig. 30. *Nebalia bipes*. Cross-section through the heart and its lateral arteries with visceral (VK) and podial (PK) components. (Slewing, 1956.) H = heart; KV = lips of the blood vessel valve; PK = paired podial blood vessel; PS = pericardial septum; TA = outer layer (connective tissue) of the heart; TM = inner layer (muscular tissue) of the heart; VK = paired visceral blood vessel.

ferences from the other Malacostraca are markedly moderated by the statement that †Nahecaris and other †Archaeostraca have a typical malacostracan organization (Fig. 31). The first antenna has a normal structure and has two flagella. The second antenna possibly possesses an exopod. The carapace seems not to be bivalved, and finally, the extremities are not phyllopod-like (Broili, 1928).

Thus †Nahecaris and other †Archaeostraca are important connecting links between Leptostraca and the lower Malacostraca. They are simultaneously original. Recently other representatives of the former “†Archaeostraca” have been totally separated from the crustaceans by Størmer (1944). A highly specific homologous organ, that connects the Leptostraca and the Stomatopoda, is the so-called pro-
cephalon (the segment of the head forward of the second antenna which is movable by a number of specific muscles).

In the Stomatopoda there appears a further articulation of the head, which makes the segment bearing the eyes movable (Fig. 32). The muscles in the head region are almost identical to those of Leptostraca, so that a near relationship between Leptostraca and Stomatopoda is very probable. Although the Stomatopoda have a considerably more exceptional organization than the Leptostraca, a position outside the Malacostraca for the last group has never been discussed.

There are a few original characters in

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**Fig. 31.** †Nahecaris, reconstruction. (Broili, 1928.)

**Fig. 32.** The procephalon of a stomatopod: (A) Dorsal view, (B) Ventral view. (Snodgrass, 1951.) 1 Ant = antennula; 2 Ant = antenna; Cp = carapace; cvMb = cervical membrane; d = fastigial plate; e = ocular plate; Epst = epistome; f = postocular plate; g = posterior dorsal plate of head; Lm = Labrum; Md = mandible; R = rostrum.
Fig. 33. Blood system of Stomatopoda: (A) Larva of the last stage of Squilla. (Balss, 1938 after Claus, 1883), (B) Adult of Squilla oratoria (Balss, 1938 after Komai and Tung, 1931). al = arteria antennularis; an = arteria antennalis; ao = aorta anterior (=cephalica), br = thoracic gill; ca. ao = aorta posterior; c. an = common origin of both arteries of first and second antenna; cao = aorta anterior (=cephalica); ce = arteries of the brain; dp = aorta posterior; en = endopodites of uropods; ex = exopodites of uropods; H = heart; lc = arteria lateralis cephalica; lp = paired lateral arteries of abdomen; o, os = ostia; oc = artery to the compound eye; oph = ophthalmic artery;
stomatopods (Fig. 33): (1) the heart with its paired segmental vessels and the segmental ostia is so original that we can take it as a model for the most primitive vessel system in the Crustacea. Paired vessels and ostia are present for nearly all segments in the thorax and abdomen, and moreover there is a pair for a lost seventh segment in the abdomen. Obviously this original organization of the central vessel system is connected with the presence of gills on the pleopods. But I would prefer to refute the argument that the gills are new organs and therefore the heart should extend secondarily into the abdomen. The heart and all marks connected with it are so clearly original that one can assume that the gills on the pleopods are also primitive relicts. In the Cephalocarida and Notostraca also we have a shift of the epipods onto the exopods. Transference of epipods we know also in amphipods and decapods. Thus perhaps it can be argued that the presence of gills on the pleopods is an original character. This last conclusion is still hypothetical, but I am sure that the heart in the stomatopods is original.

By means of the abdominal arteries one can demonstrate that in the Stomatopoda—in contrast to the other Malacostraca—the number of six abdominal segments is the result of the reduction of the first abdominal segment. This conclusion seems to conflict with the presence of a petasma. This copulatory organ in the Anaspidacea and in the whole Eucarida is formed from the appendages of the first and second abdominal segments. Since the first segment is reduced in Stomatopoda, here the petasma must be constructed by the second and third pleopods. Therefore, a homology with the petasms of other crustaceans is to be excluded. In fact the structure of the petasma in stomatopods shows very little similarity with that in the other groups (Fig. 34). It seems to be an euanaology. A convergent formation of a petasma is also demonstrable in many isopods.

After this digression we have to complete the list of original characters in stomatopods (Fig. 35). There is still to mention (2) the extension of genital organs through the whole body. As special characters we have the subneural artery with a great number of rami communicantes. Furthermore, there are five pairs of claws with the simple structure of subchelae, the surface structure of the whole body is modified in connection with the current of respiratory water, and in addition are the pereiopods and the eyes.

Judged by their original characters the Stomatopoda stand near the basis of Malacostraca and therefore near the phyllocarids. Moreover a specific homology connects these two groups: the movable procephalon with its complicated musculature. Up to the present, in Malacostraca, nowhere is found a procephalon of such a perfect structure.

Nevertheless from the Phyllocarida to the Hoplocarida there is an important phylogenetic step: the furca is replaced by the transformed last pair of abdominal extremities, the uropods. They form to-

\[ p^4-5 = \text{limit between the fifth and sixth abdominal segment}; \]
\[ p6/te = \text{limit between the sixth abdominal segment and the telson}; \]
\[ pl = \text{branches of arteries to the pleopods}; \]
\[ ro = \text{branch of artery to the rostral plate}; \]
\[ rc = \text{blood vessel branches between lateral arteries and the subneural artery (= rami communicantes)}; \]
\[ sc = \text{arteries to the frontal part of larval carapace}; \]
\[ sg = \text{paired segmental arteries}; \]
\[ sn = \text{arteria subneuralis}; \]
\[ th = \text{arteries of the thoracopods}; \]
\[ thp = \text{limit between thorax and abdomen}; \]
\[ up = \text{arteries to the uropods}; \]
\[ Z = \text{artery to the hind median spine of larval carapace}. \]
Fig. 34. The so-called petasma of *Squilla mantis*: (A) first pleopod, (B) second pleopod, showing how it differs from the petasma of Decapoda and Anaspidacea. (Giesbrecht, 1921.) *Cr* = keel; *Fol* = foliated blade; *Ir.an.di.* = frontal distal piece of armour; *Ir.an.me.3* = third frontal median piece of armour; *Ir.an.pr.* = frontal proximal piece of armour; *Pr.a.* = hook-shaped projection; *Pr.tu.* = tubular projection; *Ret* = retinacula.

Fig. 35. Schematic diagram of the organization of a stomatopod. (Siewing, 1960, fig. 4.) *Aoa* = aorta anterior; *Aop* = aorta posterior; *Art. subn* = subneural artery; *Bm* = ventral nerve cord; *Da* = intestine; *Ho* = testes; *Ki* = gills; *KoAu* = complex eye; *Ma* = gizzard; *Md* = intestinal diverticula; *P1–8* = thoracopods; *Pp* = pleopod; *Up* = uropods; *1* = mandible.
gether with the telson a broad terminal paddle. The furca is seen embryologically in a greater number of Malacostraca. An advance is also to be seen in the fusion of the four frontal thoracic segments and a part of the fifth in the stomatopods. This fusion is here, as in many other crustaceans, achieved independently.

The Stomatopoda have much in common with the Anaspidacea within the Syncarida. A specific homology is the so-called *pars ampullaris* on the entrance of the caeca into the pyloric chamber.

The superorder Syncarida is a group poor in species, with an accumulation of negative characters and having many relationships to other Malacostraca. In all species a carapace is wanting, and no breeding mechanism is evolved. Within the group, the first thoracic segment tends to fuse with the head. In this respect the Bathynellacea and the †Gampsonychidea are original—the latter because of their seven free abdominal segments, provided partly with extremities, the former because of their furca in addition to the uropods. A reduction and fusion of abdominal segments is very common in all the other representatives of Syncarida and furthermore of Malacostraca.

In the Anaspidacea, which can be anatomically studied, we see further original characters (Fig. 36): the long extended heart with vessels consisting of a podial and visceral component; the structure of the thoracic legs that carry endites and in which a well-developed praesichium is present. The gonads extend through the whole body in the male.

The statement of closer relationships is based on the following specific homologies: a real petasma and a statocyst in the first antenna connect the Anaspidacea with the Eucarida, especially with the Decapoda. On the other hand, the statocysts in the uropods of †Gampsonychidea point to the Mysidacea. Which character is the more important? That is the problem. The stem
form of syncarids surely had only one pair of statocysts, either in the uropods or in the antenna. Only one of these two can be a homologous organ, the other must be a convergence.

It seems to be uncertain whether the impressions in the uropods of †Gampsonychidea are different organs or even artifacts. If the latter, the relationship of the Syncarida would be more directed to the Eucarida on the basis of the statocyst in the basal joint of the first antenna. But perhaps, also the small depression in the antenna of Hansenomysis is a vestige of a static organ. If this is correct a closer relationship of the Anaspidacea to the Mysidacea, which represent the basic group of the Peracarida, would be indicated.

It is not yet certain whether the lacinia mobilis-like structures, recently found in some South American Anaspidacea, are homologous organs or only convergences to the similar organs in Peracarida and Pancarida. But certainly the Syncarida branched off from the main malacostracan stem earlier than the Peracarida and Eucarida. This follows not only from their geological age but also from their usually original organization in comparison with Eucarida and Peracarida.

Direct phylogenetic relationships to Isopoda and Amphipoda do not exist.

One of the most diverse superorders is the Peracarida. The Peracarida are characterised by a specific breeding mechanism that is unique among arthropods. The eggs, and the embryos after hatching, are kept in a brood pouch of the female that is periodically formed by oostegites and more or less reduced afterwards.

The relationships within the Peracarida have been clarified by the dissolution of an artificial group, the so-called “Arthrostraca,” the main categories of which were the Isopoda and Amphipoda.

In fact, there are several similarities between the two groups (Fig. 37), such as the reduced carapace and the fusion of the first one or two segments with the head. Further, the exopods of the thoracic legs and the eyestalks are reduced. The coxal joints are transformed to coxal plates and some of the thoracic legs have turned forwards, others backwards. Are these common characters specific homologies and are they sufficient to prove a natural relationship?

The greater part of these characters depend on reduction. An independent evolution of such characters is possible, and they cannot prove a close relationship between Isopoda and Amphipoda. We are facing euanalogies.

Concerning the turning of thoracic legs in the two groups, von Haffner demonstrated that it is achieved independently. Thus the coxal plates remain as the only specific character common to both groups. But it is demonstrable that such broadening of the coxal joints is present also in other crustacean groups.

Thus we have grounds for the suspicion that there are no nearer relationships between isopods and amphipods. Their union as “Arthrostraca,” in several cases together with the Syncarida, is artificial. We have to investigate characters that prove a separation of the Isopoda from the Amphipoda. In fact, there are a great number of such characters (Fig. 37): (1) the Isopoda have a maxillary gland, the Amphipoda an antennal gland; (2) gills are formed by epipods of the thoracic legs in Amphipoda but by the pleopods in the Isopoda; (3) in connection with the localisation of the respiratory organs we find the heart in the thorax in Amphipoda;
in the Isopoda it lies mainly in the abdomen. (It is highly probable that it has secondarily transferred to this situation.) Many Isopoda possess a more or less well-developed *arteria subneuralis*, which is absent in all Amphipoda; (4) the differences in the structure of abdominal extremities are important: while the Isopoda have five pairs of pleopods and only one pair of uropods, in the Amphipoda there

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**Fig. 37.** Schematic diagrams of the organization of an isopod (A) and an amphipod (B) for comparison. (Siewing, 1960, fig. 7.) **ANphr** = antennal nephridium; **Ao** = aorta; **He** = heart; **Ki** = gills (= epipodites); **Mars** = marsupium; **Mda** = anterior dorsal caecum; **Mdp** = abdominal caeca of intestine; **S Art** = segmental artery; **Te** = telson; **Up** = uropods; **I** = maxillipede; for other abbreviations see Figs. 29, 35, 36.
are three pairs of so-called uropods; (5) the Isopoda have a manca stage, but this is wanting in Amphipoda; (6) the egg-embryos in the Isopoda are curved dorsally, in Amphipoda ventrally (Fig. 38); (7) in Isopoda the oostegites are almost completely reduced after every brood, in the Amphipoda only their marginal bristles are reduced; (8) further differences are connected with the microscopic structure of the gut, especially of the stomach.

This great number of differences suggest that within the Peracarida there exist other relationships than hitherto assumed, relationships that are based on homologous correspondence.

In fact it is demonstrable that the Isopoda are much more nearly related to the Tanaidacea and Cumacea. They are connected with these groups partly by just those characters in which they differ from the Amphipoda (Fig. 39).

The Amphipoda, on the other hand, are closer to the mysids. The reconstruction of the natural system of the Peracarida by means of homologies shows that isopods and amphipods are end points of two divergent lines of evolution which arise near the mysids. One of these lines comprises the Cumacea, Tanaidacea, and Isopoda; the other line comprises only the Amphipoda. In both lines we have a reduction of the carapace, eyestalks, and thoracic exopods. Along with the reduction of the carapace as the main respiratory organ, and the restriction of the epipods to one pair, we see a functional substitution by the pleopods, which has already begun in the tanaidaceans. The transfer of the heart of isopods to the hind part of the body (Fig. 37) accompanies this secondary transfer of respiratory organs from the thorax to the abdomen. In this connection we can understand the remarkable structure of the heart with its blind caudal end, and the different insertion of arteries from that in amphipods.

Fig. 38. Embryos with rudiments of extremities of an amphipod (A) and an isopod (B), showing the different curvature of the egg-embryo. Embryo just before hatching of an amphipod (C) and an isopod (D). (Siewing, 1960, Fig. 8, after Weygoldt and Nair.)
Fig. 39. Diagram showing relationships within the Peracarida. Each line corresponds to a homologous organ. (A) Amphipoda; (C) Cumacea; (I) Isopoda; (M) Mysidacea; (T) Tanaidacea. (1) Hatching with all extremities; (2) pyloric funnel of the gastric mill; (3) Caeca anteriores dorsalia; (4) antennal nephridium; (5) pyloric bristle-chamber; (6) epipodial-gills on the thoracic legs; (7) oesophageal valve of the gastric mill; (8) tripartite cardial-ventral-piece of the gastric mill; (9) inner surface of carapace functioning as a gill; (10) embryos in the egg curved dorsally; (11) maxillary nephridium in the adult animal; (12) syncytial-like midgut-epithelium; (13) dorsal “hood-plate” in the gastric mill; (14) manca stage of the embryo; (15) stage with reduced oostegites after each brood. (Siewing, 1951.)

In the isopod line we have a greater number of radical secondary transformations, whereas the Amphipoda preserve a few original characters such as the heart and the epipods on the thoracic legs.

The degree of certainty with which we can reach conclusions can be considered a test for the quality of the morphological method. In the current investigations of the relationships within the Peracarida, I have expressed the opinion that the post-embryonic development in Tanaidacea must take a similar course to that in Cumacea and Isopoda. These two orders are, according to our investigations, more closely related to the Tanaidacea than to any other peracarian group. A few years ago Lang (1953) was able to verify this assumption. Here we see clear evidence for the exactness of the morphological method.

The Mysidacea, including the Lophogastrida which are in many respects original, represent the connecting link to other Malacostracan groups, particularly to the Eucarida and Pancarida.

One specific homology between the Peracarida and Eucarida is the arteria subneuralis. In both divisions it is very similar in structure, in the arrangement of the vessels towards the extremities, and in the position of the aorta descendens (Fig. 40).

However, we find an artery leading to
Fig. 40. Comparison of the main vessels of the blood system in Lophogastridea (A) and Decapoda (B), showing the identical position of the aorta descendens (ad) and of the arteria subneuralis (asn) and its branches.

the ventral nerve cord also in Stomatopoda, Anaspidacea and many Isopoda. A comparative investigation shows that these arteries are not altogether homologous structures, but that they have originated independently in several lines. Only for Eucarida and Mysidacea is the homology highly probable. Besides this important connecting link, we find further characters in the structure of the stomach that agree even in microscopical detail. A common root for the two superorders of Eucarida and Peracarida can be accepted.

In the neighborhood of this root stands a group of small crustaceans with very few species, the Pancarida, with the single order Thermosbaenacea (Fig. 41). They are very closely related to the Peracarida by the lacinia mobilis of the mandible. This structure is indeed a most characteristic mark of the Peracarida. But this alone does not suffice to incorporate the Thermosbaenacea in the Peracarida, particularly if we find such structures in other arthropods; it occurs in some newly discovered anaspidacean species (Noodt, 1963).

The uncommon breeding habit of the Pancarida argues in favor of making this group a separate division. The primitive structure of the maxillipeds indicates a branching off below the Peracarida but above the Eucarida. Thus, we can envision the phylogenetic connections as shown in Figure 42.

Finally I should try to answer the question of the stemform of the Malacostraca (Fig. 28). The body consists of the head, eight thoracic and seven abdominal segments; the telson carries a furca. Each of the homologously formed thoracic legs has a three-jointed protopod, an endopod with six joints, endites on several of these joints beside those of the protopod and furthermore two epipods and a flagelliform exopod. The abdominal extremities
possess a similar homologous form, but their structure is far simpler and certainly secondary. The mandible has a palp, but no exopod; the second antenna bears an articulated exopod or squama. The carapace covers all thoracic segments, and these are not fused. Stalked eyes are present. The gut has a stomach, and ventral and dorsal caeca are present in the most anterior part of the midgut. The circulatory system consists of a heart, extending through the whole body and into the hind part of the head. It is furnished with segmental, paired ostia and arteries, each of which is composed of a podial and a visceral component. There are two pairs of nephridia. In addition to the stalked compound eyes a rudimentary nauplius eye may have been present. The gonads extend through the whole body. The openings of the testes lay in the eighth, that of the ovaries in the sixth thoracic segment.

The development is indirect, there is a

Fig. 41. Schematic diagram of the organization of a pancaridan. (Siewing, 1957.) 1.A = antennula; 2.A = antenna; Aa = aorta anterior; 1. Aag = artery to the antennula; 2 Aag = artery to the antenna; Aba = abdomen; Ac = brain artery; Amp = ampulla of the brain artery; Ap = aorta posterior; Cç = carapace; Cz = further brain arteries; Dc = deutocerebrum; Ed = rectum; En, End = endopodite; Ex = exopodite; Fz = frontal blood vessel of the artery of labrum; H = heart; Hd = testes; Km = stomach; Md = mandible; Mdd = intestinal gland; Mx1, Mx2 = maxillula and maxilla; Mxp = maxillipede; Mdm = intestine; Ol = labrum; Olg = artery of labrum; Ot = ostium; Pe = protocerebrum; Pe = copulatory organ; Pip = pleopods; Pp = pereiopods; Ps = pericardial septum; Ra = circumoesophageal artery; Tc = tritocerebrum; Up = uropods; Vd = vas deferens; x = point of curving back of the vas deferens.
Fig. 42. Phylogenetic tree of the Malacostraca showing the possible relations of Malacostraca to other Crustacea (Siewing, 1960, fig. 20).
nauplius larva, and formation of segments follows serially.

This ancestor, compared with other crustaceans outside the Malacostraca, is much more original in many respects. It seems to be unjustified to maintain the opinion that the Malacostraca are the "higher" crustaceans. Certainly some groups of Malacostraca have reached a highly evolved level of organisation, but it is most probable that they branched off very early from the common crustacean stem (Fig. 42).

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VIII
Discussion Following Siewing's Paper

SANDERS: In regard to the so-called primitive second antenna of the Malacostraca, one thinks of a scale and a flagelliform endopod. In †Nahecaris, however, the endopod of the second antenna is reminiscent of the condition in many entomostracans. How is the thoracic limb to be interpreted? I presume what we see in Figure 31 are trunk limb exopods. The supposedly primitive exopod in the Malacostraca is a flagelliform structure and we do not have such an exopod here. Probably the flagelliform exopod in the Malacostraca is a secondary acquisition. It seems that we are trying to impose a caridoid pattern of limb morphology on †Nahecaris that is not necessarily indicated in the reconstruction.

GLAESSNER: †Nahecaris is the one animal of this group in which the appendages are preserved.

ROLFE: One significant feature of †Nahecaris pointed out by Gürich and Hennig, but denied by Broili (1930), concerns the structure of the carapace. †Nahecaris is preserved in pyrite and is normally cleaned with wire brushes, so that any traces of segmentation in the limb or in the carapace, would be obliterated simply by this method of preparation (although setae are beautifully preserved). As the reconstruction (Fig. 43) shows, the carapace is typically rhinocaridid in having a median dorsal plate between the carapace valves, and a movably articulated rostral plate. Thus †Nahecaris does not justify the maintenance of a discrete order †Nahecarida. The body structure shows that it

Fig. 43. Reconstruction of †Nahecaris stuertzi Jaekel, after Broili (1929, Sitzungsbl. d. Bayer. Akad. d. Wiss. math.-naturw. Abt.), carapace structure revised by W. D. I. Rolfe (cf. Fig. 31).
belongs in one of the well known sub-orders of the Phyllocarida †Archaeostraca: the †Rhinocarina. This structure of the carapace with the median dorsal plate is specialized and would seem to exclude †Vahecaris from any truly intermediate position between the †Archaeostraca and the mainly Recent Leptostraca. This is only one character, however, and I would agree with Siewing that the biramous antennules (if Broili’s 1929 reconstruction of these is genuine—cf. his 1928 reconstruction) do suggest a link between the †Archaeostraca and the Eumalacostraca.

GLAESNNER: Do you still consider the Palaeozoic phyllocarids as the ancestors of Recent Nebaliacea?

ROLFE: Yes, although we have no one genus which we can point to as the ancestor for the Leptostraca. Malzahn (1958, Z. deutsch. geol. Gesell., 110:352-359) has found the abdomen of a nebaliid in the Upper Permian of Germany, which shows that the Leptostraca are at least that old.

DAHL: The biramous antennule of the Malacostraca is peculiar; have Siewing or the paleontologists anything to tell us on that?

SIEWING: There is no known reason for this unique feature turning up in the Malacostraca. One could speculate that this is a multiplication of organs. Thus the three flagella in the first antenna of the Stomatopoda indicate perhaps an increase in the sensory surfaces of this organ. Such multiplication of organs is sometimes found in the animal kingdom.

BROOKS: Paleozoic Eumalacostraca have one pattern: a peduncle of three joints and two flagella.

MANNING: When did the three-branched first antenna show up?

BROOKS: We know little about the antennae of the Paleozoic pre-stomatopods. Peach (1908, Geol. Surv. Gt. Britain, Palaeontology, Mem., p. 39) figured †Pernecturus from Scotland with a biramous first antenna.


SIEWING: The conclusion that the first abdominal segment is reduced in Stomatopoda is based only on the comparative anatomy of the blood-vessel system. There is an artery on the limit between thorax and abdomen that leads to no extremity but ends blindly in the tissue. A pair of ostia also corresponds to this lateral artery. Therefore, here the first abdominal segment may be reduced as in Scorpionidea. But there is no embryological evidence; in the embryo, the seventh abdominal segment is reduced as in other Malacostraca.

MANTON: The embryology of a mysid and of Nebalia shows the formation of seven pairs of abdominal mesodermal somites and a seventh ganglion, but no corresponding limb develops on this segment. The uropods arise on the sixth abdominal segment, not the seventh, and the caudal furca is borne by the telson and is not a segmental appendage.

SIEWING: We can see in this a discrepancy in that the uropods are present on the seventh segment in the †Gampsonychidae.

BROOKS: This is one of the errors that has been perpetuated [see Rolfe, 1962, Palaeontology, 4:548; and Brooks, 1962a, p. 168; 1962c, p. 236 for reviews of this error.]
WATERMAN: Siewing mentioned certain similarities between Leptostraca and annelids. Is it unorthodox to assume that the Malacostraca are the central stem of Crustacea and that other so-called primitive ones are simplified or aberrant forms which come from the same basic roots or perhaps from other groups? Are the Crustacea monophyletic?

SIEWING: There are more original characters preserved in the Malacostraca than in other Crustacea. Probably these other Crustacea lost these original characters secondarily.

It is hard to say how we should derive the non-malacostracan Crustacea. It is inconsequential to assume they were derived phylogenetically independently from other Arthropoda. Furthermore, there is no evidence that other groups of the “lower Crustacea” are derived from other aberrant Malacostraca.

A possibility of the relationships of Malacostraca with the other Crustacea is given in Figure 42. I also suggest that the †Archaeostraca probably have an extensive reservoir of characters, from which may be derived the so-called lower Crustacea (Fig. 44).

I have expressed the opinion that the Malacostraca have preserved more original characters than other Crustacea; this is valid for the original groups in this subclass. There is no doubt that they have reached a high evolutionary level in the decapods. This means that other Crustacea lost their original characters more quickly than the Malacostraca (Fig. 42).

WATERMAN: Earlier, Dahl implied that the Entomostraca are more primitive.

DAHL: In the Malacostraca we find a definite number of segments and a division of the body into tagmata. It seems plausible that forms with a large and varying number of segments and a varying number of limbs are more primitive. In all Crustacea most segments are added one by one from a proliferation zone in front of the telson. It is not surprising that in a long series of segments, as e.g. in

![Fig. 44. Possible relations of †Archaeostraca to other Crustacea and to †Trilobita; by Rolf Siewing.](image-url)
the notostracan phyllopods, the posterior segments should have poorly developed limbs or no limbs at all. It seems that there exists a general tendency in a series like this to get more and more imperfect segments further back. Numerous parallels can be found among polychaetes. Such an arrangement appears to me more primitive than the arrangement in malacostracans. The mandibular palp was specially mentioned; it is true that there is no mandibular palp in adult branchiopods and cephalocarids, but it is present in the larvae, and it is well developed in many maxillopods and ostracods. A primitive heart is found in the phyllopods. The compound eyes are more highly differentiated in the malacostracans than in any other Crustacea. I think that e.g. cephalocarids, many branchiopods and, among the maxillopods, at least the mystacocarids are at a more primitive level of organization than the Malacostraca as we know them today. But the Malacostraca may have separated from other crustacean evolutionary lines at an early stage of differentiation and have certainly retained various primitive traits.

SANDERS: Claus (1876, Untersuchungen z. Erforschung d. genealogischen Grundlage des Crustaceen-Systems. Wien) long ago pointed out that the malacostracan palp was secondarily derived; from ontogeny we know that there is a biramous palp in the nauplius. The palp then disappears at the end of the naupliar series resulting in a palpless mandible. At a later developmental stage the characteristic uniramous palp appears.

SIEWING: Examples of the temporary absence of an organ in the embryogeny or morphogeny are distributed throughout the animal kingdom (e.g. lophophores in phoronid larvae, and in Bryozoa the loss of the gut during metamorphosis). A temporary disappearance of an organ does not necessarily mean that if it reappears it is to be considered secondary.

SANDERS: In this case, however, the palp in the nauplius is terminal. The secondarily acquired uniramous palp appears much more proximally on the limb, fairly close to the molar process. I interpret this to mean that these are not homologous.

SIEWING: We have more extensive translocations in the ontogeny of animals. For example, one would have to conclude on the same basis that the carapace of cirripedes is not homologous with that of other Crustacea. Another example may be derived from the Bryozoa (Membranipora), where the gut disappears in ontogeny and reappears after metamorphosis from another germ layer and in another position. Nobody doubts that the gut of larva and adult is homologous.

MANTON: The embryonic mandible of Nebalia and of Hemimysis is long and finger-like. The gnathobasic part grows out in late stages and the distal part remains as the palp. There is no degeneration of a palp and a regrowth.

SANDERS: I'm thinking of the penaeid decapod developmental series—the naupliar, protozoal, mysis and postmysis series.

GLAESNNER: Are the stomatopods primitive or could they have arisen from a modification, not of any of the existing Malacostraca, but of some primitive Malacostraca which we know only as fossils? They have a peculiar habit; their locomotion is different from that of other Malacostraca, and they developed their abdomen perhaps more strongly in connection with these habits and locomotion. The division of the head may have some-
thing to do with their habits, rather than being altogether a primitive feature. I cannot see, however, where the amphipods would come from other than somewhere near the origin of the isopods. Siewing’s diagram does not place them far from the origin of the isopods, tanaids, and cumaceans. Again, there is a peculiar habit of locomotion in amphipods. This group did not differentiate into anything, as did the decapods or isopods, but nevertheless it was successful.

On a different point, Heldt (1954, Bull. Soc. Sci. Nat. Tunis, 6:177-180) has called attention to similarity between a penaeid larva and Walcott’s \( \dagger \)Waptia. This might have been mentioned when we discussed the question of whether the Malacostraca were more primitive than we think.

ROLFE: The latter idea did not originate with Heldt; both Fedotov and Henrika (see references in Rolfe, 1962, Breviora M.C.Z., 160:5-6) discussed the similarity of \( \dagger \)Waptia to a penaeid protozoa. As they and others have pointed out, the adult must have been large if \( \dagger \)Waptia was a larva, and indeed large carapaces are found in the Burgess Shale which could be regarded as the adults. But again, as Manton has pointed out, we need to look at it and see how close is the similarity. The general \textit{facies} of it is the same but, if we are to believe Störmer, \( \dagger \)Waptia has a trilobite limb again, which is far from any protozoal limb.

HESSLER: If the Malacostraca is the most specialized and advanced subclass of the Crustacea, why is it alone in having the supposedly primitive abdominal appendages? Either this means that the primitive crustacean from which all subclasses were derived had a larger series of appendages than we find in the so-called entomostracan groups, or it means that a segment which has lost its appendages through evolution is capable of getting them back again.

GLAESNTER: I don’t think that it would get them back. Siewing’s Figure 28 shows two groups of appendages, and they don’t work together. They serve different purposes at different times: pleopods for swimming in the swimming forms are adapted to different functions where the abdomen is reduced. The pereiopods have acquired specialized functions. Preservation of abdominal appendages in the Malacostraca does not exclude the possibility that they are the more advanced Crustacea. There is much scope for reductions in the lower Crustacea, and the preservation of certain primitive features in the Malacostraca.

LOCHHEAD: On the question of whether a limb once lost could ever be regained, some interesting findings were reported by Etienne Wolff in a lecture at Woods Hole in 1961. Wolff stated that in the embryonic limbs of birds and other vertebrates it is possible to cut out some of the tissue which would develop into a dominant digit. When this is done, a suppressing effect is removed, and digits which have long since disappeared in evolution may grow in a quite normal fashion. Thus the genes for the vanished digits are still there, despite the seeming total loss of the phenotypic structures.

GLAESNER: Is it really agreed that at any stage in crustacean evolution the telson could have been lost? In the decapods the abdomen is reduced in a most extreme way and yet the telson cannot be lost.

DAHL: I never intended to imply that the telson was lost, just that segment formation stopped at an earlier stage.
SIEWING: Have you any model or perhaps an embryological clue in the Malacostraca for this assumption?

DAHL: Only that crustaceans appear with large variations in the number of segments. We have short crustaceans, such as the ostracods where limbs go all the way back and with few segments, the copepods which have few segments but no limbs on those posterior segments which should correspond numerically to segments not so far back in Malacostraca, and some of the phyllopods or anostracans, that have a far greater number of limbs than the Malacostraca.
IX

Jaw Mechanisms of Arthropoda with Particular Reference to the Evolution of Crustacea

By

S. M. Manton

British Museum (Natural History) and Queen Mary College, London

The elucidation of phylogenetic relationships within the Arthropoda is essentially speculative since the fossil record is non-committal. The facts concerning jaw mechanisms of arthropods which have recently been worked out bring to light considerable evidence concerning interrelationships and phylogeny within the Arthropoda which is not of a speculative nature. Arthropods can be classified on their head structure alone and the form and use of the mandible together with the anterior sensory equipment is all important in determining the various types of head structure. Many widespread assumptions concerning arthropod jaws have been found to be untenable. The most important of these are: (1) that the mandibles in all classes correspond, (2) that biting in the transverse plane is a primitive arthropod attribute, and (3) that many mandibles are worked by simple adductor muscles without any abductors, the abductor force being, supposedly, elasticity of the cuticle and/or hydrostatic pressure.

It is important to use living animals in order to determine the exact movements which are employed, and full use of technical methods is essential in elucidating anatomy. “Generalised” simplified anatomy as a basis for consideration of jaw mechanisms is most misleading and unsuitable. The head endoskeleton of most Arthropoda has been inadequately described. The form and function of head apodemes and segmental tendons, their movement and/or rigidity, play an integral part in the feeding mechanisms of many animals. The study of jaws must of necessity embrace a comparative survey of head endoskeleton and its associated musculature as well as the skeleto-musculature of the jaws themselves. A comparative detailed study of the anatomy and mechanism of movements of jaws shows clear evolutionary trends and in many cases points out plainly which are the more primitive and which the more specialised types.

It is generally agreed that an ability to tackle large and hard food is an advance on the feeding on soft food. The strongest biting takes place in the transverse plane but this does not appear to be a primitive attribute in either Crustacea or Hexapoda.

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1 A full account of this work, which covers the myriapods and insects, will appear in Phil. Trans. Roy. Soc., London, Ser. B.
Only in Limulus (king crab) and the Myriapoda does such biting appear to be primitive and it has certainly been independently evolved in both these cases.

It is not usually appreciated that approximation and parting of paired coxae or coxal endites does not necessarily need any specific adductor or abductor muscles or an axis of movement supported by more than one close union of the jaw on the head. When a walking or a swimming leg swings about an axis situated exactly in the transverse plane the promoter and remotor movements do not alter the distance between the coxae. It is immaterial whether the axis of swing lies horizontal, i.e. on the ventral side of the body, or whether the axis lies obliquely up the side. But if the lateral end of this axis lies a little posterior to the mesial end, as in the walking legs of an iuliform diplopod, the remotor swing brings mesially directed coxal spines or lobes together and the promoter swing parts them. Such movements can also be seen in some branchiopod thoracic limbs, and it is clear that an exploitation of this effect has led to apparent adductor-abductor movements of incisor processes which are effected by promoter and remotor muscles, very little direct coxal adduction or abduction taking place (Fig. 50).

Two movements seen in typical ambulatory limbs have been utilised in the evolution of jaw mechanisms. (1) The common promoter-remotor swing of the coxae on the body and (2) the direct prehensile movement of a telopodite or telopodite and coxa causing gripping or adduction in the transverse plane. Type (1): the promotor-remotor swing appears to have been used by the Crustacea and Hexapoda in mandibular evolution giving first a mandible capable of scratching, squeezing or grinding small particles without biting and being modified secondarily to give strong holding and cutting in the transverse plane. Type (2): leg movement has been exploited by the Myriapoda and Chelicerata in giving direct transverse biting.

Mechanical difficulties have confronted all arthropods during their attainment of biting jaws capable of dealing with hard and large food. Adduction is easy but abduction of mandibles occupying the whole head width presents important mechanical difficulties which have not previously been recognised. These microengineering problems have been resolved in different ways by the various classes of arthropods. Sometimes the resolutions are entirely different one from another and must indicate independent phylogeny. Sometimes the resolutions show convergent resemblances superimposed upon different basic morphologies, and, as with locomotory and burrowing mechanisms, the anatomical changes which become associated with each type of resolution of the biting problem become evolutionary one-way streets.

The ontogenetic development of jaws in arthropods shows that they arise in two different ways. The present-day series of mandibles of larval and of adult Crustacea shows the unquestionable derivation of the mandible in this class from the proximal endite or gnathobase and proximal part of the coxa, the distal telopodite in the adult being reduced to a bi- or a uniramous palp or it may be absent. Biting is similarly done by the leg base in Limulus and in the Arachnida and the embryonic derivation is the same. In the Onychophora-Myriapoda-Hexapoda assemblage, the mandible, on the contrary, is formed from the whole of an embryonic limb. In the Onychophora the two terminal
jaw blades resemble the two claws on each walking leg. The unsegmented mandibles of insects are developed from a whole limb rudiment, the most distal part forming the gnathal armature or mandibular tip. Most of the myriapod classes possess jointed mandibles, a feature correlated with the manner of use of the mandibles and providing flexures serving adduction in the transverse plane, as in a telopodite. There is no reason to suppose that myriapod and insect mandibles are not of the same whole limb type although the differences in the mechanisms of movement and in details of morphology are so great as to preclude the origin of the one from the other.

That a basic promotor-remotor swing has been employed by the gnathobasic mandibles of Crustacea and the whole limb mandibles of hexapods is seen to be a parallel evolution, and the basic differences in mandible derivation of these two groups must indicate the independent evolution of mandibles within them. Biting in the transverse plane has been independently evolved several times within the Crustacea and also within the hexapods. There are great differences in the use of the gnathobases in Limulus and in the Crustacea, differences which suggest a deep-seated lack of affinity between the Merostomata and Crustacea indicating that jaw evolution has proceeded independently in these two groups also.

THE MORE PRIMITIVE TYPES OF CRUSTACEAN JAW MECHANISMS

A survey of the mandibular mechanisms of the more primitive Crustacea shows a surprising uniformity in basic form, those of Chirocephalus and Daphnia among the Branchiopoda and Heminysis among the Malacostraca are extraordinarily alike and primarily serve the grinding or squeezing of soft fine food. Greater biting ability is present in Paranaspides and Anaspides. The molar areas of these mandibles do not function by a basic adduction of the jaws from their single dorsal point of closest union with the head. The primary movement is a derivative of the promotor-remotor roll of a walking leg.

Figure 45 shows a side view of the mandible of Chirocephalus (A) at the end of the promotor forward swing and (B) at the end of the remotor backward swing, the axis of movement being dorsoventral. The latter movement rolls the molar areas forwards and across each other as indicated by Figure 46. The musculature causing the promotor-remotor swing is shown in Figures 46 and 47. The head endoskeleton consists of a wide transverse mandibular tendon, anchored by struts to the cervical groove and linked with other units developed from basement membrane. The remotor muscles are the longer, larger and stronger; they comprise muscles 4, 5a and the direct muscle 5c uniting the posterior margins of the mandibles. The promotor muscles 3 and 5b roll the molar processes across each other in the opposite direction and can cause slight abduction owing to the exact shape of the mandible. Food arriving at the point marked x on Figure 46A, by a route situated close to the ventral surface of the body (see arrows on Figure 49E) emerges at y, Figure 46C, and is sucked into the mouth. The frequency of the mandibular grinding movements is much less than that of the filtratory trunk limbs.

At times slight direct abductor movements occur which part the mandibles.

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2 Paranaspides and Anaspides are essentially similar in the aspects of mandibular mechanisms here considered.
The dorsal point of close union of the mandible on the head is not a firm articulation; the mandible can slide up and down against a small sclerotised rib situated laterally in the cervical groove (Fig. 48C). Muscles 5d and 5e can strongly adduct the mandible during the remotor swing. Contraction of muscles 6 and 5f and relaxation of muscles 5d and 5e result in sliding the dorsal part of the mandible

![Diagram of Chirocephalus diaphanus](image)

Fig. 45. (A) Lateral view of the head of *Chirocephalus diaphanus* Prevost showing the mandible in its position of extreme forward roll (promotor swing) about a dorsoventral axis. The only point of close union with the head lies dorsally at the black cross (see Fig. 48C). (B) The eye and first trunk limb are in the same position as in A, but the mandible is at the end of the backward roll (remotor swing), displaying the straight anterior mandibular margin and the inward and forwardly directed molar process. (C) Transverse view of the mandible on the body.
Fig. 46. (A-C) Diagrams to show the effect of a backward remotor swing through 50° about a vertical axis of the lateral parts of a pair of cardboard shapes resembling an anostracan mandible in frontal view. (D) Represents a frontal section of the right mandible of Chirocephalus viewed from above, the position of the free ventral portion of the mandible, bearing the molar area, being indicated by a dotted line. Muscles 5a cause the backward remotor roll of the lateral part of the mandible, such as seen in A-C, which swings the molar areas forwards and against each other; muscles 5b promote the recovery swing.
Fig. 47. Transverse views of the head of *Chirocephalus diaphanus* passing in front of and through the mandible at progressively more posterior levels. A-B lies just in front of the mandible. Level A shows the oesophagus (stippled) uniting the mouth with the foregut and the cut longitudinal bar of head endoskeleton formed by an elaboration of the basement membrane. Level B passes through
slightly downwards and inwards, so abducting the molar areas. Biting in the transverse plane by more specialised Crustacea is not developed from these small adductor-abductor movements mediated by muscles 5d, 5e and 5f and 6, but by a modification of the much stronger muscles causing the promotor-remotor roll.

In Hemimysis the axis of promotor-remotor swing is no longer vertical; the dorsal end is tipped backwards a little, a position further accentuated in Paranaspides and Anaspides (Figs. 49F and 51). The axis also lies near to the anterior margin of the mandible. An incisor process used for biting projects from the mandible far from the axis. The promotor-remotor swing of the mandible now not only rolls the paired molar processes across each other as in Chirocephalus, but the shape of the mandible is such that this rotation results in approximately transverse biting by the incisor processes, as shown in Figure 50 for Anaspides. The musculature is little changed, promotor muscles 3 and 5b and remotor muscles 4, 5a and 5c correspond with those of Chirocephalus, an additional remotor muscle 2 pulls outwards from the anterior margin of the mandible, and remotor muscle 4 is much enlarged arising from a strong posterior mandibular apodeme. Muscle 6 arises in Hemimysis, as in Chirocephalus, near the dorsal apex of the mandible (Figs. 47D, 53C). This muscle arises from the anterior border of the mandible, lower down in Paranaspides (Fig. 51), where it forms an effective promotor inserting on the tendinous endoskeleton as in Hemimysis (Fig. 53C). The head endoskeleton of Paranaspides and Anaspides is mainly tendinous as in Chirocephalus but more elaborate, consisting of the segmental tendons of mandible, maxillule and maxilla linked by paired longitudinal bars, the whole anchored to the body wall by many struts (Fig. 52).

The shift in the position of the axis of promotor-remotor swing in these Syncarida enhances the apparent adductor-abductor movement of the incisor processes while still maintaining adequate grinding between the molar areas which lie close to the axis of movement.

It is clear that (1) the promotor-remotor swing of the mandibles of Chirocephalus and Hemimysis is caused by antagonistic muscles; (2) that minor direct adductor

the origin of this endoskeleton from the lateral basement membrane, the transverse connection between the longitudinal endoskeletal bars, and their fibrillar suspension from the dorsal body wall. The mandibular promotor muscle 3 inserts dorsally on to a cone of basement membrane. Two lobes of digestive gland are cut. Level C shows the anterior face of the mandible. Level D passes through the middle of the mandible and its dorsal articulation (see Fig. 48C), the posterior margin of the mandible being visible behind. The median connection between the mandibular tendon and the endoskeletal plate uniting the paired longitudinal endoskeletal bars lies on the posterior side of the mandibular tendon, and is shown also in level E. Level E passes through the posterior margin of the mandible just in front of its union by ample arthrodial membrane with the head. The endoskeletal link between the inter-paragnath groove and the transverse plate uniting the paired longitudinal endoskeletal bars lies well behind the mandible. Muscles 3, 4, 5, 5b, 5c and 6 are represented in Paranaspides and Anaspides (Figs. 51-53). The prefixes to muscle numbers “adductor” and “abductor” signify muscles causing direct movements in the transverse plane; “remotor (adductor)” and “promotor (abductor)” signify muscles primarily causing the remotor-promotor roll which facilitate the rolling together of the molar areas in Chirocephalus or secondary transverse biting in derived crustacean types (Figs. 51-53 and 55-57).
Fig. 48. Transverse sections showing the dorsal union of the mandible with the head in *Chirocephalus diaphanus*, *Hemimysis lamornae* and *Petrobius brevisyllis*. Heavily sclerotised cuticle is shown in black, slighter sclerotisation is indicated by stippling, and arthrodial membranes by interrupted lines. (A) Through the ball and socket joint of *Petrobius brevisyllis*. The ball is highly sclerotised, the inner layer of cuticle (stained blue with mallory, stippled here), becoming progressively thicker as distance from the ball increases. The socket is formed of thickened cuticle under the pleural fold, and is united by a stout fibrillar suspension to the dorsal wall of the cranium.
Fig. 49. (A-C) Diagrammatic transverse views of half of the body of an arthropod to show the several positions of the axis of swing of the coxa on the body, dotted line between the crosses. In each case the axis lies in the transverse plane of the body, (A) as in Crustacea and Diplopoda, (B) as in Symphyla, (C) as in Chilopoda. (D) Represents an end-on view of a typical coxa-body joint, the axis of swing being marked as in Figures A-C. This axis passes through the points where the arthrodial membrane (white stipple) between the coxa and body is shortest (see Manton, 1958b). (E-G) Diagrammatic views of sagittal halves of the heads of *Chirocephalus diaphanus*, *Paranasipes lacustris* and *Ligia oceanica* to show the positions of the axis of the mandibular roll which is indicated by the interrupted line between the dorsal union of the mandible and cranium (marked by a cross) and the black spot; the positions of the molar areas and incisor processes with respect to this axis; and the routes to the mouth of fine food (upper arrows) and of large food (lower arrows). The direct transverse mandibular muscle 5c and the transverse mandibular tendon are cut. Promotor, muscle 3, and remotor, muscle 4 (abductor and adductor), are homologous in the three animals, muscles 3 and 4 both possess apodemes in *Ligia*, and a posterior remotor (adductor) apodeme is present in *Paranasipes*. Further details are shown in Figures 45-47, 51-52, 54, 55.

(B) Through the point of closest union of the head and mandible of *Hemimysis lamornae*, no articulation is present and the thick arthrodial membrane is united by a fibrillar suspension to the basement membrane of the side wall of the head. (C) The dorsal articulation of the mandible of *Chirocephalus diaphanus*, formed between the sclerite of the cervical groove and the apex of the mandible, is often in the position shown, but the sclerite can project above the mandible, according to the position of the latter. The basement membrane is enlarged dorsally as shown.
Fig. 50. Ventral view of the mandibles of *Acanthodes tasmaniae* Thomson to show the extreme range of movements about the axis of roll (see Figs. 49F and 51), which are possible to the animal. The dorsal end of the mandible and its point of closest union with the head lie far below the plane of the paper. The black spot bearing an arrow marks the same spot on the mandible in all figures. A shows the extreme end of the forward (promotor) movement, rather more extreme than usual in normal feeding. B-D show the progressive backward (retractor) roll which brings the incisor processes together in the transverse plane, moving along a hollow in the labrum.
Fig. 51. Lateral view of the head of *Anaspides tasmaniae* Thomson to show the positions of mandibular muscles and the direction of the principal mandibular movements. The cross indicates the close dorsal union of the mandible and head under the shallow pleural fold whose free margin is shown by a heavy line. The dotted line between the cross and black spot marks the axis of the rolling movement. The lightly dotted line shows the anterior margin of the mandible on to which muscles 3 and 6 pull. The posterior margin of the mandible gives origin to the hollow apodeme bearing dorsolateral muscle 4, and from the posterior edge and posterior part of the mandibular face arises transverse muscle 5c. Muscle 3 and part of muscle 6 arise from arthrodial membrane near the mandibular edge. The lateral part of the transverse mandibular tendon is shown in black; from it muscles 5a and 5b pass outwards and backwards and outwards and forwards, respectively, to the concavity of the mandibular cuticle.
and abductor movements occur in Chirocephalus and Hemimysis, and the tilt of the axis of swing, more marked in the Syncarida than in Hemimysis, results in the promotor and remotor muscles indirectly causing adductor and abductor movements of the incisor processes. These crustacean mandibles are not worked by only three muscles comprising no abductors, as claimed by Snodgrass (1950), and no elastic forces reside in arthrodial membranes sufficient to cause either abductor or promotor movements. Only sclerotised cuticle can provide such a force and arthrodial membranes linking the mandible to the head are typically lacking in sclerotisation which, if present, would be a hindrance to the effective movements. In certain cases sclerotised cuticle does provide a mechanism for recovery movements, e.g., abduction of the maxillule by the elasticity of the maxillulary sclerite (Jackson, 1926).

**TRANSVERSE BITING IN CRUSTacea**

Strong transverse biting in Crustacea has been evolved many times, but by different means, and two examples will be considered below, that of the Isopoda, of particular interest because of certain superficial resemblances to hexapods, and the resolution adopted by the crayfish Astacus fluviatilis (Potamobius astacus L.) and the crab Carcinus maenas (L.) among the decapods. Ligia is a large-food feeder capable of biting into food masses and swallowing sizeable particles via a wide oesophagus, the route for the food being from below upwards (see lower arrow in Figures 49F, G; cf. the narrow oesophagus of fine-food feeders, Fig. 49E). The axis of promotor-remotor swing of the mandible, already sloping backwards in the Syncarida, is approximately horizontal in Ligia and the pre-axial part of the mandible is short, forming a very robust hinge extending along the dotted line between the cross and the black spot on Figure 54. The promotor-remotor swing now becomes a wide adductor-abductor movement in the transverse plane, the gape being also wide (cf. small gape in fine-food feeders). The musculature moving the mandible is a derivative of the primitive malacostracan type, and the head endoskeleton is more robust. The small pair of maxilla 1-2 apodemes of a mysid or Parapaspides is very large in Ligia, forming paired bars (the sternal alae of Jackson) extending through the head, and anchored on to the surface cuticle, entirely replacing the tendinous endoskeleton, which consists of transverse mandibular, maxilla 1 and maxilla 2 tendons and their longitudinal connections in Hemimysis and Anaspids.

Reference to Figures 47 and 53 shows that the presence of a large mandibular tendon linking transverse mandibular muscles must inhibit wide abduction since great changes of length in the transverse muscles would be necessary if the gape should be wide. The elimination of the transverse mandibular tendon and the reduction of the transverse muscles arising from the mandibular concavity to a remnant (5a on Figure 56A), free the mandible of this restriction and permit the employment of a wide gape. Remotor muscle 4 in Ligia is very elaborate, arising in many sectors from a large and complex apodeme corresponding with that of the lower Malacostraca. These muscles fill a major part of the head cavity (Figure 55). The abductor mechanism is very ingeniously contrived. A long thin apodeme leaves the pre-axial margin of the mandible and slopes upwards and out-
wards into the “cheek” (Fig. 54 and left side of 56A), and from the tip of this apodeme four small sectors of muscle 3 slope towards the middle line (Figs. 55 and 56A). Contraction of muscle 3 pulls the tip of this apodeme slightly towards the middle line and this movement results in wide abduction of the incisor processes and the extension of muscle 4. The remains of the transverse muscle 5a inserts now on the longitudinal head apodeme and serves as a weak adductor pulling at a rather poor mechanical advantage. The molar areas are still present on the mandible but their triturating ridges are restricted to the proximal edges which alone come in contact as the mandibles swing together.

Thus transverse biting and a wide gape have been achieved in the Isopoda by the adoption of a horizontal position of the axis of swing of the mandible, a dissolution of the segmental tendon system of the head, together with most of the transverse muscles, and by the great elaboration of promotor and remotor muscles 3 and 4,

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**Fig. 52.** Sagittal half of the head of *Anaspides tasmaniae* Thomson with the alimentary canal and digestive gland removed to display the cephalic endoskeleton and mandibular musculature. The posterior mandibular apodeme and the transverse segmental tendons and their connectives are shown in white, the median endoskeletal bridges cut in the sagittal plane are hatched. The positions of the mandibular margins and of the axis of movement between the dorsal union with the head (a cross) and the black spot are indicated. The web of fibrous connections between the transverse mandibular tendon, the lateral longitudinal tendinous bars and the three dorsolateral struts are more complex than shown. The levels A-D mark the planes of sections shown on Figure 53.
Fig. 53. *Paranaspides lacustris* Smith. (A-D) Thick diagrammatic transverse sections of the head at the levels indicated on Figure 52, at A-D, to show the mandibular muscles and cephalic endoskeleton. The position of the axis of movement passing from the dorsal union of the mandible and head, marked by a cross on D, to the black spot on A is projected on to the other figures which show only part of the obliquely situated mandible. The designations (adductor and abductor) to the muscles shown are made in the sense described in the text; these do not signify a basic adduction and abduction in the transverse plane, but a remotor-promotor roll. Level A shows the cuticular unions ii and iii of the paired longitudinal tendinous bars, iii being close to the oral angle braced by the termination of the transverse mandibular tendon shown in level B. Level B shows the lateral longitudinal tendinous bar, the anterior dorsolateral mandibular remotor (adductor) 2, and the anterior extension of the transverse mandibular tendon. Level C shows the transverse mandibular tendon bearing remotor (adductor) and promotor (abductor) fibres (see labelling on level B), the transverse union of the paired longitudinal endoskeletal bars at the level where they bear promotor (abductor) 6 (see the labelled dotted outline of the origin of the muscle in Fig. 52), and promotor (abductor) 3 arising mainly from the arthrodiral membrane below the carapace fold. Level D shows the longitudinal endoskeletal bar and its tendinous suspensions iv and v, the hollow posterior mandibular apodeme with its dorsolateral remotor (adductor) 4, and the transverse mandibular remotor (adductor) 5c lying behind and independent from the mandibular tendon. (E) Oblique horizontal section just below the mouth to show the mandibles and their molar processes at the end of the remotor roll, the transverse mandibular tendon, which supports the lower end of the axis of movement (black spot), and the transverse muscles.
which now become, in effect, abductor and adductor in function. The triturative ability of the mandibles, favoured by a vertical position of the mandibular axis of swing (as in Chirocephalus), is decreased by a slope of the axis shifting towards the horizontal, a position giving maximum efficiency to incisor process biting by muscles pulling from the same side of the hinge as the cutting blades.

The decapod transversely biting mandibles are derived from the same basic malacostracan pattern seen in Hemimysis and Paranaspides, but lever principles are employed and different muscles from those of Ligia become the effective abductors and adductors. A strong hinge is present but the cutting blades and the muscles supplying the adductor force are situated on opposite sides of the hinge in contrast to Ligia.

Fig. 54. Ligia oceanica Roux. Lateral view of the head with the pleural plate and leg of the second thoracic segment cut short. The heavy dotted line marks the axis of movement of the mandible, passing through the same morphological points marked by a cross and black spot as shown for Chirocephalus, Paranaspides, and Anaspides on Figures 45, 47, 49, 51, 53. Arthrodial membrane is indicated by white stipple on black. The “tergal ala” apodeme of the head is visible through the arthrodial membrane passing to the second thoracic segment, here stretched a little. The notch, marked by a small circle, carries a cuticular thickening, suspending: the maxillipetal sclerite, the alar bar of the superficial sclerite system of the head wall, and the inferior lateral pterygoid process which forms one arm of the base of the “sternal ala”—a principal head apodeme (see Fig. 55).
Fig. 55. Ligia oceanica Roux. Sagittal view of left half of the head to show the longitudinal apodermal endoskeleton, the mandible and mandibular muscles. The mandibular cuticle is drawn alone in Figure 56, B from the same aspect. The cut through the ventral cuticle of the head passes along the "median bar" (a superficial scute), and one arm is shown of its anterior bifurcation which ends on the paragnath, the cut end of the other being hatched. The antennal muscles passing to the genal fossa region of the cranium (between the circle and cross on Fig. 54) are removed; they pass between the mandibular adductor and abductor muscles. The extrinsic muscles of the maxillule and maxilla from the tergal ala and sternal ala (see dotted arrow) and the maxillipedal muscles from the maxillipedal sclerite andalar bar are also omitted. The mandibular hinge on the head lies between the cross and black spot. The broad mandibular adductor apodeme leaves the parasagittal edge of the mandible and passes directly upwards (see Fig. 56, A). The narrow mandibular adductor apodeme leaves the anterodorsal edge of the mandible close above the hinge and passes outwards and upwards (see left side of Fig. 56, A). The mandibular adductor muscle forms three main sectors; a posterior sheet passes from the proximal posterior edge of the apodeme upwards and backwards to the tergal ala. The most bulky sector fans out from the apex of the apodeme to the whole dorsal and anterodorsal face of the cranium above the "frontal line" (half of it is cut away to expose the adductor muscles); and an anterior sector arises from a tuft of fibres half way along the anterior edge of the apodeme and inserts on and around the "supra-antennal line" (see Fig. 54) of the cranium. The mandibular adductor comprises 4 sectors: two pass to the dorsal cranial wall just median to the eye; one passes to the " marginal line" (see Fig. 54) behind the eye; and another to the anterior face of the tergal ala. The principal head apodeme the "sternal ala" arises from a maxilla 1-2 intucking (white stipple) bearing the inferior lateral pterygoid process and the maxillary pterygoid process in its outer and inner angles, respec-
Figures 57A, B, show side views of the mandibles of the crayfish and crab with the lateral parts of the head removed as far as the union of the mandible with the head. The axis of swing of the mandible, marked by a dotted line, is oblique and in both animals allows biting in the transverse plane. In the crayfish the main hinge is formed by the elongation of the dorsal articulation along the anterior margin and there is no freedom at the point marked by the black spot as in the weaker rolling type of mandible (Chirocephalus and Paranaspides). In the crab the dorsal articulation is very weak and a strong anterior articulation near the black spot lies between the epistome and mandible at the base of the mandibular palp.

The muscular system of Hemimysis and Paranaspides is clearly recognisable in decapods but additional apodemes are present. A small one projects from the anterior margin of the mandible in the crayfish and a much longer one in the crab (white on Figure 57A to D). In the crab the anterior ventral position of the hinge enables the morphologically dorsal part of the mandible to be in line with the anterior apodeme so that the two form a very long lever (as noted by Snodgrass, 1950) which is responsible for the strong bite of the crab.

In the crayfish, muscle 4 remains the principal adductor, but becomes very small in the crab. Remotor (adductor) 2 (adductor lateralis mandibulae of Schmidt, 1915) from the anterior apodeme passes outwards to the lateral head wall in both decapods, pulling at a much more advantageous angle than in Anaspidns and Paranaspides (Figs. 51, 53B and 57D) owing to the presence of the anterior apodeme. This muscle in the crab is very large and pulls from a tendinous flap set at a sharp angle to the tip of the apodeme, so providing plenty of surface far from the hinge for the origin of muscles 1 and 2. Muscle 2 of Hemimysis and Paranaspides corresponds with the separate adductor 1 and 2 of the crab, passing forwards to the front wall of the head (Figs. 57B, C, D). Muscles 1 and 2 in the crab are now the principal adductors superseding muscle 4. Part of transverse muscle 5a is present in the crayfish but inserts on the head endophragmal skeleton, no transverse tendon being present, and muscle 5c is absent; these features facilitate the wide gape of the mandibles. In the crab muscle 5c is absent and 5a further reduced. Promotor (abductor) muscles 3 and 6 are present in crayfish and crab as in Paranaspides, but with the dissolution of the transverse tendon muscle 5b is absent. Muscle 6 leaves the anterior apodeme in crab and crayfish and passes inwards and backwards to the endophragmal skeleton (Fig. 57A, B, C, the "abductor major" of Schmidt, 1915, and the "internal abductor" of Pearson, 1908). In the crab muscle 6 is much more bulky than muscle 3 and forms the principal antagonist of muscles 1 and 2.

The lever formed from the combined upper mandible and anterior apodeme in the crab is several times the distance between the anterior mandibular articulation and the cutting edge. An extensive dis-
Fig. 56. (A) Posterior view of the head of Ligia oceanica, intact dorsally and laterally as far as the notch surrounded by the circle, marked as on Figures 54, 55. Ventrally the mouth parts are removed leaving the left mandible and the right paragnath and mandible. The principal head apodeme, the sternal ala, is cut, and its process bears the very small remains of mandibular remotor (adductor) 5a (cf. Figs. 51 and 53.). (B) Sagittal view of the mandibular cuticle devoid of muscles seen from the same aspect as in Figure 55.
Fig. 57. Diagrams showing the mandibles and their movements (A) in the crayfish Astacus fluviatilis (Potamohipus astacus L.) and (B-E) in the shore crab Carcinus maenas (L.) for comparison with Chirocephalus, Anaspides and Ligia. The direction of pull of muscles 1 to 6 is shown by arrows on A and B. For further details of the muscles see Schmidt, 1915, for Astacus and Pearson, 1908, for Cancer. (A and B) Lateral views of the right mandible of crayfish and crab with the head cut back; a tendon passes forwards from the anterior mandibular apodeme to muscles 1 and 2 in the crab. (C) Dorsal view of the crab to show anterior and posterior mandibular apodemes and their muscles, the position of the gnathal lobe being shown by white dotted lines. (D) Anterior view of the crab with the head cut back to show the anterior mandibular apodeme and its muscles together with the anterior articulation of the mandible with the head. The mandible and its muscles are foreshortened in both B and D. (E) Ventral view of mouth region of the crab with the mandibles fully open disclosing the labrum between the mandibular palps.
Fig. 58. (A) The prosoma of *Tachypleus tridentatus* Leach cut transversely in front of legs 5 and viewed from in front to show the extrinsic limb muscles. The digestive gland is omitted; portions of the heart, pericardial floor and intestine are indicated but unlabelled; pedal nerves are stippled and arthrodial membranes are shown by white dots. Ventrally the anterior end of the sternite is passing upwards towards the oesophagus (see Fig. 59). The endosternite is cut transversely; its ventral surface and that of the ventral (pleural) surface of the carapace are foreshortened. Muscle numbers are those of Benham (*in* Lankester, Benham and Beck, 1885). Muscles 52 attach the dorsal cornua of the endosternite to the carapace and muscles 18 comprise the branchio-thoracic muscles which pass forwards from the branchial limbs to the prosomal carapace. The coxa of leg 5 is entire on the left, and on the right it is cut away as far as its articulation with the pleurite, disclosing the "dorsal flange" (marked) which is covered externally by
placement of the tip of the apodeme results in a lesser but stronger displacement of the biting cusps. Large movements of the tip of the anterior apodeme can only be effected by long muscles (note the great length of muscles 1 and 2 in the crab compared with the size of the gnathal lobe, made possible by the wide carapace; Fig. 57C, D). Long muscles 1, 2 and 6 are easily housed in the wide cephalothorax. Their bulk is presumably quite sufficient for the needs because the head space could easily house more bulky adductor muscles. This contrasts with the locust and Ligia where the head capsule is filled to capacity by the mandibular adductor muscles. There is no reason to suppose that biting and holding by the mandible of a crab is in any way less efficient than that of isopods and pterygote insects.

These two examples show how the basic musculature associated with the promotor-promotormuscular roll of the primitive Malacostraca has independently given rise to strong transverse biting, the principal antagonistic muscles being 3 and 4 in Ligia and muscles 1-2 and 6 in the crab. Transverse biting has been independently evolved in other specialised Crustacea which will not be considered further here.

**THE BITING MECHANISM OF THE CHELICERATA**

The Chelicerata share with the Crustacea the utilisation of pairs of biting and chewing mesially-directed coxal lobes or gnathobases, but the Chelicerata differ from the Crustacea in that their biting is done primarily by direct adductor-abductor movements in the transverse plane and not, as in Crustacea, by a derivative of the anteroposterior swing of the coxa on the body used in locomotion.

In Limulus both locomotory and feeding movements are carried out by prosomal limbs 2 to 5, and fairly soft but large food, such as worms and molluscs, can be shredded and eaten entirely with rapidity. The arachnids, on the contrary, are fluid feeders, chewing portions of their prey with the coxae of the pedipalps for long periods; the distal parts of these limbs are usually not locomotory. However, the coxal-feeding movements of the Xiphosura and Arachnida are essentially similar.

When walking, each pair of prosomal legs 2 to 6 is moved in similar phase by a promotor-promotor swing on the body effected by muscles pulling on the anterior and posterior proximal coxal margins (Fig. 58, promotors 27 and 41a, remotor

a fold of arthrodial membrane (see Fig. 60, A). On the right, one limb of the Y-shaped pleurite, with which leg 5 articulates, and the entire pleurite articulating with leg 6, are shown. The extrinsic muscles attached to the anterior thickened rim of the coxa are indicated in white on the left, some of the more posterior muscles being indicated in black. The extrinsic muscles attached to the posterior thickened rim of the coxa are shown on the right where the anterior rim and its muscles are cut away. The coxal endite is cut short on the right to show the sternite. (B) Anterior view of the mesial part of the gnathobase of leg 5 to show the heavy spines (with black tips) and the endite set in ample arthrodial membrane which allows the proximal rim of the endite to tip into the rest of the gnathobase on forward flexure of the endite (see Fig. 59, B). (C) Posterior view of the same to show the straight hinge between the endite and the rest of the gnathobase and the muscle extending from the endite to the posterior rim of the coxa. Contraction of this muscle returns the endite into line with the rest of the gnathobase after the endite has been pushed forwards by adductor movements of the coxa which press the endite against food or against the roof of the food basin.
29 and 41p). The phase difference between successive legs is small.

Food found in or on the substratum by the terminal pinchers of the prosomal legs during burrowing or walking is placed deep in a food basin extending between the coxal gnathobases, the labrum anteriorly and the chilaria posteriorly (Fig. 59). The walking coxal movements are replaced by adductor and abductor movements in the transverse plane. Projecting dorsally above the ball and socket pleurocoxal articulation (Figs. 58, 60) are two flanges carrying abductor muscles 25 and 26. A small inward displacement of these flanges results in considerable abduction of the coxal bases. The adductor muscles 42 and 43 (Fig. 58) insert ventrally on the endosternite. The forward slope of the mesial proximal corners of the coxae, brings the movable coxal endites of legs 3 to 5 close to the mouth (Fig. 59). Adduction of the paired coxae results in elevation of these endites because each coxa moves from a laterally situated articulation (Fig. 58). The posterior face of the movable endites slides against the sternite, thus pushing food into the mouth. Lamellibranchs are subjected to a preliminary "nutcracking" treatment. The shell is gripped by the chilaria, bitten and cracked by the very strong cusped sixth pair of coxae, and the chilaria swing forwards passing the broken prey to the more anterior shredding gnathobases (a fuller account of the feeding movements will be given elsewhere).

The skeleto-musculature of the prosomal limbs of Limulus is suited to produce all the observable movements. Abductor muscles are not absent as stated by Snodgrass (1952). The direct transverse biting by means of movements taking place at right angles to the basic promotor-remotor am-
Fig. 59. (A) Sagittal half of the prosoma of _Tachypleus tridentatus_ Leach to show the form and positions of the gnathobases, the mouth, and the endoskeleton with its attachments. The lateral prosomal ridge and the posterolateral margin of the carapace are shown by a dotted line. Muscle numbers are those used by Benham (in Lankester, Benham and Beck, 1885). The heart, oesophagus, proventriculus and intestine are not labelled. Numbers 2-6 mark the gnathobases of legs 2-6; the moveable coxal endites of legs 3-5, which are directed towards the mouth, are not labelled. The positions of the coxal margins of legs 2-6, which are attached by arthrodial membrane to the flanks of the animal, are indicated by dotted lines and marked 2-6. The anterior face of coxa 2 is visible lateral to leg 1. The supra- and suboesophageal ganglia are cut. The cut endosternite and its foreshortened dorsal face are shown, the anterior cornu and two lateral cornua are attached by muscles (not shown) to the anterolateral part of the carapace; the dorsal cornu is attached by muscle 52 to the carapace and by muscle 53 from the base of the dorsal cornu, and muscles 54 and 55 from the dorsal face of the endosternite pass to entapophysis 1. A small "transverse endoskeletal connective" lies below the nerve cord above the gnathobase of leg 6; this skeletal bridge is united laterally with the endosternite and carries a muscle to the anterior part of the sternite as shown (the occipital ring of Patten and Redenbaugh). The oblique and ventral longitudinal muscles are shown diagrammatically (for details see Benham, in Lankester, Benham and Beck, 1885, pls. 74-5, figs. 1-3; Patten and Redenbaugh, 1900, pl. 8, fig. 4). Three extrinsic cheliceral muscles insert on the carapace; the largest and most posterior is the flexor and the most anterior is the extensor. (B) View of the gnathobase of leg 5 from the sagittal plane to show the free anterior and tight posterior union of the endite with the stiff cuticle of the rest of the gnathobase, and the range of movement of the endite in the parasagittal plane (see also Figs. 58, B and C).
only in the proximity of the mouth, since a series of such endites all along an undifferentiated body could not have possessed similar functions to those of Limulus.

RELATIONSHIPS OF CRUSTACEA, MEROSTOMATA AND TRILOBITA

The basic movements of the locomotory limbs of Limulus and of Crustacea are the same, a promotor-remotor swing. The

![Diagram](image)

**Fig. 60.** (A) External lateral view of the dorsal ends of the coxae of legs 5 and 6 of *Tachypleus tridentatus* Leach to show their articulations with the Y-shaped pleurites lying at the junction of the under surface of the carapace and the pleural arthrodial membrane. A fold of this membrane covers the intucked dorsal flange of each coxa. (B) Internal view from the sagittal plane of the coxae of legs 5 and 6 after removal of the viscera and endosternite. The cuticular thickenings forming the coxal rims and internal ridges are shown in white. (C) Dorsal view of the upper end of left coxa 5 to show the size of muscles 25-29 and the position of their carapace insertions. Muscle 27 is attached to a tendinous sheet projecting below muscle 25 from the lateral groove of the carapace (see Fig. 58). The dorsal flange of the coxa is foreshortened, and the anterior and posterior coxal margins slope downwards and to the left because the proximal rim of the coxa does not lie in the exact transverse plane (see Fig. 59, A, dotted outline of the base of the coxa of leg 5).
fundamental difference between the feeding movements of mandibular gnathobases of Crustacea and of the prosomal gnathobases of Limulus is of great importance. This, and the associated differences in limb morphology, including coxal articulation with the body, must surely mean that the merostome and crustacean gnathobases have been independently acquired as a parallel evolution not indicative of affinity, although both groups bite with a gnathobase and not with the tip of the limb. If a common basis for the Limulus and crustacean gnathobasic mechanism has ever existed it could only be sought for in a minute arthropod, possessing no basal articulations to its limbs, in which an undifferentiated link by arthrodiad membrane permitted a variety of slow movements by promotor, remotor, adductor and abductor muscles. Increase in size or in strength of movement must have been accompanied by the evolution of closer articulations at the limb bases. Thereafter, the Crustacea have used direct adductor-abductor mandibular movements only to a minor extent (as in Chirocephalus and Hemimysis), the direct abductor muscles 6 of these two animals corresponding in general principle, but not in detail, with abductors 25 and 26 of Limulus prosomal limbs 2 to 6, while the Chelicerata have exploited this biting movement to a maximum.

It is significant that the second feature which the Merostomata and Crustacea have in common, the biramous leg, is one of quite different construction. The outer ramus in the Merostomata and in the Trilobita is a proximal exite (pre-epipodite of Störmer, 1939), while the outer ramus in Crustacea is a more distal structure borne on the end of the protopodite, and one or two proximal exits may be present as in Anaspides.

A third contrasting feature shown by Limulus and the Crustacea lies in the ventral flexibility of the limb-bearing body wall in the former and the rigidity of the trunk insertions of the locomotory limbs in the latter. The pedigerous ventral surface of the prosoma of Limulus can shorten when feeding to 60 per cent of the length shown when walking, a flexibility serving opposite needs. Coxae when closely packed one behind the next can chew without lateral escape of food from the food basin, while some spreading out of successive coxae is essential for the locomotory promotor-remotor movements.

Thus, the study of jaw mechanisms emphasises the depth of the cleft between the Merostomata-Chelicerata and the Crustacea. The Trilobita have clear general resemblances in leg form to the limbs of Limulus, but the Trilobita lack as good a gnathobase and possess pre-epipodites all along the series. There is also the resemblance in trilobation of the carapace which may have a functional significance such as it has in Limulus (bracing the cuticle against the deformatory pull and the extrinsic limb muscles). Thus the evidence, as far as it goes, supports Störmer, 1944, in suggesting closer affinity between Chelicerata and Trilobita than between either of them and the Crustacea.

In attempting to assess the taxonomic position of early arthropodan fossil animals, many showing some resemblances to Crustacea, one would like to see a much more careful study of the basal regions of the head and trunk limbs where the state of preservation may allow it. There appears to be much too great a readiness to state that limbs are of the biramous trilobite type when in fact this is not proved. Details of the coxal articulations and outer rami of the appendages might
indicate the type of biramous limbs and type of gnathobasic or jaw-like movements which existed and would be of service in correctly interpreting the fossil record.

THE RELATIONSHIPS OF CRUSTACEA, MYRIAPODA AND HEXAPODA

There is reason to suppose that the present-day Onychophora, Myriapoda and Hexapoda represent a related series of animals whose origin may have been far removed from that of either the Crustacea or the Trilobita-Chelicerata assemblage. The unsegmented whole-limb jaws of Peripatus place the Onychophora squarely with the Myriapoda-Hexapoda assemblage, a conclusion in keeping with the many other considerations brought forward by Tiegs, 1947, Manton, 1949, and Tiegs and Manton, 1958. The limited cephalization indicates perhaps a very early adoption of a jaw technique in feeding. The unique alternate anteroposterior slicing by entognathous jaws (Manton, 1937) is related to the onychophoran accomplishment of outstanding importance, that of being able to deform the body extremely so that access is gained, without pushing, to damp cavities where predators cannot follow (Manton, 1959, 1961a). Large sclerotised mandibles working on a transverse mandibular tendon would be an impossible mechanism for such a habit of life.

The four types of jaws indicated by the vertical columns on Figure 61 appear to have been independently evolved, since the details of their mechanisms and structure preclude any one type giving rise to another. Since the crustacean mandible is primarily a gnathobase and the hexapod mandible a whole limb, it would be surprising to find more than convergent resemblances between them, as indeed is the case. No support has been found for the assumption (Snodgrass, 1951) that these mandibles are homologous coxal derivatives. It is the coxa-body joint only which is constant in all types of mandibles. Since only two movements of ambulatory limbs appear to have been used in jaw evolution, it is not surprising to find each of these movements to have been exploited more than once.

The whole-limb jaws of the Hexapoda are unsegmented and the mandibular mechanism, which most nearly approaches a central primitive type among hexapods, is that of Petrobius. As in Crustacea, Petrobius uses a promotor-remotor rolling movement of the mandible (but with very many differences in detail) about an approximately dorsoventral axis. The dorsal point of closest union with the head forms a ball-and-socket joint in Petrobius, permitting very free rotation (Fig. 48A). The corresponding point of closest union of the mandible and head of Hemimysis is shown in Figure 48B; here there is no articulation at all, just a link of thick flexible arthrodiad membrane braced by a fibrillar suspension from the basement membrane above. Petrobius possesses a well developed transverse mandibular tendon functioning as in the more primitive Crustacea, but this is a potential attribute of all body segments (Manton, 1928, 1934 and 1956) and is no evidence of close affinity. The mandible of Petrobius essentially rotates in a slot, and food is scratched, sucked up, and ground by molar processes. The combined action of the mouth parts, the hypopharynx and super-liguueae gives hydraulic efficiency around an oral cone, copious salivary secretions being produced by the labial segmental organs.

The mandibular mechanisms of (i)
Ctenolepisma and the more primitive Pterygota and of (ii) the entognathous Apterygota (Collembola and Diplura) present two divergent types of mandibular evolution which could have originated from an archi-Petrobius type. Trend (i) leads towards an absence of the Petrobius type of hydraulic efficiency and to the acquisition of strongly hinged transversely biting mandibles, by changes in the position of the axis of movement much as in the Isopoda, together with a parallel utilisation of the same type of adductor-abductor musculature. The superficial resemblances between the mandibles of Ctenolepisma and the Pterygota and of the Isopoda are no more than convergent. Trend (ii) leads towards a proximal freedom of the mandibles permitting protractor-retractor movements, as well as free rotator and counter-rotator movements, made possible by the growth of a pleural fold, such as is present in Petrobius, and leads to entognathy. The differences in the protractor-retractor mechanisms of Collembola and Diplura suggest that their

Fig. 61. Diagram showing the conclusions reached concerning the distribution of the principal types of mandibles or jaws (below) and the derivation of the jaw mechanisms (above). The heavy vertical lines indicate an entire absence of common ancestry between the jaws referred to on either side; an interrupted vertical line indicates separate evolutions of the jaw mechanisms of Hexapoda and Myriapoda which probably had a common origin; and the shaded areas indicate mandibular mechanisms showing convergent similarities derived from unlike origins.
entognathy has been independently acquired. All these changes indicate a closer relationship between some archi-Petrobius type of thysanuran and a pterygote than between either Collembola or Diplura and the Pterygota. No hexapod which has embarked upon the evolution of one or another type of entognathous mandible is at all likely to have been able to reverse its evolutionary trend back to a generalised state and then progress towards the pterygote condition.

The closer affinity of the pterygote and apterygote groups to each other than to the Myriapoda is shown by their mandibular mechanisms, by the details of the structure, musculature and functions of the anterior and posterior tentorial apodemes and segmental tendons (described in the full account of this work for the first time) and by their hexapodous state.

The mandibles of the Myriapoda, comprising two segments in the Symphyla, three in the Diplopoda, three to five moveable scutes in the Chilopoda and unjointed in the Pauropoda, undoubtedly represent whole limbs comparable with the unsegmented mandibles of the Hexapoda. The basic mandibular movement in the Myriapoda appears to be direct biting in the transverse plane, such as is employed by the gnathobase of Limulus, but using the tip and not the base of the limb. The usual difficulty concerning the abductor mechanism has had to be resolved. Segmentation of these mandibles facilitates adduction and all utilise the mobile anterior tentorial apodemes, to different extents, to promote mandibular abduction. The advantages of entognathy, namely protrusibility of mandibles and great freedom of movement, have been independently acquired in the Chilopoda and Pauropoda. The basic form and modes of action of myriapodan mandibles point to a unity among these classes and a cleft between them and the Hexapoda.

The Symphyla, in some ways so suggestive of originating from the ancestors of insects, differ basically from the hexapods in mandibular mechanism, in structure and mode of action of maxilla 1, in the presence of maxilla 1 segmental organs, and in the presence of the myriapodan type of head endoskeleton; these differences are so great as to make it clear that a suggested archi-Symphylan ancestry of insects must be abandoned. The very great apparent differences in external trunk characters of the myriapodan classes are correlated in detail with habits of life and could readily have been derived from a common type (Manton, 1954, 1956, 1958, 1961a and b, Parts 8 and 9 in preparation). The Diplopoda and Chilopoda show the result of early habit divergence between fast moving predatory animals and burrowing feeders on decaying vegetation. The stimulus for the evolution of the entognathy of the Chilopoda has been the predatory crevice-living habit and the advantage of extreme head flattening.

CONCLUSIONS

Thus the evidence derived from mandibular mechanisms supports the view concerning a deep separation between (i) the Onychophora-Myriapoda-Hexapoda stem, (ii) the Crustacea, and (iii) the Merostomata-Chelicerata-Trilobita assemblage. A biting gnathobase has been independently evolved in the Merostomata and in Crustacea, and a whole-limb mandible has evolved independently in the present day land forms, usually in segmented form in the Myriapoda, and unsegmented, using a different basic movement, in the Hexapoda.
A parallel evolution of jaws in arthropods must date from the earliest differentiation of the major classes, but there is no indication of the stage of advancement from which they came. There appears to be no justification for the use of the term "Mandibulata" in a taxonomic sense uniting the Crustacea, Myriapoda and Hexapoda. Similarly the "Entognatha" and "Labiata" indicate grades of advancement and not taxonomic groups.

To some persons the parallel evolution of a mandible is a most improbable supposition. Yet Hinton (1957-1962) has demonstrated the independent evolution of spiracular gills of pupae and plastron respiratory structures of eggs of insects in a very large number of cases, and the similarity holds down to the electron microscope level. Clearly, deviations from the resolution of the respiratory problems are impracticable and consequently the same type of respiratory structure has been evolved many times. Mandibles are not quite like this. There are a limited number of ways of acquiring a mandible, and following them out throws much light on the past history of the arthropods.

Increase in knowledge of the fossil record shows that reptilian and mammalian grades of organization have been reached independently many times. "The mammals are a polyphyletic group—by which is meant that mammals have no common ancestor which was itself a mammal. The common ancestor must be found among the reptiles" (Kermack and Mussett, 1959). In view of these conclusions on the evolution of major vertebrate classes it would indeed be surprising to find no trace of polyphyletic evolution among so large a group as the Arthropoda. Some polyphyletic conception of arthropod evolution indeed seems inescapable, but it is one thing to demonstrate the existence of clefts between modern groups of animals and quite another to speculate upon the depths of these clefts in geological time and to suggest what common type of animal preceded the divergent lineages.

REFERENCES

———. 1937. The feeding, digestion, excretion


MANTON: It is of great importance to recognize that there are two quite different ways in which animals react to a definite need. If there is only one or a very limited range in resolutions of the problem, the same morphological (and physiological) features turn up independently in unrelated animals, as in the case of compound eyes and plastron respiratory structures within the Arthropoda. Some resolutions may persist in spite of all other changes; for example, the fine structure of a cilium is constant throughout the plant and animal kingdoms. If, on the other hand, there are various but a limited number of ways of meeting a need, the same resolution may be independently adopted by unrelated animals, giving well known convergent similarities. Phylogenetically related animals inheriting the same resolution of a problem show resemblances due to affinity. "Unique" mechanisms may account for very detailed convergent similarities. Mandibular mechanisms are not "unique." There are a limited number of resolutions of the need for jaws, and an understanding of them shows which characteristics are indicative of phylogenetic affinity or the reverse, and which are convergent.

HESSLER: In Hutchinsoniella the mandibular muscle pattern is clearly derived from that of the thoracic limbs. The extrinsic muscles for each thoracic limb come from four main areas of origin (Fig. 62): two are dorsal, just lateral to the dorsal longitudinal trunk muscles; two are ventral (VM), either the ventral intersegmental tendon anterior or posterior to the segment. Of the dorsal extrinsic muscles, the anterior (DAM) and posterior (DPM) groups have corresponding anterior and posterior insertions on the limbs. The dorsal anterior muscles fall into groups which abduct (ABD) or adduct (ADD) as they exercise their main function of promotion. Observation shows that there is a mediolateral component to the primarily fore-aft swing of a thoracic limb, so that the path of the limb is elliptical.

The extrinsic muscles of the maxillule fall into the same basic groups found in thoracic limbs. The abductor-adductor groups of the dorsal muscles are more strongly differentiated than those of more posterior limbs. This change is related to the greater importance of abduction-adduction in a limb primarily concerned with moving food into the atrium oris. With this change in function, the origin of the largest ventral extrinsic muscle has shifted along the posterior intersegmental tendon to the midline, thus increasing its power as an adductor.

In the mandible, the changes are of the same sort found in the maxillule, but more extreme. The origins of nearly all the powerful ventral extrinsic muscles
Fig. 62. Limb musculature of *Hutchinsonella macracantha*. A, thoracic limb; B, first maxilla; and C, mandible. Muscles in black are on the posterior face of the limb; those in white are on the anterior face. DAM-ADD, adductor group of dorsoanterior extrinsic limb muscles; DLM, dorsoanterior extrinsic limb muscles; VLM, ventral longitudinal trunk muscles; VM, antero- and posteroventral extrinsic limb muscles. By R. Hesker.
have shifted to the midline. The origins of the abductor and adductor subgroups of dorsal anterior muscles have shifted even further apart. The abductor group is the only set of muscles with an origin lateral to the single hinge point of the mandible and therefore is the only muscle group capable of abducting the jaws, the same function it had in the more posterior limbs. I agree with Manton that the primary motion of the mandible is a promotor-remotor swing, but just as in the posterior limbs there is still a muscularily controlled abductor-adductor component.

LOCHHEAD: On the question of turgor and the role of the exoskeleton in the earliest arthropods: usually emphasis is placed on some sort of rigid exoskeleton, providing advantages such as hinge joints and muscle attachments. But may not the turgor type of organization have been more primitive?

MANTON: A turgor type of organization is basic for most phyla. It is difficult to visualize an animal in which the internal pressures are not of vital importance. Hydrostatic pressure is essential in coelenterates, annelids and mollusks as well as arthropods, and a pressure system is essential even to a sponge.

I suggest that the absence of basal articulations to the legs of Cephalocarida and of Anostraca and many other Branchiopoda is correlated with the large anterior and posterior area of the legs in proportion to the transverse sectional area of the body. This of necessity results in very wide basal unions with the body. It is mechanically simple to devise basal articulations between leg and body permitting much movement when the leg base is small, but much less easy when the base is large. The incurled posterior margin of the mandible of Chirocephalus (Fig. 46D) is a means of easing the swing of so large a limb base, and the absence of any firm proximal rim to the trunk limbs of Anostraca and Cephalocarida is another resolution (necessitating also the origin of extrinsic leg muscles on the anterior and posterior faces of the legs and not on the proximal margins).

BROOKS: Thus far in this conference, we have not defined a crustacean. Crustacea are of great diversity but one thing that characterizes them is the structure of the head. There are two pairs of antennae, a pair of mandibles and two pairs of maxillae. These are not comparable to the cephalic appendages of a trilobite. Trilobites and Crustacea represent two phylogenetic lines, and the structures mentioned are not homologous.

Yesterday it was stated that trilobites were filter-feeders. I believe Størmer was correct in drawing an analogy between the feeding habits of trilobites and Recent king crabs. Thus, the trilobites were probably lowly scavengers and predators. Whether we believe the crustacean jaw primitively was for scraping, for a molar purpose, or for biting is not important. The significant fact is that all primitive Crustacea have heavily sclerotized, strong jaws. Are we to believe that this structure originated through natural selection in a filter feeder? The crustacean jaw structure must not be disregarded in phylogenetic considerations.

MANTON: Chirocephalus is a typical filter-feeder with a very large mandible, but this mandible is not heavy. The whole cuticle of Chirocephalus is thin and delicate and that of the mandible is a trifle more fully sclerotized than that of the trunk. To describe the mandibles of filter-feeding Crustacea as “heavy” is mislead-
ing when their specific gravity approximates that of water. I have shown how the simplest crustacean mandibles suit the squeezing or grinding of small particles of soft food, however the food is collected. A heavy mandible is only found in large-food feeders capable of strong biting, and this is a repeated end term in crustacean evolution.

BROOKS: But we have to be careful about secondary modification. The biting triturating mandible is a diagnostic characteristic of Crustacea.

LOCHHEAD: Chirocephalus has a large, heavy mandible, which it uses when filter-feeding. However, like most filter-feeders, Chirocephalus does not always filter-feed. Sometimes it goes down to the bottom and scrapes up material with the tips of its trunk limbs. Perhaps the heaviness of the mandible is associated with this habit.

GORDON: Filter-feeders are so highly specialized that I think the whole mechanism has arisen secondarily. Euphausia has a marvelous filter-feeding method for a pelagic crustacean. Even in the Nebaliacea Cannon has shown that the filter-feeding limbs are secondarily acquired.

MANTON: I do not believe that an elaborate filter-feeding mechanism was ever primitive. With Lochhead I would emphasize that a crustacean can feed on minute food without any filter mechanism, as in Triops. Trilobites may have done the same, all limbs cooperating, but these animals could not have cut up their food as effectively as does Limulus since the paired limbs apparently could not meet ventrally. A case can be made for supposing that the primitive malacostracan was a bottom-liver. Such a habit could account for the typical differentiation of thorax and abdomen, and such an animal probably was a bottom-feeder on soft or small food. Filter-feeding may have turned up with the adoption of the pelagic habit, probably convergently in Syncarida, Eucarida, and Peracarida.

GLAESSNER: When we discuss the feeding of the trilobites, we should not forget the paleobiological evidence. Seilacher has somewhat confused the evidence by referring to †Cruziana as a trilobite resting-track. However, at least from Ordovician time, trilobites scraped up material from the bottom incidentally creating large and conspicuous sedimentary structures, which show that they were searching for coarse material. We have here the possibility of looking not only at the organization of the limb but also at actual traces of its activity left in the rock.

BROOKS: †Cruziana is also found in Lower Cambrian strata. There are many specimens on which it is possible to see that the trilobites were plowing in search of food just as does the Recent king crab.
XI

Evolution of the Branchiopoda

By
Paul Tasch
Department of Geology, University of Wichita, Wichita, Kansas

INTRODUCTION

The subclass Branchiopoda, as now understood, consists of seven orders, three of which are extinct. There is agreement at present on the classification shown in Table 5.

Three of the orders made their first recorded appearance in Lower Devonian time. These are the Conchostraca, Anostraca, and †Acerostraca. The order †Lipostraca apparently (Tasch, 1957) originated and became extinct during Middle Devonian time. The first recorded appearance of the Notostraca was during the Upper Carboniferous. A recently described order, †Kazacharthra, first appeared in the Upper Jurassic. The Cladocera apparently arose sometime between late Mesozoic and the older Tertiary (Fig. 63).

DUBIOUS PRE-DEVONIAN CONCHOOSTRACANS

The family †Lepidittidae (Kobayashi, 1954) consists of calcareous-phosphatic and calcareous forms that Tasch considers

TABLE 5
Classification of the Branchiopod Orders by Various Workers

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<th>SERIES A</th>
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<td>BROOKS, TASCH</td>
<td>BROOKS, TASCH</td>
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<td>DAHL</td>
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<td>Superorder 1</td>
<td>Superorder 3</td>
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<tr>
<td>Notostraca</td>
<td>Anostraca</td>
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<tr>
<td>†Kazacharthra</td>
<td>†Lipostraca</td>
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<tr>
<td>†Acerostraca</td>
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<tr>
<td>Superorder 2</td>
<td></td>
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<tr>
<td>Conchostraca</td>
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<td>Cladocera</td>
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The three superorders will be named in the “Treatise on Invertebrate Paleontology, part R.”
unacceptable as conchostracans. Other workers are of the same opinion (Novoji-lov, 1960). Reference is often made to this family to prove the marine origin of conchostracans. Adamczak (1961), for example, accepts at least one of the genera of the above-named family, the genus †Fordilla, and considers it to be the Cambrian ancestor of both conchostracans and †Eridostraca-type ostracodes. He refers further to a conchostracan found in Professor Kozlowski’s collections from the Polish Silurian. A line drawing shows a fragment of the dorsal and ventral sector of a valve. No photograph or description accompanies the drawing. It can readily be interpreted as an †Eridoconcha-type of ostracode. The valve of this alleged Silurian conchostracan is calcareous. All that can be said in light of the present published evidence is that documentation of a Polish Silurian conchostracan is inadequate and

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**Fig. 63.** First recorded appearance of each of the seven branchiopod orders.
cannot be accepted. That does not deny, of course, that marine Silurian conchostracan fossils may be found at some future time.

Therefore, it must be concluded that no undisputed conchostracans older than Lower Devonian have been reported.

**CONCHOSTRACA**

Novojilov (1958) has reclassified all fossil and some living conchostracans chiefly on fine structure of the valves. The late Dr. N. T. Mattox (1957), a leading investigator of living conchostracans, demonstrated that valve ornamentation could not effectively discriminate between genera and families. The use of valve ornamentation as a classificatory device was introduced by Baird (1849) and rejected by all subsequent workers. Mattox showed that several kinds of ornamentation occur in species belonging to the same genus. Tasch (1958) and others (e.g. Defretin, 1958) rejected this approach to the classification of fossil conchostracans.

There are several valve characteristics which are distinct, variable, and not readily amenable to subjective interpretation, as is fine sculpture. These include: ribbedness of the valve, spinosity of the larval valve, serration of the dorsal margin, and posterior recurvature of growth lines. Such valve characteristics display traceable, clearcut, evolutionary trends, which will be discussed below.

Additional features that can be used taxonomically are: position of the umbo relative to the dorsal margin, valve configuration, and size. However, in employing the last-named features, it is important to be aware of the fact that an individual conchostracan changes its configuration as it grows. Furthermore, in any population represented by fossil valves, size of the valve cannot be employed indiscriminately in taxonomy. Tasch has collected giant-sized individuals of *Cyzicus mexicanus* (greater than 25 mm.) in long-persisting ponds in Hesston, Kansas, while smaller individuals of the same species occurred in contemporaneous ponds that were more ephemeral.

**Ribbedness.**—The family †Leaiidae Raymond, as redefined by Tasch, embraces conchostracans bearing one to five radial ribs, carinae, or flat, diagonal edges which are divergent from the umbo. During Middle and Upper Devonian time, leaiids with five, four, and three ribs, are known, for example, †*Praeleaia* Lutkevitch from Estonia, and †*Pteroleaia* Copeland from the Upper Devonian of the Canadian Arctic (Fig. 64).

Bedding planes on which the last-named leaiid occurred, contained five, four, and three-ribbed individuals apparently belonging to the same species. It is inconceivable that in a puddle or in the shallows of a pond in a contemporaneous population, three distinct genera defined by number of ribs on the valve would be represented. More plausible, in the light of the writer’s study of living forms in cultures, and their natural habitats, is the explanation that number of ribs on the valve is a genetically variable character within the same population as well as between different populations through time.

During the Permo-Carboniferous, two and three-ribbed valves are dominant. Many of these valves, as those of the genus †*Leaia*, also bear a rib-like thickening along the dorsal margin. Within the context of this general tendency, considerable variability in ribbedness occurred. †*Monoleaia* bears a single rib; †*Paraleaia* bears two ribs and between them is a groove where a rib should have occurred.
†Massagetes bears one complete posterior rib and an embryonic, or partial, anterior rib. A partial rib, or a groove where a rib should be, is an obvious modification of the gene complex controlling ribbedness.

By Lower Cretaceous time, true ribbedness is extinct and in its place, two flat diagonal edges occur on the subquadrate valves of †Japanoleaia.

The evolutionary trend in the character "valve-ribbedness" may be summarized as a general tendency to decrease the number of ribs through time. The exact function of ribs on the valve is unknown. However, the writer suggested that it might have served to strengthen the valve structurally. Another possibility is that it was related to the burrowing habit. Living con-

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Fig. 64. Ribbedness of valve in conchostracans. Left column: lower figure, †Pteroleaia, Upper Devonian of the Canadian Arctic (after photograph by Copeland) with five, four, and three-ribbed individuals on same bedding plane; middle figure, †Leaia, common in Permo-Carboniferous beds, bearing two and three ribs. Bracketed Permo-Carboniferous types in right column: lower figure, †Monoleaia, single ribbed form; middle figure, †Paraleaia, two ribs with medial furrow; upper figure, †Massagetes, with one complete posterior rib and an embryonic, or partial anterior rib. Left column, upper figure, †Japanoleaia, from the Lower Cretaceous, with flat, diagonal edges where ribs had been in Paleozoic leaiids.
chostracans burrow in bottom muds with ventral valve agape on the sediment-water interface. The ribs of extinct forms, rising above the general surface of the valve, might have aided departure from the burrow as waters shallowed and mud dried on the valve.

Spinosity, serration, and posterior recurvature.—Three valve characters which are related and in which evolutionary trends are traceable from Carboniferous to Recent time, include spinosity of the initial (larval) valve, serration of the dorsal margin, and posterior recurvature of growth lines (Fig. 65).

The genus †Cornia (=†Pemphicyclus) of the Permian bears a small node, spine base, or hollow spine in a central position on the initial valve. Tasch (1961) re-studied †Estheria ortoni Clark from the Conemaugh of Ohio. He found it to possess both a larval valve spine and posterior recurvature of growth lines. Accordingly, it was placed in a new family. Research of the past few years on Permian conchostracans from Kansas and Oklahoma brought to light new evidence on the evolution of various valve characters in conchostracans. Thus, in addition to †Cornia, †Gabonestheria, with a large anterior spine
on the initial valve, appears to be ancestral to the genus †Vertexia and also to have given rise to the genus, †Curvacornutus. The latter bears a curved or looped initial valve spine.

Another genus apparently derived from †Cornia, is †Protomonocarina. This unusual genus possesses a series of bead-like components that form a partial rib. If, as postulated by Tasch, this genus did arise from a †Cornia population (Fig. 66), then a mutation of the gene or genes governing larval node or spine could have caused a shift of such a node or spine from the center to the periphery of the valve. As the first five growth bands were laid down during successive molts, a repetition of the mutant condition could account for the beaded, partial rib. Mississippian and Pennsylvanian leaiids studied by the writer often show bead-like components of valve ribs. Novojilov raised the condition of leaiid ribs with bead-like components to generic status in his genus, †Igorvarentsovia. Such recognition seems hardly warranted since the condition of bead-like components of leaiid ribs, as already noted, is visible in eroded specimens of many species of the genus †Leaia.

Nevertheless, the widespread occurrence of bead-like components in leaiid ribs of Carboniferous specimens appears to strengthen the view that the leaiid rib originated by the steps indicated earlier. This would not exclude other modes of development of ribbedness in conchostracans. Another genus from the Oklahoma Wellington Formation, †Limnadiopsileaia, possesses a single leaiid rib as well as posterior recurvature of growth lines. It apparently derived from a contemporaneous unribbed palaeolimnadiopsiid population. One can explain this occurrence if the palaeolimnadiopsiid line is traced back to †Estheria ortoni from the Conemaugh of Ohio. As noted earlier, this species bears an

![Diagram](image-url)

**Fig. 66.** Gene modification of initial valve node and origin of the leaiid rib.
initial valve spine and also has posterior recurvature of growth lines. Another possibility is the derivation from an Upper Mississippian unribbed palaeolimnadiopsid that did not bear an initial valve spine but may have carried the gene(s) for it as recessives. At any rate, †Protonomonocarina at one end, and †Limnadiopsileaia at the other (see Fig. 65), appear to relate back to a pre-Carboniferous †Cornia ancestral type. This type is envisioned as having had an initial valve spine but lacking posterior recurvature of growth lines.

Since five, four, and three-ribbed leaiids are known from the Upper Devonian of the Canadian Arctic, it is apparent that the leaiid rib has a long prehistory in the oldest Devonian or pre-Devonian. Until such specimens are found, the question of "rib origin" cannot be resolved.

The Permian †Palaeolimnadiopsis line could have given rise to † Keratestheseria in the Jurassic and also to Limnadiopsis. The last-named genus is characterized by a serrated dorsal margin. The Triassic †Echinestheseria, and the Permian †Vertexia, appear to be derivatives of the Permian genus †Gabonestheria.

TAXONOMY AND ITS BEARING ON EVOLUTIONARY TREND

Novojilov (1960) expanded the number of fossil conchostracan families to twenty. Tasch, in the "Treatise on Invertebrate Paleontology," has found that these can be reduced to eleven. The reason for this reduction stems from completely divergent interpretations of what constitutes specific, generic, and familial characters. Having rejected fine sculpture and ordinary shape variants of valves as being within the variability to be expected in a given conchostracan population, it follows that new categories erected on such premises should be placed in synonymy. When that is done, different evolutionary trends may be discerned.

The eleven conchostracan families recognized by Tasch embrace forty-eight genera. During the Devonian, four new families appeared, while five new families first occurred in the Carboniferous. Thus, nine new families apparently made their first appearance during the late-Middle to Upper Paleozoic, a span of some 130 million years. By the Mesozoic, five of these Paleozoic families became extinct and only two new families arose during Jurassic to Cretaceous time, a span of some 110 million years.

Two new conchostracan families arose in post-Cretaceous time, a span of seventy million years. The Cyclestheriidae certainly is a post-Cretaceous family. Permian through Cretaceous genera, assigned by Novojilov (1958) to the Leptestheriidae, have been shifted elsewhere by Tasch in the "Treatise" for reasons already mentioned. That leaves only Recent forms under this family. Thus, Leptestheriidae appears to have arisen during post-Cretaceous time.

It is apparent that Middle to Upper Paleozoic time represents the heyday of conchostracan evolution. That, in turn, can account for the variability in certain extinct valve features discussed above. Since the end of the Paleozoic to the Recent, only four new families have made their appearance. By contrast, an equivalent number arose in the Devonian alone. The entire geological history suggests that, in an evolutionary sense, the conchostracans represent a stagnant group.

Only three of the five living families, which embrace fourteen genera, have a good fossil record. The Cyzcidae range from the Devonian to the Recent; the
Limnadiidae from the Carboniferous to the Recent; and the Lynceidae from the Upper Cretaceous to the Recent.

Soft-part anatomy.—Evidence on soft-part anatomy preserved in the fossil record is limited to a very few well-documented examples. †Limnesteria ardra from the Kilkenny Coal Measures of Ireland had antennae, mandibles, trunk, telson, and appendages preserved. Specialization of the first and/or second appendage in males for clasping the female during copulation was apparently established in its modern aspect by Carboniferous time.

†Cornia cebennsis described by Deschaseaux (1951) had mandibles, fragments of a biramous antenna, impression of an ocellus, and of the interior of the digestive tube, as well as caudal furca, preserved. This Carboniferous conchostracan possessed a head with a modern profile, somewhat larger appendages than living forms, shorter antennae, and a longer caudal furca. In addition, eggs fossilized with the valves were both fewer in number and larger in size than in modern forms. Deschaseaux noted that by Triassic time, conchostracan eggs became smaller and more numerous in a given individual.

It is apparent that, except in varying dimensions which might fit a normal curve of distribution in a given population if more fossil examples had been found, Carboniferous conchostracans were modern in most aspects of soft-part anatomy. However, Deschaseaux’s observation suggests that the reproductive process in females differed from modern forms at least in egg production.

It is plausible to assume that larger eggs in Carboniferous conchostracans may reflect the transition from a marine to a freshwater environment via an estuary. Needham (1930) pointed out that the transition from salt water to fresh water via the estuarine environment would involve eggs with larger yolks to accommodate to the brackish conditions. A further bit of evidence on this theme is Kummerow’s (1939) conchostracan from the Lower Carboniferous of Germany, †Quadriasmussia hercynica. This form definitely lived in a marine environment, having been fossilized with trilobites and brachiopods. Gross (1934) described a species of Cyzicus from the Lower Devonian of Germany that had been fossilized with marine ostracodes. The fossil record of conchostracans from Devonian through Permian time thus contains examples of marine, estuarine, and freshwater environments. †Limnesteria ardra, for example, clearly lived in an estuarine environment.

From these considerations, one may postulate that the Carboniferous was a time of transition from marine to fresh water for some conchostracans. Furthermore, there probably were several pulses, or times of transition, since freshwater Devonian forms are known.

CLADOCERA

Fossil record.—The ephippia of †Daphnia fossilis from the Oligocene brown coal of Germany, is the oldest presently known fossil cladoceran. Calcified ephippia of Miocene daphniids have also been reported from the late Tertiary Humboldt formation of northeastern Nevada. Interglacial and postglacial cladocerans are quite numerous. As many as forty-three species and subspecies of living central European chydorids occur in such deposits along with species of other families (Frey, 1958).

Evolution of Cladocera.—Frey assumed that cladoceran species from late glacial lake sediments could be compared mor-
phologically to living equivalents because no extensive change had occurred in the past 11,000 years. J. L. Brooks concluded that certain Daphnia species from deep glacial lakes arose during the Pleistocene, while southern species in shallow waters arose prior to that time. Scourfield indicated that Bosmina species occurring in his glacial lake cores, when compared to living equivalents, suggested a less-evolved condition.

These observations, which are essentially confined to the Pleistocene and post-Pleistocene, can now be extended to the older Tertiary. The mode of shedding ephippia containing eggs in order to withstand the increasing severity of the environment was operative in its modern aspects some 40 million years ago. In turn, this suggests that Oligocene to younger Tertiary cladocerans possessed a soft-part anatomy closely similar to that of modern forms, with perhaps minor modifications.

CLADOCERAN-CONCHOSTRACAN RELATIONSHIP

The cladoceran genus Leptodora is considered an “aberrant conchostracan.” It is the only living cladoceran with a larval form that goes through a naupliar stage as do conchostracans. Its shell is reduced to an egg case. The conchostracan species Cyclectheria hislopi, by contrast, is very cladoceran-like. Unlike conchostracans in general, it bypasses the naupliar stage, and the young have the full complement of appendages and a well-developed valve at birth. The eyes are united into a single cyclopean organ as in cladocerans (Sars, 1887).

As observed in the discussion on Conchostraca, the family Cyclectheriidae arose sometime during the post-Cretaceous to older Tertiary. Since Oligocene cladocerans are known, the origin of cladocerans can be further restricted to post-Cretaceous pre-Oligocene time. Cyclectheria hislopi, a living species, seems to be the most likely candidate for the transitional type leading from conchostracan to cladoceran. Living Leptodora, while an aberrant form, is a cladoceran. It is also known from post-glacial deposits. It probably arose during the older Pleistocene. If so, the fact that it has a naupliar stage merely relates back to the ancestral condition, i.e. the original derivation of cladocerans from conchostracans.

ANOOSTRACA—†LIPOSTRACA

The fossil record of anostracans is very sparse. The oldest reported fossil anostracan is †Gilsonicaris rhenana from the Upper Devonian of Germany (Van Straelen, 1943). This species possessed eighteen trunk segments, eleven of which bore appendages. It had closest affinities to the Eocene †Branchipodites vectensis but differed in the greater number of segments. †Branchipodites anthracinus from the Upper Carboniferous possessed eight trunk segments with lateral appendages resembling those of the lamellar branchial feet of living Branchipus. †Rochdalina parkeri from the British Coal Measures had eleven segments. Palmer’s Miocene anostracans also possessed eleven trunk segments.

Exclusive of the family Polyartemiidae, extant families of anostracans all have eleven thoracic segments. Thus, by Carboniferous time, in this respect, anostracans had a modern aspect. Branchipus-type appendages, noted above, also are known from the Carboniferous. In turn, this suggests that appendages also had a modern aspect at that time.

The chief trend discernible in the fossil record of anostracan evolution is a de-
crease in number of segments between Devonian and Carboniferous time.

The order †Lipostraca known only from the Rhynie Chert of the Devonian Old Red of Scotland bears closest affinities to the Anostraca. Scourfield (1926) was impressed by the combination of primitive characters (such as the biramous II antenna) with greater specialization than is found in living anostracans. He cited fifteen points of difference between lipostracans and anostracans. Nevertheless, other workers have considered lipostracans to be primitive anostracans. Scourfield elsewhere (see Tasch, 1957) remarked that in the earlier stages, the mandibular palp in lipostracans was “remarkably identical” with that found in the anostracan Chirocephalus diaphanus. He thought that this pointed to a pre-Devonian ancestry for both. If we follow that line of reasoning, a pre-Devonian ancestral type gave rise to two branches, anostracans in Lower Devonian (perhaps a †Gilsonicaris-type) and lipostracans in Middle Devonian time. Since Lipostraca are unknown after Rhynie Chert time, it appears that this order with two distinct series of appendages (branchiopod and copepod) was an unsuccessful evolutionary experiment. By contrast, once reduction of segments was achieved by Carboniferous time, the Anostraca continued to the present day relatively unchanged in basic plan while differentiating into several families.

†ACERCOSTRACA, NOTOSTRACA, AND †KAZACHARTHRA

The †Acercostraca known only from the Hunsrück shale, Lower Devonian of Germany, closely resemble the notostracans in general, and Triops (=Apus) in particular. The common characteristics include: a dorsal carapace, a pair of sessile eyes, small antennae, and about fifty pairs of appendages. However, the acercostracans lack the characteristic notostracan telson and furca (Lehmann, 1955).

Notostracans known as fossils range from the Upper Carboniferous to Recent. Fossil forms are closely similar to living forms. This evaluation applies to species of both Triops and Lepidurus. The last-mentioned genus is known from the Triassic of South Africa and the Lower Cretaceous of Turkestan. There is little doubt that by Carboniferous time notostracans had a modern aspect. It appears that Triops, possessing a telson and rudimentary supra-anal plate, gave rise to Lepidurus, which possesses both a telson and a supra-anal plate, somewhere between Permian and the dawn of Triassic time.

A recently named new order, †Kazacharthra, known only from the Lower Jurassic of Kazakhstan, possessed a telson without a terminal segment. The mouth parts were of the notostracan type. In general plan, it closely resembles notostracans.

However, notostracan resemblance loses its taxonomic importance in Novojilov’s view because the number of short appendages in the anterior portion of the ventral face is fewer in †Kazacharthra than the number found in notostracans (Novojilov, 1957).

The three orders mentioned above show close affinities as well as marked differences (Fig. 67). There are alternative interpretations of the evolutionary relationships between them. Either †Acercostraca was directly ancestral to Notostraca, or both orders arose from a common pre-Devonian ancestral type. If the last alternative is accepted, then the †Acercostraca represent an unsuccessful Devonian offshoot while the Notostraca are late Car-
boniferous descendants that persist to the present time. †Kazacharthra, in turn, may either be a synonym of Notostraca, or an unsuccessful branch of the notostracan stock in Lower Jurassic time. In this way, we are afforded a long-range view of notostracan evolution from pre-Devonian time on.

Thus, notostracans, as was the case with the conchostracans, are clearly a stagnant group in an evolutionary sense (Longhurst, 1955). This might not have been the case if the unsuccessful orders, †Acerostraca and †Kazacharthra, had survived.

**SIGNIFICANCE OF THE PRE-DEVONIAN FOR BRANCHIOPOD EVOLUTION**

It is apparent from the discussion above that pre-Devonian marine and non-marine deposits (specifically Ordovician and Silurian beds) should contain crucial evidence bearing on the origin of several branchiopod orders: Conchostraca, Anostraca, and †Acerostraca. The problem
narrowed down to the derivation of these three orders that made their known first appearances in Devonian time. All the other orders arose directly from one or another of these or from collateral lines: Cladocera arose from Conchostraca; Lipos- traca and Anostraca probably had a common ancestor; & Acerostraca and Noto- straca may have had a similar origin; and Kazacharthra appear to be a derivative of the Notostraca.

H. L. Sanders (this volume, p. 172) presents the interesting thesis that the ancestral crustacean was not too distant from living Cephalocarida. He indicated five steps leading to the branchiopod mode of development by modification of the common ancestral type. These steps included, among others, reduction, modification, and loss of appendages in the ancestral crustacean that ultimately led in the branchiopod direction. These steps must have involved a considerable number of genetic mutations and countless generations of cephalocarid-like populations. Sanders' fourth stage in the transition from the ancestral type to true Branchiopoda is the "evolving of the branchiopod nauplius." As a tentative theory attempting to place in time the various parts of this sequence, the present writer suggests the following time scale:

(1) Late Pre-Cambrian to Lower Cambrian ... origin of the cephalocarid-like crustacean ancestor.

(2) The rest of the Cambrian to older Ordovician ... head and trunk appendage reduction, modification, and/or loss.

(3) Middle to Upper Ordovician time ... evolution of the branchiopod nauplius.

(4) Close of the Ordovician ... establishment of branchiopod mode of development.

(5) Silurian ... adaptive radiation, ultimately giving rise to three distinct branchiopod lines: ancestral stock of Devonian conchostracans, common ancestral stock of anostracans and lipostracans, and common ancestral stock of acerostracans and natostracans.

If Sanders' outline of the steps leading to the branchiopod mode of development by modification of a cephalocarid-like ancestral crustacean is plausible (and the consensus of crustacean specialists appears to be in favor of it), then the theory of small-step evolution leading from species to higher categories requires large time spans in which such evolution could have occurred. Without having any claim to accuracy, the proposed geologic time schedule outlined above for the pre-Devonian evolutionary events provides a useful frame of reference to be improved, modified, or corrected as new fossil data become available. It is possible, for example, that steps 2 to 4 of this time schedule may have to be pushed back to the Cambrian. However, at the present writing the available evidence supports the time schedule as outlined.

REFERENCES


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Discussion Following Paper by Tasch, and Summaries of Recently Published Papers by Brooks\(^1\) and Rolfe\(^2\)

SAUNDERS: In the conchostracan *Lync"e"us*, the valves of adult and nauplius are different. A paleontologist finding the flat larval valve would not put it into the Conchostraca; he would probably make it a nitostracan. Perhaps some difficulties in identifying fossils may be due to such differences in developmental stages?

TASCH: That's true for the Lync"e"idae which are known as fossils only from the Lower Cretaceous of the Transbaikali. For the other families, we have the addition of growth bands. Various studies have shown that individuals molt approximately every three days. You can count how long a given individual lived. Some of these individuals get to be quite a size. I ac-


knowledge what you say as a caution, but I think workers on fossil conchostracans have been aware of this fact.

GLAESNER: In a recent paper (Jux, J. Paleont., 1960, 34:1129-1152) a large number of †Archoeosteca were considered as Malacostraca. Has this been definitely ruled out?

ROLFE: It is interesting historically that the argument over the Leptostraca being Branchiopoda or Malacostraca has always been present to some extent with the fossils. We have just had a renaissance of this problem by Ulrich Jux, who has suggested that all the †Archoeosteca are Branchiopoda. He bases this on one genus which he has studied: †*Montecaris*. And it is exactly this problem that I outlined previously: a maximum of three segments is preserved, projecting from the carapace of one specimen available to Jux; this is different from any malacostracan number and hence he concluded that †*Montecaris* must be a branchiopod. Now, however, we know that †*Montecaris* has seven pleomeres and at least seven thoracomeres. Impressions of the mandibles were interpreted by Jux as the labrum. To my mind there is no basis for even this one genus being a branchiopod. Some
archaeostracan genera are certainly malacostracan (see Rolfe, 1962a, p. 930); others are incertae sedis.

BROOKS: Tasch has eliminated pre-Devonian forms from the Branchiopoda. What would he do with †Fordilla, †Bradoria, and the various Middle Cambrian fossils from Nova Scotia?

TASCH: I cannot place them in the Branchiopoda, but other workers consider that some of these belong to a transitional group.

BROOKS: What do you think of the Ordovician †Douglasocaris, which was described as a phyllocarid rather than a branchiopod? It has cercopods rather than a furca, and a single ramus in the antenna. It is not a malacostracan.

ROLFE: It does not have the produced archaeostracan telson.

BROOKS: It has nine abdominal somites: it is a branchiopod. So the branchiopod record does go back further than the Devonian.

TASCH: I agree. You can infer this from the high development in Devonian forms. We have to distinguish between the acceptable (i.e. the undisputed) fossil record of branchiopods and their pre-Devonian origins inferred from biological data of living branchiopods and related forms. The undisputed fossil record of branchiopods that is presently available begins in the Devonian.

BROOKS: About the feeding habits of Paleozoic Crustacea. All the older syn-nectas and a range of Anaspides which scrape material and in feeding take in a lot of detritus. Paleozoic forms and †Anaspidites in the Triassic, show that they probably had the same feeding habits as Anaspides or Paranaspides: they have intestinal tracts filled with enough detritus to reveal the course of the intestine through the body. These intestinal fillings are so characteristic of the different genera (none of the forms that I would say was predaceous ever has them) that when we get to †Palaeocaris, all we have to do is look at the intestinal filling, because it is a generic character.

MANTON (subsequent written comment): Brooks states that Paranaspides and Anaspides scrape material and take in a lot of detritus, with no further qualification. I think that I am the only person who has studied these animals alive (1930, Proc. Zool. Soc. London, pp. 791-800, 1079) and I would not endorse this statement. Paranaspides is largely a pelagic feeder in a lake rich in plankton. I stated that "the stomach contents consisted of an unrecognizable mass of detritus, finely divided and containing numerous diatoms," a common type of content of alimentary canals of filter-feeders. I did not use the term "detritus" in the sense in which Brooks uses it to denote a mass of mineral particles. We need a careful definition of detritus, and much more work on the gut contents of extant Crustacea before we can interpret fossil alimentary canals with the certainty suggested by Brooks. Anaspides is partly predatory and it scrapes algae off stones. Particles are collected from an enclosed space by the filter mechanism which prevents food being swept away by the flowing streams in which the animals live.

I should also like to question the basis of the statement that all the older syn-nectas had raptorial appendages. I should like to see much more detail of all the limbs before accepting this statement.

GLAESSNER: What about the origin
DISCUSSION

161

and history of the carapace in these early stages? Is it the archaeostacan carapace that undergoes these changes? Why do these groups get rid of it and how? Particularly the syncarids.³

BROOKS: I have no proof that the Malacostraca are monophyletic, but rather that they are polyphyletic. Possibly †Anthracocaris was a stage in the reduction of the carapace from the primitive caridoid Malacostraca. There is an alternative interpretation of this: that, as in the branchiopods, there are those with and those without carapaces. It is possible that some of these forms, for example the Tanaidacea, are different, and that amphipods, isopods, and syncarids represent a different phyletic line that never had a carapace to start with. I think we have to admit that all lines that we can draw on from the study of Recent Crustacea indicate that the caridoid facies in the Malacostraca is primitive. I think that the Eumalacostraca were derived from within the complex of the Phyllocarida. If this is so, the primitive eumalacostracan must have had a carapace. We can reject this alternative interpretation. The stratigraphic record now supports Calman and other theorists that the caridoid facies is primitive.

MOORE: From all we have heard in this conference it makes eminent sense to group together, as a reservoir of ancient Crustacea, those forms that have these divergent relationships to known modern groups.

DAHL: Do you think that your line leading up to the Stomatopoda has to be derived from the Phyllocarida too?

BROOKS: I suspect so because of con-

³ See also discussion of Peracarida problem, p. 181.

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**Fig. 68.** Phylogeny and classification of fossil and Recent Eumalacostraca, by H. K. Brooks (1962, Bull. Amer. Paleont., 44, text-plate 16).
spicuous differences in the articulated rostrum. There is other morphological evidence to suggest the same thing. I could not see them grouped with other Eucarida.

DAHL: You still think it probable that they are not a separate line, but join the others at the phyllocarid level?

BROOKS: Yes. The problem is that we don’t know anything within the Phyllocarida that would be a suitable ancestor. Our unknown would be a good link there. Interestingly, †Eocaris does not have a rostrum. A rostrum in the regular caridoid is a secondary development.

ROLFE: Would Manton care to comment on the “furcal rudiments” on the telson that Brooks has emphasized? Are they genuine furcal rudiments, or could they be interpreted as anything else?

MANTON: It seems to me a good interpretation, although I don’t know much about furcal rudiments. I only know them from following them out in Nebalia and a mysid. In the mysid they are formed directly from the telson cuticle and at the first ecdysis they are shed with the old cuticle and are not re-formed.

BROOKS: Furcae are still found in the euphausiids and in the Bathynellacea. There is no question but that the furca is a primitive crustacean characteristic. We even have it in the Eumalacostraca; the furca is more widespread in Malacostraca than we realize.

MANTON: The basic evolution of Crustacea probably took place in a marine environment. We know a large number of fossils from freshwater deposits. Have we in fact a reasonable representation of the marine Crustacea? We should not build evolutionary castles on a preponderance of freshwater forms.

BROOKS: I am confident that the oldest forms are marine. I believe that the evolution and adaptive radiation as we know it was in the marine environment. Much of the fossil record, is, however, in freshwater deposits, and is sporadic.

GLAESSNER: Could you name the genera that are associated with marine fossils?

BROOKS: †Palaeopalaemon, from the Ohio Shale, and †Devonocaris from the Moscow Shale of New York and also from Belgium are associated with marine fossils. †Eocaris is found in the uppermost Middle Devonian of Western Germany and is associated with the phyllocarid †Montecaris and a dominantly marine fauna. The records of the others are sporadic; even when many are found, it is only in abnormal environments. They were not preserved in a marine environment, just as there is no record of the king crab in marine deposits, even though the modern form comes into estuarine waters and fresh water only to breed. Otherwise it is truly marine, and are we to believe that the king crab existed throughout the Tertiary in fresh water and then became marine in the Recent? No, it is selective preservation.

GLAESSNER: May I add two or three unpublished facts to the record. Birrshtein in Moscow has a Devonian crustacean of this general character; I think it was obtained in marine strata from a borehole. Malzahn in Hanover has found fossils from the Upper Permian, which are primitive tanaids and Cumacea with eye-stalks.
XIII

Significance of the Cephalocarida

By

Howard L. Sanders

Woods Hole Oceanographic Institution

Woods Hole, Massachusetts

INTRODUCTION

This paper is concerned with external anatomy, and internal anatomy is considered only insofar as it impinges on problems relating to external morphology. The objectives are to: 1, justify the subclass ranking of the Cephalocarida; 2, indicate possible malacostracan-cephalocarid relationships; 3, demonstrate branchiopod-cephalocarid relationships; 4, indicate the basic phylogenetic position of the Cephalocarida among the Crustacea.

The intent is not to show that the present-day Cephalocarida represents a close replication of the original "Ucrustacea," but rather an early grade of development in the crustacean series.

A more extensive work (Sanders, 1963) should be consulted for more detailed consideration of the Cephalocarida and documentation of topics discussed here.

SERIAL HOMOLOGY

One of the most characteristic features of the Cephalocarida is the pronounced serial homology of the limbs (Figure 69). The trunk limbs and second maxilla are essentially identical appendages consisting of a foliaceous exopod, a lateral foliaceous pseudepipod, an ambulatory endopod, and a flattened, although slightly posteriorly

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1 Contribution No. 1230 from the Woods Hole Oceanographic Institution. This research was supported by National Science Foundation Grants G-4812 and G-15638.
concave, protopod with a series of endites on the medial edge. The entire limb is concave posteriorly. This limb series represents the most primitive state of tagmosis known in the Crustacea.

The identity of the second maxilla has been questioned, since in the branchiopods this limb is frequently reduced to a minute protuberance and therefore easily overlooked. However, there can be no doubt that this limb is the second maxilla, for the large maxillary gland opens on its protopod.

The first maxilla with its foliaceous exopod, ambulatory-like endopod, and protopodal endites is obviously related to the more posterior limbs, particularly in the larvae.

The second antenna and larval mandible are structurally alike. In both there is a many-segmented exopod with similar setation, and the endopod is two-segmented. The enditic spines are found on the protopod of these limbs and on both pairs of maxillae and all the trunk limbs as well.

The external morphological evidence for pronounced serial homology in *Hutchinsonsoniella* finds strong support in Dr. Robert R. Hessler's studies (unpublished) on the skeletal musculature of this crustacean. The muscle pattern is the same in all the thoracic limbs and the second maxilla. In the first maxilla and mandible the musculature departs progressively from the pattern of the more posterior limbs but, nevertheless, is clearly derived from it.

The limbs reflect their high degree of serial homology in their multiplicity of function. All limbs participate in the trophic function. Current production is generated by the movements of the first maxilla, second maxilla, and trunk appendages. The first antenna, second antenna, larval mandible, second maxilla and trunk limbs are locomotory. The second maxilla, trunk limbs, adult first maxilla, and larval second antenna, as well as the setal combs on the terminal abdominal segment and telson and the long terminal spines on the telson, contribute to grooming activities. The sensory function seems to be restricted to the first antenna.

**MODE OF NAUPLIAR DEVELOPMENT**

To clarify the relationship of the Cephalocarida to other Crustacea, particularly the Branchiopoda, a comparative study was made of the one type of larva common to all the crustacean subclasses: the nauplius. The word "nauplius" is used here to mean both nauplius and metanauplius.

The primitive mode of development in the Crustacea was most probably a continuous and sequential addition of segments and limbs through a large number of moultts (Calman, 1909). In Figure 70 the mode of naupliar-metanaupliar development in the Cephalocarida, Branchiopoda, Cirripedia, Copepoda, and Mystacocarida is compared.

The pattern in the Cirripedia departs appreciably from the proposed primitive pattern. Neither segments nor limbs are added during the first five stages. At the sixth or terminal stage a segment and the first maxilla are added. At the moult to the first cyprid stage a large number of segments and limbs are added.

The Copepoda conform more closely to the suggested pattern. There is a gradual addition of segments up to stage 6 when three segments are added. The addition of limbs is not continuous, a single limb being added at stage 3, and two limbs each at stages 5 and 6.

Mystacocarid naupliar development shows a fairly regular addition of segments
through a long series of 10 stages. The addition of limbs is highly irregular with a single limb appearing at stages 2 and 3, none during stages 4, 5, and 6, two at stage 7 and not in sequential order, and three at stage 8.

The mode of development in the Branchiopoda is characterized by the addition

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**Fig. 70.** Mode of naupliar development in the Cephalocarida, Branchiopoda, Cirripedia, Copepoda, and Mystacocarida. The bar denotes the number of segments; circles denote limbs present. Black circles represent limbs with the definitive form, open circles represent limbs that are rudimentary. The graphs are derived from the descriptions of Heath (1924), Oberg (1906), Delamare Deboutteville (1954), and Sandison (1954).
of numerous segments and limbs at a single moult during the early naupliar stages. The full complement of segments and most of the limbs are already present midway through the naupliar series. Such a developmental pattern is applicable to both the phyllopod and anostracan branchiopods.

The cephalocarid naupliar development approximates the suggested primitive pattern more closely than does any other group. There is a continuous addition of segments through a long series of 13 naupliar stages. The addition of limbs is much more regular than it is in other Crustacea. Differentiation of the limbs proceeds at a

Fig. 71. Representative branchiopod nauplii: A, reconstruction of the liposstracan †Lepidocaris rhyniensis (from figures of Scourfield, 1940); B, the conchostracan Limnadia lenticularis (adapted from Sars, 1896); C, the notostracan Triops cancriciformis (adapted from Claus, 1873); and D, the anostracan Artemia salina.
nearly constant rate, and usually only the terminal appendage at any given stage is rudimentary.

NAUPLIAR AFFINITIES

If we disregard the Cephalocarida for the moment, a study of naupliar morphology reveals that crustacean nauplii can be clearly separated into two groups. The Branchiopoda make up one group (Fig. 71), which can be characterized by: (1) a small and unsegmented first antenna with setation restricted to the distal edge; (2) the length of the protopod on the second antenna, which is more than half the total length of the limb; (3) the

![Fig. 72. Representative nonbranchiopod nauplii: A, the copepod Temora longicornis (adapted from Oberg, 1906); B, the mystacocarid Derocheilocaris remanei (adapted from Delamare Deboutteville, 1954); C, the cirripede Balanus balanoides; and D, the decapod malacostracan Penaeus duorarum (adapted from Dobkin, 1961).](image-url)
presence of a single large spine on the medial surface of the distal protopodal segment of the second antenna; (4) the absence of setae from the medial surface of endopod on the second antenna; and (5) a uniramous mandible.

In contrast, the nonbranchiopod group (Fig. 72) has (1) a first antenna that is long and segmented, with setation not limited to the distal edge; (2) a protopod on the second antenna less than half the total length of the limb; (3) two or more small spines on the medial surface of the protopod of the second antenna (absent in penaeids since the nauplii do not feed); (4) setation on the medial surface of the endopod of the second antenna; and (5) a biramous mandible.

MALACOSTRACAN RELATIONSHIPS

Except for the Leptostraca, the more primitive representatives of the major groups within the Malacostraca have a common type of morphology from which the more specialized elements diverge widely. The anatomical features comprising this general type of morphology are referred to as the caridoid facies, and it is assumed that these features were present in the hypothetical ancestor of the Eu-malacostraca.

The major factor obscuring the past history of the Malacostraca is the almost universal tendency for development to continue within the egg to a very late stage; the juvenile that finally emerges has already acquired the adult features. The stomatopods, euphausiids, and decapods do have free-living larval stages, and it is in the penaeid decapods that development retains many of what we may suppose to be its primitive features.

Analysis of the larval stages of Peneaus setiferus (Fig. 74) demonstrates that, by and large, the caridoid facies appear late...
in larval development. The incipient biramous first antenna, the scale-like exopod and flagelliform endopod of the second antenna, the palp on the mandible, and the functional uropods are first evident during the mysis stages. The functional pleopods make their appearance during the post-mysis stages, and the flagelliform exopods of the maxillipeds are not present until the juvenile stages.

From this developmental series it seems apparent that a number of the caridoid features—the uniramous mandible, the flagelliform exopod on the maxillipeds, the scale-like exopod and flagelliform endopod of the second antenna—are, at least morphologically, secondarily derived.

The morphology of the penaeid larva at the protozoal stages, before the appearance of most of the caridoid features, is much closer to certain entomostracan groups, particularly the Cephalocarida, than to its own later developmental stages. This morphological similarity can be demonstrated for each limb. Only the penaeid and cephalocarid second antenna will be compared here. (For a detailed comparison of other limbs see Sanders, 1963.) In both there is a many-segmented exopod with each segment, except the most proximal two or three, carrying a large stiff seta on the ventral surface and with the terminal segment bearing three setae. A two-segmented endopod carries 4-5 setae or spines distally and bears two or more setae on its medial margin, and a two- or three-segmented protopod.

It is concluded that the caridoid mor-
Phylogeny is acquired late in development. In those few malacostracan groups having a fairly complete series of larval stages, the morphology before and after the acquisition of the caridoid facies is decidedly different. The pre-caridoid morphology is remarkably similar to the morphology found in the Cephalocarida and suggests that the Malacostraca arose from a crustacean stock that had many features in common with the present-day Cephalocarida.

**Branchiopod Relationships**

Cannon (1933), on the basis of his detailed and elegant functional study of the feeding mechanisms of the Branchiopoda, has presented a very convincing scheme (see Fig. 75) explaining the relationships of the various branchiopod limb patterns. He postulated that the proto-branchiopod trunk limb most probably had six unmodified, medially directed endites with spines along the enditic ridge.

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**Fig. 75.** Interrelationships of the filtering trunk limbs within the Branchiopoda (from Cannon, 1933). For interpretation see text.
and with a series of widely spaced anterior and a series of widely spaced posterior setae. From such a pattern two types of limbs evolved. One line led to the modern Notostraca and was brought about by the enlargement of the basal endite which turned forward and so overlaid the proximal endite of the limb in front. The other line led to all the remaining branchiopods and was brought about by the backward projection of the proximal endite. The latter condition was realized in the anterior limbs of the mid-Devonian †Lepidocaris rhyniensis. The backward projection of the other endites and the conversion of the widely spaced row of posterior setae into a closely meshed row of filter setae gave the condition present in the Conchostraca, Cladocera, and Anostraca.

Both the Cephalocarida and Cannon’s protobranchiopod have, in contrast to all known branchiopods, six unmodified endites, i.e. the proximal endite has not been transformed into a gnathobase and then further altered. The Cephalocarida share the following features with the Notostraca and †Lepidocaris among the Branchiopoda: endites (distal endites only in the Notostraca and †Lepidocaris) medially or slightly posteromedially directed; a row of spines present on crests of endites; a row of widely spaced posterior and a row of widely spaced anterior setae (distal endites only in the Notostraca and †Lepidocaris).

Because of the large degree of agreement between the cephalocarid and the proposed protobranchiopod limb, and since the Cephalocarida share morphological features with only the most primitive branchiopod components (Notostraca and †Lepidocaris), it seems probable that the limb structure in the Cephalocarida represents a condition precursory to that found in the Branchiopoda.

The limbs in the cephalocarid move with a marked metachronal beat which is initiated posteriorly and passes forward. The metachronal limb movements create currents which are used by the animal in conjunction with feeding (Fig. 76). In the adult, a strong flow of water is drawn posteriorly, medially, and dorsally into the median chamber between the paired thoracic limbs and thence into the inter-limb spaces on the forestroke or suctional phase (Fig. 76, positions 1–6). On the backstroke, with the reduction of the inter-limb space, water is forced out posterolaterally as a series of jets between the exopods and pseudopipods (Fig. 76, positions 7–9).

Detritus is put into suspension by the broom-like action of the second antennal exopod and the distal endopodal spines of the second maxilla and trunk limbs. This secondarily suspended detritus is drawn into the median chamber on the forestroke and is caught on the posterior setal row of the endites and endopod. Because of the interdigitation of the anterior with the posterior setal row (Fig. 76, positions 9 and 1), these relatively large detrital masses are scraped back into the median chamber where they are carried dorsally on the next forestroke. The enditic spines of the protopod then move the detrital mass forward from limb to limb to the enditic process of the first maxilla, which passes it into the atrium oris.

It requires no stretch of the imagination to derive the most primitive known branchiopod trunk limb feeding mechanism from the cephalocarid mechanism. All that is required is the loss of the endopod (pos-
Fig. 76. Sagittal view of the trunk limbs in *Hutchinsoniella* showing the various positions during a metachronal cycle together with the associated water currents. The arrow above each trunk limb indicates the relative movement.

possibly as an adaptation to pelagic life) and the modification of the proximal endite.

On the other hand, the cephalocarid trunk appendage uniquely has all the components present in the nebalid malacostracan trunk limb feeding mechanism. In fact, it is much easier to derive the leptostracan feeding mechanism from one similar to the cephalocarid type (Sanders, 1963) than from a eumalacostracan scheme, since such a derivation does not entail loss of parts, acquisition of new parts, or a significant number of hypothetical stages.

The ladder-like arrangement of the ventral nerve tracts found in many branchiopods (Anostraca, Conchostraca, and certain Cladocera) has been considered to be a retention of the pattern found in some Annelida (Calman, 1909). However, those branchiopods that lack a food groove, the Notostraca and certain Cladocera, also lack the ladder-like arrangement of the ventral nerve tracts.

*Hutchinsoniella*, like the Notostraca, has the paired ventral nerve tracts close together. They are just dorsal to the food groove; in fact, the nerve ganglia protrude ventrally into the ventral gully. The more deeply invaginated food groove of the Anostraca and Conchostraca is directly opposed to the midgut, and the ventral nerve tracts are situated lateral to the food groove. Probably the wide, ladder-like nerve tracts are merely the result of lateral displacement by the deepening food groove.

THE CEPHALOCARID-LIKE CRUSTACEAN PROTOTYPE

If there is any justification for the belief that the Cephalocarida represent a retention of an early stage of morphological development in the Crustacea, then it should be possible to relate the diverse patterns in each limb of the various subclasses to that found in the Cephalocarida. This has been done for each of the appendages. The limb patterns present in
Fig. 77. Relationship of the first maxilla of various crustacean subclasses. The length of the heavier portion of the radiating lines gives a measure of the similarity of those limbs to their cephalocarid counterpart. Upper cephalocarid limb is naupliar and lower is adult. Copepodan limb A is naupliar and B is adult. Malacostracan limb A is decapod protozoeal and B is the adult decapod.
the various crustacean groups were found to be either directly comparable to their cephalocarid counterparts or could be derived from them by reduction and simplification (see Sanders, 1963).

As an illustration, the first maxilla will be considered here (Fig 77). The larval cephalocarid limb consists of a flattened, leaf-like exopod, bearing setae laterally and distally, a multi-segmented endopod with each joint bearing two setae on its medial surface and carrying three or more spines or setae distally, and a protopod with two or more endites bearing gnathic spines or setae. In the protozoa of the penaeid Malacostraca these features are all present, except for the fewer endopodal segments and a reduction in the size of the exopod. Among both the Copepoda and Ostracoda there has been a fusion of the endopodal segmentation, but otherwise all the components persist. The first maxilla of the Mystacocarida is precisely the cephalocarid larval pattern lacking, however, the exopod. In the adult Cephalocarida the naupliar endites disappear and are replaced by a larger, more proximal enditic process bearing a number of anteriorly directed spines. The highly reduced branchiopod first maxilla is morphologically and functionally similar to the enditic process of the adult cephalocarid first maxilla.

This analysis of comparative limb morphology demonstrates that: (1) only the Subclass Cephalocarida, among the known subclasses, possesses a limb series sufficiently generalized to indicate a central position within the Class Crustacea; (2) most crustacean groups can be derived

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**Fig. 78.** A scheme for the derivation of the Branchiopoda and Malacostraca.
from an ancestor having most of the morphological features of the Cephalocarida; (3) crustacean evolution probably consisted of simplification, reduction, and specialization.

A suggested scheme for the derivation of the Branchiopoda and Malacostraca is shown in Figure 78.

REFERENCES


XIV

Discussion Following Sanders’ Paper

MANTON: The primary difference between the second maxilla and the limbs behind is that it has one less endite.

HESSLER: The skeleto-musculation systems of the Leptostraca and the Cephalocarida have much in common. Both have a segmentally repeated, ventral inter-segmental tendinous bar in the thorax, and in the cephalon a ventral endoskeleton formed from the fusion of such bars. In both groups the longitudinal trunk muscles run straight from segment to segment, a pattern quite unlike that in the caridoid facies. The Leptostraca, Cephalocarida, Branchiopoda, Mystacocarida, and Cirripedia, have dorsoventral thoracic trunk muscles. The only other Malacostraca clearly possessing such muscles are the Stomatopoda. These muscles are so similar in leptostracans and cephalocarids as to suggest specific homologies. Because of data such as these, the position of the Malacostraca does not seem to be so isolated as has been thought.

DAHL: The Malacostraca and the Maxillopoda resemble each other in various respects. Brooks mentioned that he could think of deriving the Malacostraca from some copepod-like crustacean. I don’t agree; I think that such an ancestor must lie well below the copepod level of organization. But I agree that the malacostracan and maxillopodan groups of evolutionary lines appear to be closer to each other than either of them is to the branchiopod lines. From what we have heard it appears probable that the Cephalocarida play a central part in the discussion concerning a possible common ancestor.

SANDERS: There is a danger of representing the present-day cephalocarid as the primitive condition. Dahl has pointed out one feature which certainly is not primitive. This is the nature of the brain, which he has related to the fact that the animal is blind.

DAHL: In preliminary observations on the brain of Hutchinsoniella we have found what appears to be a complete change-over from visual to chemical orientation. Some structures are unique. There is a pair of, comparatively speaking, enormous lobes lying in front of the labrum which we can only interpret as the lobi olfactorii. In any case, they are connected with the antennules. There are also some very large and dense masses of neuropileum in the anterior part of the protocerebrum located in an area more or less corresponding to the one where you find the olfactory association centers of the corpora pedunculata in the Malacostraca. These two observations tend to give independent support to the suggestion that the olfactory sense is the principal one in Hutchinsoniella. This in its turn will certainly have to be inter-
interpreted as an adaptation to the peculiar habitat.

GORDON: With regard to the table of larval and adult characters, I would agree with you if you cut out caridoid and merely talk about larva and adult.

TASCH: On Figure 75 of the proto-branchiopod, what is the significance of the arrows, because there is one from \(\text{Lepidocaris}\) through \(Sida\), a cladoceran, to \(Estheria\)?

SANDERS: I don’t believe Cannon was attempting to present a rigid phylogeny. He was merely arranging the limb series from a functional point of view.

SIEWING: In 1960 I expressed an opinion on the interrelationships in the Crustacea (Fig. 79). The Cephalocarida are shown near the base of the Superorder Anostraca (comprising Cephalocarida, \(\text{Lipostraca}\) and \(\text{E anostraca}\)), but also not far from the root of \(\text{Malacostraca}\) and \(\text{Maxillopoda}\). What evidence is there against this view?

SANDERS: First, the head appendages of the Cephalocarida and Branchiopoda are almost diametrically different. Second, the purpose of showing the branchiopod and non-branchiopod nauplius was to demonstrate that the cephalocarids cannot be included within the Branchiopoda, since their larval morphology is entirely non-branchiopod. Third, limbs and segments are added in large blocks early in the naupliar series in the branchiopods, while in the cephalocarids there is a continuous, gradual addition of limbs and segments throughout the long series of naupliar stages.

SIEWING: Yes, but you have proved that the feeding mechanism is so similar to that of \(\text{E anostraca}\), and Hessler has

![Fig. 79. Relationships within Crustacea, by Rolf Siewing.](image)
shown that they have turgor extremities too, like Euanostraca. Furthermore, there are other similarities between Cephalocarida, Euanostraca and †Lipostraca. There is the eggsac connected with the position of gonads in the abdomen, and the external openings of the gonads. And there are, as you have demonstrated in former papers, similarities in the body shape between the forms in question. These similarities seem to speak for a nearer relationship.

SANDERS: A malacostracan, mystacocarid or copepodan adherent could similarly present good morphological reasons for including the Cephalocarida in his group. But I tried to point out that there are good reasons for keeping the cephalocarids separate. The fact that the Cephalocarida share morphological features with most of the other subclasses and, at the same time, have features that are distinctively their own is the most exciting part of the story.

HESSLER: With reference to the feeding type, there is just as good reason for seeing close similarity to the Leptostraca as to the Branchiopoda.

SANDERS: Hessler’s studies of the endoskeleton indicate a non-branchiopod condition in the Cephalocarida. Branchiopoda have a laminar type of endoskeleton that is quite different from any other group.

MANTON (subsequent written comment): Since I have described the endoskeleton of a leptostracan and have looked at the endoskeleton of several Branchiopoda, may I say that I do not think that there is an important fundamental difference between the two.

GLAESSNER: Are the Notostraca so far from the Cephalocarida?

SANDERS: That is a matter of degree. I’d rather not consider that the cephalocarids are any closer to the branchiopods than to any other group.

SIEWING: Near the phylogenetic ancestor of the Anostraca perhaps?

SANDERS: Not particularly; it is generalized enough, but it is not an immediate branchiopod ancestor.

GLAESSNER: These are not the ancestors but they are the present-day representatives of the ancestors, and some of our difficulties in assigning them a specific place arise from the fact that something has happened to all of them, particularly the Malacostraca.

SANDERS: We haven’t the third dimension of time.

DAHL: Yes, we have to project them all into Recent time. When scanty material of the cephalocarid was first known, I took up exactly the same position as Siewing is taking now, that the Cephalocarida would have to be connected to the branchiopod line. That was why I created a new group, the Gnathostraca, to receive both. But the material presented has convinced me that there is no such close connection and that the Gnathostraca cannot be regarded as a natural unit. It may be that the present-day Cephalocarida in certain respects resemble the branchiopods, perhaps even more than they resemble other things, but we have to accept the fact that there are also fundamental differences, and to place them accordingly.
Discussion of the Peracarida Problem

In a discussion arising from earlier sessions, Manton drew attention to the unity of the Peracarida, as drawn up by Calman, and used by Gordon, Siewing, etc. and to the parallel loss of the carapace in the Isopoda and Amphipoda, resulting in convergent similarity with the Syncarida. Basic peracaridan features—the *lacinia mobilis*, and brood pouch—are features not easily seen in fossil animals.

BROOKS: The seminal receptacle has a polyphyletic origin in the Eumalacostraca. Thus, the presence of a seminal receptacle in the Syncarida cannot be used to exclude them from consideration as possible ancestors of the Peracarida. The Paleozoic Eumalacostraca show divergence toward the different Recent taxa.

GLAESSENNER: I have one or two questions here. Now, if we take the Peracarida as they are, how far back should those characters go? Do we always have to have Peracarida if we go back in the geological record, or do we lose all those groups, the Amphipoda, Isopoda, Tanaidacea, Cumacea and Mysisacea when these characters, that you mentioned as characters of the Peracarida, were not yet in existence? At what stage do these characters necessarily belong to all these groups? Or are there other characters which may have been present in ancestral forms of these various groups to enable us to trace them back? I think the difficulty of the problem that is placed before the paleontologists here is that these characters are so specific and so unusual that without them we cannot even talk of ancestors of those groups. How would you trace back those groups which are now peracaridan?

MANTON: Back to primitive mysid-like animals, which had a carapace and progressively lost it. Where you have mysid records of an early nature one would put back the origin of the rest of the peracaridan groups to an earlier stage than that, but from the mysid line, and not from the syncarid line.

GLAESSENNER: Now the difficulty here is that we can trace the mysids back and we end up with lophogastrids with a very strongly developed character. We arrive at an ancestral group which we originally called †Pygocephalomorpha, and now they are called †Eocarida, and which contain the ancestors of the decapods. You have to assume that the true peracaridan characters evolved at a certain time which is presumably also the Palaeozoic. I did not connect them all that closely with the Syncarida.

BROOKS: I do not believe in a close relationship between Syncarida and the Amphipoda and Isopoda. An alternative interpretation is that the syncarids originated independently of the Eumalacostraca with a carapace. Malacostraca with a carapace tend to have the thoracic

181
somites reduced in size. Another interesting point is the forward imbrication of the anterior thoracic somites. How did the carapace originate if its point of origin is covered by an overlap from the first thoracic tergite?

GLAESSNER: The second pleura of the abdominal tergite in the Caridea has a very strong forward and lateral overlap and I don't think anyone has ever been able to find out why.

MANTON (subsequent written comment): The forward overlap of the first free thoracic tergite in the Syncarida or of the second abdominal tergite of the Caridea have a clear functional explanation: the facilitation of flexure. The former example is necessary because of the tapering form of the body, the larger tergite more easily overlapping the smaller, and the caridean condition permits maximum freedom of flexure at the point where it is most needed. Within the Chilopoda there are many examples of forward overlap by tergites, but the same tergite does not always imbricate in the same direction, depending always on body shape. When the body does not taper, the tergites overlap posteriorly.

GORDON: Calman thought that the syncarids never had a carapace, and that the isopods and amphipods had lost it secondarily.

SIEWING: The different reconstructions of malacostracan phylogeny made by zoological and paleontological morphologists derive from their different methods. The paleontologist proceeds in the reverse direction from that of the zoologist. He presumes that one can read the phylogeny directly from the geological succession. Thus, the zoologist reconstructs the phy-

![Diagram](https://example.com/diagram.png)

Fig. 80. Relations of Peracarida, by Rolf Siewing.
logeny on the basis of the natural system, the paleontologist the natural system from the phylogeny. The effect is that the paleontologist gets more parallel lines of evolution than the zoologist. Another cause for this may be the lack of material and the overestimation of superficial characters. Paleozoologists and neozoologists must compromise in their methods to get a mutually consistent system.

As demonstrated earlier, the Isopoda and Amphipoda are derived from a common ancestor near the Mysidacea. The Isopoda are connected with the Mysidacea by transitional groups, such as the Cumaceae, Tanaidacea, and perhaps the Spelaeogriphacea. All these groups are peracaridan crustaceans and therefore have in common the physiologically complex marsupium, and a lacinia mobilis. But the latter is also found in the Thermosbaenacea and some recently discovered Anaspidacea (Stygocaris, Parastygocaris) from South America. I can see no reason for an independent derivation of peracaridan groups from one another. The Peracarida are connected via the Mysidacea with the main stem of the Malacostraca, that leads to the Pancarida and Eucarida (Fig. 80). At the fork the Syncarida and Peracarida are not far apart, but we have no proof of a direct derivation of Peracarida from Syncarida.

GLAESSNER: What is the biological explanation for the independent loss of carapace in the two lines shown on Figure 80?

SIEWING: The reduction of organs occurs much more frequently than the new building of an organ. Carapace reduction occurs in the Crustacea in many lines (Copepoda, Mystacocarida, Anostraca sensu lato, Syncarida, Amphipoda, Tanaidacea, Isopoda, Spelaeogriphacea). Absence of carapace alone, therefore, by no means proves a nearer relationship between Syncarida and the Isopoda-Tanaidacea-Amphipoda.
Index

This is a subject and systematic index—authors are not indexed. Throughout the volume the sign † precedes the name of a fossil taxon.

Abdomen, 5-6, 8, 109
displacement of organs from, 3-4
and locomotion, 3, 17-18
muscles of, 17-18
number of segments in, 88, 93, 95, 107-108
structure of, 3
Abduction-adduction of muscles, 111-138, 141-143
Acclimation [Acclimatization] (see also Temperature, Salinity, etc.), 28-34
†Acercostraca, 145, 154-156
Adaptation, 3, 21, 25, 27-45, 79-84, 178
antiquity of, 82
freshwater, 37-38, 40-42
functional, 5, 28, 33-34, 45
 genetic, 28, 34-45
non-genetic, 28-34, 45
to salinity, 34, 35-43
serial, 28
structural, 28, 33-44, 43, 44-45
terrestrial, 34, 35, 40, 43-45, 59-76
Adaptive characters, viii
Adaptive radiation, 21, 84, 156, 162
Aedes, 43
†Agnostida, 19
Amandibulates, 19
Amphipoda, 3, 8, 9, 10, 96-99, 109, 161, 181, 182, 183, Table 1, Figs. 37-39
Anaspidacea, 88, 93, 95-96, 100, 159, 183
Anaspidites, 18, 113, 117, 122, 127, 135, 160, Figs. 36, 50, 51
†Anaspidites, 160
Ancestors (see also Common ancestor), vii, 39, 177, 179
crustacean, 17, 20
of Leptostraca, 106
of Peracarida, 181
reconstruction of, 6, 85
Ancestral branchiopod, crustacean, etc. (see Primitive branchiopod, crustacean, etc.)
Annelida, 20, 21, 107, 143, 172
Anomura, 51-57, 84
Anostraca, 1, 2, 3, 5, 6, 7, 8, 10, 11, 12, 24, 110, 132, 143, 145, 153-154, 155-156, 166, 171, 172, 179, 183, Table 1, Fig. 1
Antennal gland, 38, 39, 42, 43, 96
Antennule, 88, 90, 91, 105, 106, 167, 168, 169, 177
†Anthracostraca, 161
Apodemes, 111-138
Appendages (see also Antennules, etc., Trilobitan limb), 4, 5, 19-20, 88-90, 111-139, 141-144, 178
biramous, 21, 135-136, 154, 168, 169
of Branchiopoda, 152-156, 178
of Cephalocarida, 163-174, 178
differentiation of head, 5
evolution of, 21
and feeding, 17-21
of fossil Conchostraca, 152
of Malacostraca, 88-101, 105, 106
and primitiveness, 107, 109
Apterygota, 80, 137-138
Apus (see Triops)
Arachnida, 80, 112, 131
†Archaeostraca, 90, 106, 107, 159-160, Fig. 44
Archetype, archetypal evolution, vii
Argulus, 11
Armadillidiidae, 44
Armadillidium, 32, 44
Artemia, 29, 30, 32, 35, 38-39, 82, Figs. 3, 4, 8, 71
Arteria subneuralis, 93, 97, 99
Arteries, paired, 88, 93, 101
Arthrostral membrane, 62, 135, 136, Fig. 60
Arthropoda (see also various groups), 2, 23, 83, 141, 143
Arthrostraca, 96
Ascothoracica, 1, 2
Asellus, 31, 41
Astartidae, 40, 41
Astacus, 29, 31, 34, 41, 42, 43, 122, 127, Figs. 9, 57
Atomism, 24
†Aysheaia, 21
Bahamas, distribution of terrestrial crabs, 73-75, Fig. 25
Balanus, 10, 28, 33, Fig. 72
Bathynellacea, 95, 162
Behavior, 33, 39-40, 44, 81
Benthic habit, 3-4, 6, 45, 144

185
INDEX

Biramous appendages, 21, 135-136, 154, 168, 169

_Birgus_, 35, 40, 45

_Bosmina_, 153

Brachyura, 8, 51-57, 59-76, 83

†Bradoria, 160

Brain, 90, 177

Branchial chambers, 40, 43, 59, 62, 74

Branchiopoda, 1, 11, 12, 13, 18, 23, 28, 108, 113, 143, 145-156, 159, 160, 161, 163-166, 167, 168, 170-172, 175, 177, 178, 179, Table 5, Figs. 1, 2, 63, 67, 70, 78

†Branchipodites, 153

Branchipus, 42, 153

†Branchipusites, 153

Branchiura, 1, 2, 8, 11, 12, Table 1, Fig. 1

Brood pouch, 43, 44, 96, 98, 181

Bryozoa, 108

Caeca, caecum, 7-8, 95, 101

_Calanus_, 9-10

_Calanoida_, 83

_Callianassa_, 35

_Callinectes_, 60, 65, 67, 75, Tables 2-4, Fig. 19

†Canadaspis [†Hymenocaris], 19

_Cancer_ 35, 59, 62, 65, 67, 69, 75, Tables 2-4, Fig. 18

Carapace, 2, 88, 90, 108, 109, 154, 159, 161

absence of, 2, 94, 161, 183

loss of, 181-183

in †Nahecaris, 105-106

parallel evolution of, 2, 181

reduced, 96, 98, 161

as size indicator, 65-67

_Carcinus_, 34, 35, 36, 38, 40, 60, 68, 69, 122, 127, Fig. 57

_Cardisoma_, 59, 62, 65, 66, 67, 72, 74, 75, 76, Tables 2-4, Figs. 16, 25

Caridea, 182

Caridoid facies, 3-4, 17, 105, 161, 162, 168-170, 177, 178

Cephalization, 5, 136

Cephalocarida, 1, 2, 3, 5, 6, 7, 8, 10, 12, 13, 18, 20, 93, 108, 141, 143, 156, 163-175, 177-179, Figs. 1, 2, 70

†Ceratiocaris, 159

Cercopods, 160


adaptive, viii

external morphological, 2-6

internal morphological, 7-12

and habits, 21, 80-81

loss of, 107, 108, 109, 156, 181-183

of Malacostraca, 85-102

phylogenetic, viii

primitive, 6-7

Chelicera (see also various groups), 112, 131-134, 138

Chilopoda, 6, 80, 138

Chirocephalus, 42, 113, 117, 122, 125, 135, 143-144, 154, Figs. 45-49, 75

_Chironomus_, 43

Chydoridae, 152

Cilia, 24, 141

Circulatory system (see also Arteries, Heart, etc.), 8, 11, 101, Figs. 33, 40

Cirripedia, 1, 2, 8, 11, 12, 13, 28, 108, 164, 177, Figs. 1, 70

Cladocera, 33, 82, 145, 152-153, 156, 171, 172, Table 1

Classification, 1-2, 12-15, 85, 88, 138, 139

of Anomura, 51-57, 84

of Branchiopoda, 145, 147, Table 5

of Eumalacostraca, Fig. 68

single character, 83

Coelenterata, 143

_Coenobita_, 40, 45

Cohorts, 13, Fig. 2

Collembola, 137-138

Common ancestor, vii, 24, 177

Communities, physically and non-physically controlled, 81-83

Compensation, 32

Compound eyes, 10-11, 12, 22-25, 93, 108, 141, Table 1

Concavity of limbs, 164

Conchostraca, 7, 145-152, 153, 155, 156, 159, 171, 172, Table 1, Figs. 64-66

Connective tissue, 67

Convergence, convergent evolution, 2, 7, 25, 141, 144, 181

of brain, 9

of habits, 144

of lacinia mobilis, 96

of mandibles, 112, 136, Fig. 61

of petasma, 93

of statocysts, 95-96

Copepoda, 1, 2, 3, 4, 5, 8, 9, 12, 13, 20, 28, 33, 83, 110, 164, 174, 179, 183, Figs. 1, 70

Copepodoidea, 2

†Cornia †Pemphicyclus, 149, 150, 151, 152, Fig. 65

Coxal plates, 96

_Crangon_, 35, Fig. 8
Craterostigmus, 83
Crustacea (see also various groups), 143
Crustacea/Insecta relationship (see Insecta)
†Cruziana, 144
Ctenolepisma, 137
Cumacea, 98, 99, 109, 162, 181, 183, Fig. 39
†Curvacornutus, 150, Fig. 65
Cuticle, 41, 43, 60, 67, 68, 73, 111, 135, 143, 162
Cyclestheria, 153
Cyclesterilidae, 151, 153
Cyclodorippae (see Tymolae)
Cyclodorippae (see Tymolus)
Cyclomorphosis, 33
Cyclops, 29
Cymonomae, 53
Cymonominae, 57
Cymonomus, 52-53, Figs. 10, 11
Cypris-stage, 28, 164
Cyzicidae, 151
Cyzicus, 147, 152

Daphnia, 25, 29, 33-34, 41, 113, 152, 153, Figs. 9, 75
Decapoda, 9, 22, 24, 28, 51-57, 83-84, 95, 108, 109, 125, 181, Table 1, Fig. 40
Decapoda peditremen, 55-57
Decapoda sternitremen, 55-57
Derocheilocaris, Fig. 72
Dietritus (see also Feeding), 160, 171
Development, 75, 108, 151, 164-167, 168-170, Figs. 70, 74
†Devnonocaris, 162
Diaphanosoma, Fig. 75
Diaptomus, 29
Digestive tract (see also Intestine, Mouth, etc.), 7-8, 12
Diplura, 80, 83, 138
Diplura, 137, 138
Displacement of organs, 3-4, 9
Distribution, 41, 73-75, 76, Fig. 25
Divergence, divergent evolution, vii, 21, 80, 98, 139, 161, 181
Dorippidae, 83, 84
Dorippidae peditremen, 55
Dorippidae sternitremen, 55
Dorippinae, 51, 55
†Douglasocaris, 160
Dromia, 51
Dromiacea, 51-57, 84
Dromiidae, 51
Ecdysis, 69-70, 159, 162, 164, 166
of Conchostraca, 159
and pericardial sacs, 69-70, 71, Fig. 24
†Echinestheria, 151, Fig. 65
Ecology, 27, 28, 34, 152
Eggs, 38, 42, 44, 152, 153, 168
Eggsac, 179
Elasticity of cuticle, 11, 122
Embryology, 21, 108, 109-110, 112-113
of Amphipoda-Isopoda, 98, Fig. 38
of Notostraca, 23
of Stomatopoda, 106
Emerita, 35
Endites, 18, 21, 95, 100, 112, 132, 134, 164, 170, 171, 174, 177
Endophragmal skeleton, 54, 55, 56, 57, 84, Figs. 13, 14
Endoskeleton of head, 111, 113, 117, 122, 127, 138, 177, 179, Figs. 52, 53, 55
Entognatha, 139
Entognathy, 136, 137, 138
Entomostraca, 107, 109
Environment (see also Oxygen, Temperature, etc.), 45, 80, 81-82, 83
acclimation and, 28, 34
of basic crustacean evolution, 162
and divergence, 21
fitness of, 24
Enzymes, 24
†Eocaris, 162
Ephippia, 82, 152, 153
†Eridoconcha, 146
†Eridostraca, 146
Eriochir, 33, 34, 38, 40, 42, 43, Fig. 9
Eriphya, 34
Eryonidea, 57
†“Estheria”, 149, 150, 178, Fig. 75
Euanalogy, 93, 96
Euanolastraca, 178-179
Eucarida, 93, 96, 99, 100, 144, 162, 183, Fig. 80
Eumalacostraca, 106, 159, 161, 168, 181, Figs. 68, 78
Euphausia, 144
Euphausiacea, 162, Table 1
Euryhaline (see Salinity)
Evolution (see Adaptation, Phylogeny, etc.)
Evolutionary lines, 13-15, Fig. 1
Excretion, 39-41
Exoskeleton, 20, 143
Eyes (see Compound eyes)
Eystalk, 9, 70, 96
Feeding, 5, 6, 17, 20–21, 136, 143–144, 160, 164, 170, 171, 172, 178, 179

†Fordilla, 146, 160
  Freshwater (see Adaptation)
  Frontal organs, 9–10
  Fusion, 132
  of segments, 20, 95, 96, 106, 174

†Gabonestheria, 149, 151, Fig. 65
  Gammarrus, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42, 
  Figs. 5, 8, 9

†Gampsonychidae, 106

†Gampsonychidea, 95, 96
  Gecarcinus, 39, 44, 59, 62, 63, 65, 66, 67, 69, 71, 
  72, 74, 75, 76, 77, Tables 2–4, Figs. 15, 20–25

Gene modification, 148, Fig. 66
Genetic adaptation (see Adaptation)
Genetic potentiality, 25, 109
Genitalia, 51–57, 83, Figs. 10–14
Genotype, 24, 29
Gills, 59, 60, 62, 71, 73, 74, 76
  and osmoregulation, 35–40, 42
  on pleopods, 44, 93, 96, 98
  structural adaptations, 43, 44, 45
  on thoracopods, 96

†Gilsonicaris, 153, 154
Glands (see Antennal gland, Maxillary gland, etc.)
Gnathobasic mandible, 112, 113–135, 136, 138
Gnathostraca, 1–2, 12, 179, Fig. 42
Gonads, gonoduct, gonopore (see Reproductive system)
Grades, 139, 163
Grooves, 132
Gymnopleura, 56, 57

Habits, 83, 108–109, 138

and divergence, 21, 80–81
and macroevolution, 45
Hansenomysis, 96
Harpacticus, 9
Head, 2–3, 5, 12, 44, 109, 111, 143
Heart, 3, 4, 12, 88, 93, 95, 96–97, 98, 101, 108, 
  Fig. 5
“Heavy” mandibles, 143–144
Heloeius, 31, 35
Hemigrapsus, 34, 35
  Fig. 48
Hemoglobin, 24
Hermit crab, 80
Hexapoda (see Insecta)
Histology, of pericardial sacs, 67–69, 75–76
Holeuryhaline (see Salinity)
Homerus, 30, 43, Figs. 6, 7
Homolidae (see Thexiopidae)
Homolodromiidae, 57
Homology, vii, 5, 9, 10, 93, 98, 99, 100, 101, 
  108, 111, 136, 143, 163, 164, 177
Homology investigation-method, 85, Fig. 39
Hoplocarida, 93
Hutchinsoniella, vii, 141–142, 164, 172, 177, Figs. 
  69, 73, 76
Hyas, 35

†Hymenocaris (see †Canadaspis)
Hyperia, 8

†Igorvarentsovia, 150, Fig. 66
Insecta, 3, 21, 22, 37, 111, 112, 113, 132, 136–139
Insecta/Crustacea relationship, 3, 22
Intestinal filling, 160
Intestine (see also Midgut, Proctodaeum, etc.), 
  3, 7–8, 42, 43, 108, 152, 160
†Ipsilonia, Fig. 65
Isopoda, 3, 8, 9, 10–11, 43, 44, 96–100, 109, 123, 
  137, 161, 181, 182, 183, Table 1, Figs. 37–35

†Japanoleaia, 148, Fig. 64
Jaws (see Mandible)
Juvenile stage, 11, 168–169

†Kazacharthra, 145, 154–155
†Keratestheria, 151, Fig. 65
Koonunga, 18

Labiata, 139
Labrum, 17, 18, 22, 159
Lacinia mobilis, 95, 100, 181
INDEX

Larval stages (see also Juvenile, Nauplius, etc.), vii, 75, 108, 109, 159, 168-169, 178
†Leaia, 147, 150, Figs. 64, 66
†Leaïidae, 147, Figs. 64, 66
Leander, 9
†Lepidippidae, 145-146
†Lepidocaris, 18, 171, 178, Figs. 71, 75
Lepidurus, 154
Leptodera, 153
Leptograpsus, 152
Leptestheriidae, 153
Leuia, 150, 151, Fig. 65
†Leuiaidae, 152
Lepisma, 60
Ligia, 32, 122, 125, 131, 132, Figs. 49, 54-56
Ligidae, 44
Limbs (see Appendages)
Limnadia, Fig. 71
Limnadiidae, 152
†Limnadiopsetiaea, 150, 151, Fig. 65
†Limnadaeopsis, 151, Fig. 65
†Limnesteria, 152
Limulus, 21, 112, 113, 131-135, 138, 144
†Liposcuta, 145, 154, 156
Locomotion, 4, 6, 35
and abdominal structure, 3, 108-109
and macroevolution, 45
Locusta, 131
Lophogastrida, 99, 181, Fig. 40
Lophopanopeus, 35
Loss of characters, 107, 108, 109, 156, 181-183
Lyncidaeidae, 152, 159
Lyneus, 159

Macroleon, 45
Macrura, 83
Maja [Maia] 35, 54, 55, 60, 68, 69, Fig. 14
Malacostraca (see also various groups), 1, 3, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14, 19, 30-102, 106, 107, 108, 109, 110, 122, 132, 159, 160, 161, 162, 177, 178, 179, 181, 182, Figs. 1, 2, 26, 27, 28, 42, 78
Manca-stage, 98
Mandible, 19-20, 21, 23, 111-139, 141-144, 152, 159, 164, 168, 169, Figs. 45-57, 61, 62
gnathobasic, 112, 113-135, 136, 138
“heavy”, 143-144
whole-limb, 112-113, 136, 138
Mandibular palp, 101, 108, 154, 169
Mandibulata, 19, 139
Marine fossil Eumalacostraca, 162
†Marrella, 19
Marsupium (see Brood pouch)
†Massagetes, 148, Fig. 64
Maxilla, 163, 164, 171, 174, 177, Fig. 77
Maxillary gland, 42, 96, 164
Maxilliped, 100
Maxillipoda, 1, 2, 3, 4, 8, 10, 11, 12, 13, 23, 108, 177, 178, Figs. 1, 2, 42
Meganyctiphanes, 18
Membranipora, 108
Merostomata, 113, 132, 134-135, 138
Metabolic rate, 28, 29, 30, 32, 34, 35, 60
Metachronal limb movements, 171, Fig. 76
Metamerism, 5
Metanauplius (see also Nauplius), 12
Metapenaeus, 34, 35
Midgut, 7, 8, 101, 172
gland, 39, 59
Mitochondria, 24
Mollusca, 23, 143
Molting (see Ecdysis)
†Mouleoida, 147, Fig. 64
Monophyly, 88, 161
†Montecaris, 159, 162
Morphological series, vii
Morphology, 85-102
exactness of method, 99
importance of, 7
internal and external, 2-12
Mosaic evolution, viii, 19
Mouth, 6, 17, 18, 19, 20, 22
Mouthparts (see also Mandible), 3, 12
displacement of, 9
evolution of, 4-5
of †Kazacharthra, 154
Muscles, 3, 4, 17-18, 84, 91, 111-139, 141, 143,
164, 177, Figs. 46-48, 51-53, 55-60, 62
Myriapoda, 21, 22, 81, 112, 113, 136, 138, 139
Mysidacea, 8, 95, 96, 99, 100, 106, 162, 181, 183,
Table 1, Fig. 39
Mysis-stage, 169
Mystacocarida, 1, 2, 3, 4, 5, 8, 12, 13, 20, 108,
164-165, 174, 177, 179, 183, Figs. 1, 70
†Nahecans, 90, 105-106, Figs. 31, 43
Natantia, 9, 55, 57, 83
Natural selection, 23-24, 27, 143
Natural system, 2, 13, 183
Nauplius, 28, 102, 108, 153, 159, 164-168, 178,
Figs. 70-74
Nauplius eye, 9, 11, 12, 23, 101
Nebalia, 8, 106, 108, 162, Fig. 30
Nebaliacea, 106, 144
Neomysis, 29
Nephridia, 88, 101
Nephridial canals, 43
Nervous system (see also Brain), 3, 8-11, 172
Neuroendocrine system, 69-70
New steady state, 29, 30, 31-32, 34
Niches, 21, 81-82, 83
Non-genetic adaptation (see Adaptation)
Non-physically controlled community, 82
Notopoides, 53-54, Fig. 13
Notostraca, 5, 7, 23, 93, 108, 145, 154, 155, 156, 159, 171, 172, 179, Table 1
Ocypode, 34, 35, 39, 44, 45, 59, 60, 62, 65, 66, 67, 72, 74, 75, 76, Tables 2-4, Figs. 17, 21, 25
Oesophagus, 122
Olenellid trilobites, 19
Olfactory sense, 177
Oligohaline (see Salinity)
Oniscidae, 44
Oniscus, 32, 44
Ontogeny, 7, 108, 112, 147
Onychophora, 21, 80-81, 112, 136
Organs (see also Frontal organs, etc.), 9-12
displacement of, 3-4, 9
“Original” structure, 85, 107
Ornamentation, of Onychopodida, 147
Osmoconcentration, Figs. 8, 9
Osmosis, 35-42, 60
Ostia, 93, 101, 106
Ostracoda, 1, 2, 7, 8, 11, 12, 13, 28, 108, 110, 114, Table 1, Figs. 1, 2
Overlap of pleura, 182
Overshoot response, 29-30
Oxygen, consumption and acclimation, 29, Figs. 3, 4
Oxystomata, 56, 83
Pachygrapsus, 33, 35, 39, 40
Pagurus, 34, 35
Palaemon, 35, 39
Palaemonetes, 34, 35, 37, 39, 40, 41
†Palaecaris, 160
†Palaeolimnadiopsis, 151, Fig. 65
Paleontology, 82, 84, 85
adaptation and, 80
method of, cf. zoology, 182-183
need for, 4
†Palaeopalaemon, 162
Palinura, 57
Palinurus, 35
Pancarida, 96, 99, 100, 183, Figs. 41, 80
Pandalus, 9
Panopeus, 60
Panulirus, 67, 69
†Paraleaia, 147, Fig. 64
Parallel evolution, vii, 25, 83, 183
of carapace, 2, 181
of compound eyes, 22-23
of mandibles, 135, 139
Paranaspides, 18, 113, 117, 122, 125, 127, 160, Figs. 49, 52, 53
Parastygocaris, 183
Particle-feeding (see Feeding)
Pauropoda, 138
Pelagic habit, 3-4, 6, 45, 144, 160, 172
†Pemphicyclus (see †Cornia)
Penaeidea, 109, 168, 169, 174
Penaeus, 35, 168, Figs. 72, 74
Peracarida, 3, 4, 96-100, Figs. 39, 80
Pericardial sacs, 44, 59-77, Figs. 15-24
function, 69-73, 76
gross anatomy, 60-67
histology, 67-69, 75-76
surface area, 62, 63-67, 75, Tables 2-4
†Perimetcurs, 106
Peripatus, 80, 136
Petasma, 93, 95, Fig. 34
Petrobius, 18, 136, 137, 138, Fig. 48
Phoronid larvae, 108
Phyllocarida, 93, 106, 159, 160, 161-162
Phyllopoda, 1, 5, 6, 7, 8, 10, 11, 12, 24, 108, 110, Fig. 1
Phylogenetic series, vii, 143
Phylogeny, vii-viii, 24-25, 27, 85, 107, 112, 141, 182-183
of Arthropoda, 11, 134-135, Fig. 44
of Branchiopoda, Fig. 67
of Crustacea, 6, 7, 9, 13-15, 177-178, Fig. 79
of Eumalacostraca, 161, Fig. 68, 80
of Malacostraca, 4, 85-102, 161, 177, 178, Figs. 68, 80
reconstruction of, 85
Physically controlled community, 82
Pleopods, 18, 52-53, 54, 56
respiratory, 44, 93, 96, 98
†Plesiosauria, 80
Pleura, overlap of, 182
Polyartemidiae, 153
Polychaeta, 88, 108
Polyphylly, 139, 161, 181
Polystenohaline (see Salinity)
Porcellio, 32
INDEX

Porcellionidae, 44
Porifera, 143
Post-Mysis stage, 169
 Potamobius (see Astacus)
 Potamon, 31, 34, 37, 40, 42, 43, Fig. 9
 Potentiality, basic genetic, 24-25
 †Praecaia, 147
 Preadaptation, 83
 Precoxal segment, 132
 Pre-epipodites, 135
 Primitive (see also Ancestors), 2, 17, 85, 107-108
 anomomerism, 107
 branchiopod, 156, 171, 179, Fig. 75
 characters, 6-7
 crustacean, 102, 107-108, 143, 163, Fig. 78
 adaptation and, 45
 ?benthic or pelagic, 3
 and Cephalocarida, 6, 12, 13-14, 156, 177
 characters of, 6, 162
 development of, 164
 limb(s) of, 4-5, 20-21, 109
 organization, 3, 6
 and tagmosis, 6
 eumalacostracan, 161
 feeding mechanism, 17, 144
 habit, 144
 jaw mechanism, 111
 Malacostraca, 144, 168
 malacostracan, 3, 6, 85, 100-102, 105, 107,
 144, 168-170, 177, Fig. 28
 tagmosis, 164
 Primitiveness, 6-7, 17
 and appendages, 107, 108, 109
 of Cephalocarida, 177
 of Malacostraca, 107-109
 secondary, 85
 and segmentation, 107
 of Stomatopoda, 108-109
 of turgor organization, 143
 Procambarus, 41
 Procephalon, 90-91, 93, 108
 Proctodaemum, 8
 Promotor-remotor movements of coxae, 112-136,
 143, Figs. 45, 46, 50
 Protobranchiopod (see Primitive branchiopod)
 †Pseudocrustacea, 6, 19, Fig. 42
 Pseudotracheae, 43, 44
 †Pterygota, 147, Fig. 64
 Pterygota, 137-138
 †Pygocephalomorpha, 181
 †Quadriasinussia, 152
 Ranina, 53, 54, 56, Fig. 12
 Raninidae, 51, 53-54, 56, 57, 83
 Raptorial appendages, of Syncarida, 160
 Recapitulation, vii
 Reduction, of organs and structures, 17, 93, 95,
 98, 106, 109, 154, 156, 161, 174, 175, 183
 Relative growth, 34
 Reproductive system (see also Genitalia), 17, 179
 of ancestral malacostracan, 101
 of Copepoda, 4
 displacement of, 3-4
 of fossil Conchostraca, 152
 position of gonopore, 3-4, 5
 Reptantia, 55
 Reserve cells, 69
 Respiration, 4, 20, 34, 43, 44-45, 59, 73, 93, 139
 Respiratory organs (see also Gills, etc.), 96, 98
 Responses, 28, 29-30, Figs. 3, 4
 undershoot and overshoot, 29-30
 Reversal, evolutionary, 138
 †Rhinocarididae, 105
 †Rhinocarina, 106
 Rhithropanopeus, 35, 36, Fig. 8
 Rhodopsin, 23
 Ribs, of Conchostraca, 150-151, Fig. 64
 †Rochdaia, 153
 Rostral plate, rostrum, 105, 162
 Salinity, 30-42, 82, Figs. 8, 9
 Scorpionidea, 80, 106
 Scutes, 21, 132, 138
 Secondary derivation, 85, 108, 144, 169
 Secondary modification, 144
 Segmentation, 5, 6, 20, 88, 164, 166, 174, Fig. 70
 of abdomen (see Abdomen)
 of †Archeostraca, 159
 of Branchiopoda, 153-154
 inherited from annelid, 20
 of Malacostraca, 88
 of mandibles, 138
 and primitiveness, 107
 variation in, 110
 Selection pressure, vii, 24, 27
 Selective preservation of fossils, 162
 Sella turcica, 55
 Seminal receptacle, 181
 Sense organs (see also Compound eyes, etc.),
 9-12
 Serial adaptation, 28
 Serial homology, 163-164
Setae, 17, 18-19, 22, 62, 71-72, 75, 76, 164, 167, 168, 169, 171, 174, Figs. 20, 21
Shape, changes in Conchostraca, 147
Sida, 178, Fig. 75
Simoccephalus, 29
Single character classification, 83
Size, 65-67, 147
Speciation, 82
Species, abundance, 81, 83
Spelaeogriphacea, 183
Speocarcinus, 35
Spermathecae, 51-57
Spermatophores, 51
Sphaeroma, 44
Spriggma, 20
Squilla, Figs. 33, 34
Stabilization phase, 30-31
Statocyst, 9, 95-96
Steady state, 29-33, 34
Sternal furrows, 51
Stomach, 88, 95, 98, 100, 101
Stomatopoda, 3, 4, 20, 90-95, 100, 106, 108-109, 161, 177, Table 1, Figs. 32, 33-35
Stomodaeum, 7, 8
Streptocephalus, 32
Stress, 82
Structural adaptation (see Adaptation)
Structure, and function, 80
Stygocaris, 183
Sutures, 132
Symphyla, 80, 138
Syncarida, 95-96, 117, 118, 122, 144, 159, Table 1
Tachypleus, Figs. 58-60
Tagmosis, 5-6, 107, 164
Tanaidacea, 98, 109, 161, 162, 181, 183, Fig. 39
Telopodite, 112, 113
Telson, 95, 100, 106, 107, 109, 154
Temora, Fig. 72
Temperature, acclimation, 29, 30, 32-34, 35, Figs. 5-7
Tendons, 111-138
Terrestrial adaptations (see Adaptation)
Terrestrial crabs, 59-76
Thelxiopidae [Homolidae] 51
Thermosbaenacea (see Pancarida)
Thoracica, 11, 13, Table 1
Thorax, 5, 6, 51-52
Thysanura, 3, 138
Tigriopus, 32
Time scale, for branchiopod evolution, 156
Tolypeutes, 44
Tomopteris, 20
Trends, vii, 27, 111, 137, 153-154
Trichoniscidae, 44
Trilobation, 135
†Trilobita, 19, 21, 132-135, 136, 138, 143, Fig. 44
Trilobitan limb, 19-20, 21, 109, 132, 135, 143, 144
†Trilobitomorpha, 19
Triops [Apus], 10, 18, 21, 41, 144, 154, Figs. 71, 75
Turgor, 143, 179
Tymolae [Cyclodorippae], 53
Tymolidae, 56-57
Tymolinea, 51-53, 55-57
Tymolus [Cyclodorippe], 51-52, Figs. 10, 11
Uca, 33, 34, 35, 39, 44, Fig. 8
Undershoot response, 29-30
Unique solutions, 22-24, 141
Upogebia, 35
Urcrustacean (see also Primitive crustacean), 163
Uropods, 44, 93, 95, 96, 97, 98, 106, 169
Urspriinglich, 85
Variation, 27, 147
Varuna, 38
Vertebrates, 23, 109
†Vertextia, 150, 151, Fig. 65
Vision (see Compound eyes)
†Waptia, 109
Water uptake, 70-76
Weight of Brachyura, 62, 65, 66, 67
Whole-limb mandible, 112-113, 136, 138
Xeinostoma, 51
Xiphosura, 131, 143, 144, 162
X-organ, 9-10, 12