PART R

ARTHROPODA 4

CRUSTACEA (EXCEPT OSTRACODA)

MYRIAPODA—HEXAPODA

By H. K. Brooks, F. M. Carpenter, M. F. Glaessner, Gerhard Hahn, R. R. Hessler, R. L. Hoffman, L. B. Holthuis, R. B. Manning, S. M. Manton, Lavon McCormick, R. C. Moore, W. A. Newman, A. R. Palmer, W. D. I. Rolfe, Paul Tasch, †T. H. Withers, and V. A. Zullo

VOLUME 1

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[Volume 1, p. i-xxxvi, *R*1-*R*398; Volume 2, p. *R*399-*R*651; Volume 3 (to follow)]

INTRODUCTION

By Raymond C. Moore

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This unit of the *Treatise* to which the letter R was assigned in original plans has been exceptionally slow in taking form and more difficult that any other yet published to organize. For example, the first major sections of systematic descriptions and illustrations were received from O. W. Tiegs and T. H. Withers in 1954. After editorial work had been approved by the authors, the materials were placed in files as Part R "nest eggs." Prior to 1960, F. M. Carpenter, M. F. Glaessner, and Paul Tasch had accepted Part R assignments, and in the period 1961-65 the list of contributing authors was enlarged to include H. K. Brooks, Isabella Gordon, Gerhard Hahn, R. R. Hessler, R. L. Hoffman, L. B. Holthuis, R. B. Manning, S. M. Manton, W. A. Newman, A. R. Palmer, W. D. I. Rolfe, and V. A. Zullo.

Completed first drafts of sections, varying considerably in length, or revisions of previously submitted typescripts and figures were received by me as follows: 1956—Tasch; 1960—Tasch; 1961—Hessler, Rolfe, Tasch; 1962—Carpenter, Hessler, Manton, Palmer, Rolfe, Tasch; 1963—Carpenter, Glaessner, Hessler, Holthuis & Manning, Manton, Rolfe, Tasch; 1964—Brooks, Carpenter, Glaessner, Hessler, Rolfe; 1965 — Carpenter, Glaessner, Hahn, Hoffman, Holthuis & Manning, Palmer, Rolfe; 1966—Carpenter, Glaessner, Manton, Newman & Zullo, Rolfe; 1967 — Carpenter, Hahn, Newman & Zullo.

With expectation that unfinished portions of Part R would be ready for the press within a few months at most, type-setting was begun in June, 1965, and continued steadily through November of that year. Then, owing to the unavailability of awaited typescripts, it was necessary to halt press work until June, 1967, only to shut down again in less than three weeks' time. The final stage of type-setting was delayed until February, 1968. This record amply demonstrates the arduousness of coordinating the labors of numerous specialists, each of whom is needed to round out a taxonomic "package" in manner aimed at maximum comprehensiveness and authoritativeness. I am very grateful to all of the *Treatise* contributors who have conscientiously worked to meet our objectives by able completion of their accepted assignments, but from the viewpoint of all concerned—participating authors and an anticipated host of persons who will be benefitted by use of this and other *Treatise* units —I deprecate the slowness in accomplishing publication.

I call special attention to the two chapters of general scope next following this short introduction. They have been contributed by Sidnie M. Manton in response to invitations extended by me, that on classification of Arthropoda after she and other *Treatise* authors concerned with arthropodan groups had criticized (1965, *in litt.*) the so-called subphylum assemblage named Mandibulata or Antennata as quite outmoded and therefore unacceptable in classification. The breadth and thoroughness of Dr. Manton's many years of investigations on most important morphological features of virtually all main divisions of living arthropods, coupled with studies of their anatomy, physiology, interrelationships, and evidence bearing on their evolutionary changes and phylogeny, especially qualify her for a comprehensive appraisal of the phylum—granting that groups known only as fossils have received little first-hand attention from her. For these, judicious dependence on the work of paleontologists has been requisite.

Manton's discussion of the problems of arthropodan major classification in the light of multitudinous factual observations which have been accumulated points to the need for emending the outline of main divisions of the Arthropoda given in *Treatise* Part O (1959, p. *O*15-*O*16). This is now given in her chapter (p. *R*13) and adopted as a guide for arranging most of the sections of systematic descriptions.

Comparison of the chapter on *Introduction to Classification of Arthropoda* with the next one on *Evolution and Affinities of Onychophora, Myriapoda, Hexapoda, and Crustacea,* written earlier, shows how one complements the other in stressing important common features of main groups as contrasted with equally important differences.

The chapter on *General Feaures of Crustacea* by MOORE & MCCORMICK is substitute for one which ISABELLA GORDON had agreed and expected to prepare, but which cirsumstances prevented her from submitting. Invitations to other crustacean specialists were declined. Such a chapter by GORDON may yet be offered for later *Treatise* publication in a supplement or revision of Part R.

Authorship of systematic descriptions of crustaceans, myriapods, and insects is indicated with each division. Mostly it was arranged several years ago. On the basis of counsel received from *Treatise* advisers and on my own responsibility, the contributions received in 1954 from WITHERS on Cirripedia and from TIEGS on Myriapoda have been considerably revised by others, including changes of illustrations. Late submissions (June, 1966) were valuable self-originated sections by ROLFE on Arthropleurida and Arthropoda Incertae Sedis and by HAHN on Bostrichopodida.

A departure from previous practice in publication of *Treatise* units is made in issuing two volumes of Part R, here given, in advance of a third one containing text and illustrations for fossil insects. This is a comparatively large section which is not yet ready for the press. The index for Part R is divided accordingly.

INTRODUCTION TO CLASSIFICATION OF ARTHROPODA

By S. M. MANTON

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[Chapter submitted January, 1966]

Different parts of this *Treatise* refer to a variety of classifications, either of the Arthropoda as a whole, or of parts of this vast assemblage of animals. Fossil remains do not demonstrate either the origin of the Arthropoda or of its classes. When the fossil record provides no decisive evidence of interrelationships, classifications can be, at best, only working hypotheses. But such hypotheses must conform to the ever-growing body of evidence relating to past history of living animals which stems from all available sources. Classifications should be based upon facts and not upon speculations. The practical necessities of taxonomic and other work makes subdivision or classification of arthropods an imperative requirement. It is not surprising that some of the imperfectly known fossil arthropodan remains cannot be referred with certainty to any modern group and others appear to be decidedly unlike animals in any extant class.

A classification of arthropods should be based upon phylogeny, but in the absence of sufficient fossil evidence, taxonomic groupings must rest largely upon the comparative anatomy of living species, on embryology, and life histories, and probably to some extent also on biochemistry and biophysics. The available evidence concerning the extinct arthropods is more limited and much less detailed. A very large measure of convergence is shown by the morphology and physiology of living arthropods whose past histories, it is inferred, must have been fundamentally different. An appreciation of such convergences is of immense importance in the elucidation of arthropodan relationships. No simple scheme of classification which ignores convergence can provide a basis for the reconstruction of past history and relationships of arthropods. A review was given by TIEGS & MANTON (25) of theories of arthropod phylogeny and classification which had been advanced prior to 1958. In recent years important new factual evidence concerning these matters has been obtained. This introduction for *Treatise* Part R is intended to be a brief summary of the present position of arthropod classification based upon older considerations and newer factual evidence.

Abundant evidence concerning the evolution and relationships of living arthropods, at first unexpected, has been provided by an increasing body of studies of functional anatomy and of the habits of life with which the morphology is intimately associated, a line of work not easy to apply to fossil materials. Vast arrays of complex anatomy, such as those shown by crustacean limbs or the trunk skeletomusculature of myriapods, takes on a new and ordered meaning. An understanding of the manner of working of different morphological systems, together with the circumstances under which they work, lead to two advances in our appreciation of arthropodan evolution. Firstly, the different morphologies which characterize many of the larger groups of living arthropods have been shown to be related to habits of life which are not adaptations to particular environmental niches. Evolutionary advances in morphology and physiology can enable an animal to live better both in the same and in a variety of environmental circumstances. The end terms of evolution within a particular order or other category, on the contrary, often form adaptive radiations to particular niches, and these adaptations, superimposed upon the more basic characters of each group, have less far-reaching evolutionary significance in that they do not give rise to new forms of evolutionary significance (p. *R*21). Secondly, when the functional advantages, or the mode of action, of various morphological set-ups are known, any postulated evolution from one to another which entails a functionally impossible intermediate or one which negates the functional advantages already achieved, at once becomes apparent. The factual matters brought forward by this type of work are of basic and essential importance in any attempt to arrive at a natural classification of the Arthropoda. These lines of work are as yet in their infancy, and for their successful development the comparative approach is essential. Detailed study of one animal alone gives few clues, but a knowledge of the functional assets of animals showing very different and closely similar habits at once becomes revealing as to the possible manners in which their evolution can have proceeded.

The Arthropoda have in common a metamerically segmented body with a differentiated anterior end which forms either a localized head or the anterior part of a cephalothorax or prosoma, according to the class. They possess serially repeated limbs along a trunk; an ostiate heart and a hemocoelic body cavity; and a cuticle, which even when thin and flexible, is constructed in a definite arthropod manner. Growth is intermittent, owing to periodic ecdysis of the cuticle. The features which link the arthropods together are thus few in number. The conspicuous sclerites on the body and limbs of most arthropods are not necessarily basic arthropodan features (see below). Many arthropods have a cuticle which is little sclerotized and bends easily. Many sclerites are not associated in any way with muscles and perform protective and other functions (1, 15). Muscles insert upon subcutaneous sheets of connective tissue, on basement membranes and on internal tendon systems far removed from the body surface. Muscles frequently pull on arthropodial membranes (13, 14, 15). Muscles are attached to sclerites only indirectly by tonofibrils traversing ectodermal cells from the subectodermal connective tissues. Extreme sclerotization, coupled with the formation of elaborate joints, lever-like apodemes, etc., represent arthropodan advances which are far less basic than the hemocoel, although found among the earliest recognizable arthropodan remains.

The head end is formed ontogenetically in a manner unlike that in other phyla. Ventrolaterally the anterior segmental mesodermal somites (which form most of the internal tissues of the adult) and the corresponding ectodermal areas, many of which bear limb rudiments, grow forward relative to the mouth. The oral aperture with the unsegmented rudiment forming the upper lip (labrum), shifts backwards, as shown diagrammatically in Figure A. Some of the anterior limb rudiments are thereby carried to a preoral level, while the mouth becomes subterminal and ventrally directed, unless other specializations ensue. A preoral cavity is frequently formed by these shifts, and into it the mouth parts crush, grind, or bite the food. The mouth does not shift out of one segment and into another (23; 25, p. 269). It is the lateral parts of the segments which bend forward around the mouth. The anterior segments are not even roughly cylindrical in shape, as are those of the trunk. The dorsal tissue of much of the head is formed by unsegmented acron, tissue which has persisted from the embryonic or developmental stage previous to that in which segmentation is initiated (Fig. A). The figure by WEBER, reproduced in the *Treatise* Part O (Fig. 6) is a purely theoretical concept. The varying amounts of yolk in arthropodan eggs determines the early distance (large in Fig. A) between the unsegmented dorsal blastoderm and the ventral segment rudiments at the future anterior end of the body. Comparative embryology of the more primitive members of the larger arthropod groups does not substantiate WEBER's theoretical concept, accepted by STØRMER in the *Treatise*.

The limbs which become preoral in position tend to become sensory or trophic, in whole or in part, and perform other functions according to the group. Limbs just behind the mouth are usually specialized for feeding to some extent, and the unsegmented acron provides eyes of various kinds.[1]

The major classes of arthropods each have characteristic head structure which alone is sufficient to separate one class from another. The differentiating characters comprise: 1) number of segments which have shifted to a preoral position, one in the Onychophora, two in the Chelicerata, and three in Crustacea, Myriapoda, and Hexapoda; 2) number and nature of preoral limbs—prehensile chelicerae characterize the Chelicerata (Merostomata, Arachnida), two pairs of antennae occur in Crustacea, and one pair in the Onychophora, Myriapoda and Hexapoda; 3) presence or absence of mandibular appendages just behind the mouth and nature of these limbs—the mandibles in Crustacea are formed by the leg base and those of the Onychophora, Myriapoda, and Hexapoda by a whole limb which bites with the tip and not with the base; 4) number of paired postoral limbs used in feeding; the Chelicerata usually employ one or more pairs of gnathobases for chewing or cutting and use a movement (and associated morphology) quite unlike that operating the crustacean gnathobases. The Crustacea, Myriapoda, and Hexapoda show two pairs of limbs largely or entirely devoted to feeding (maxillules, maxillae) and further limbs may be used in part, or entirely, for such purposes in Crustacea and certain Myriapoda. Cephalic segmentation and limb equipment in fossil arthropods is seldom known with certainty. We do not know whether trilobite antennules correspond with the antennules or antennae of Crustacea, and the four following biramous limbs of some trilobites may be common to the class and may correspond with the postantennulary head appendages of Crustacea. The many middle Cambrian merostome-like arthropods cannot be assigned with certainty to Crustacea, Trilobita, or Merostomata on their imperfectly known cephalic features (17, 19, 21). There is every probability that many extinct Arthropoda, such as *Sidneya* (19), do not belong to any of the well-known classes.

The arthropodan trunk region may or may not be divisible into definite tagmata, but these regions when clearly defined are characteristic of only certain classes and orders. The tagmata shown by the Arthropoda are well known and need not be enumerated here.

In some arthropods all trunk segments are laid down embryologically before hatching, and in others only a few segments are so formed, additional segments being added progressively during early life. The details

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[1] The table in *Treatise* Part O (p. O11) suggesting homologies of anterior segments in arthropods is not in accord with factual knowledge (*see* footnote, Part R, p. R42).

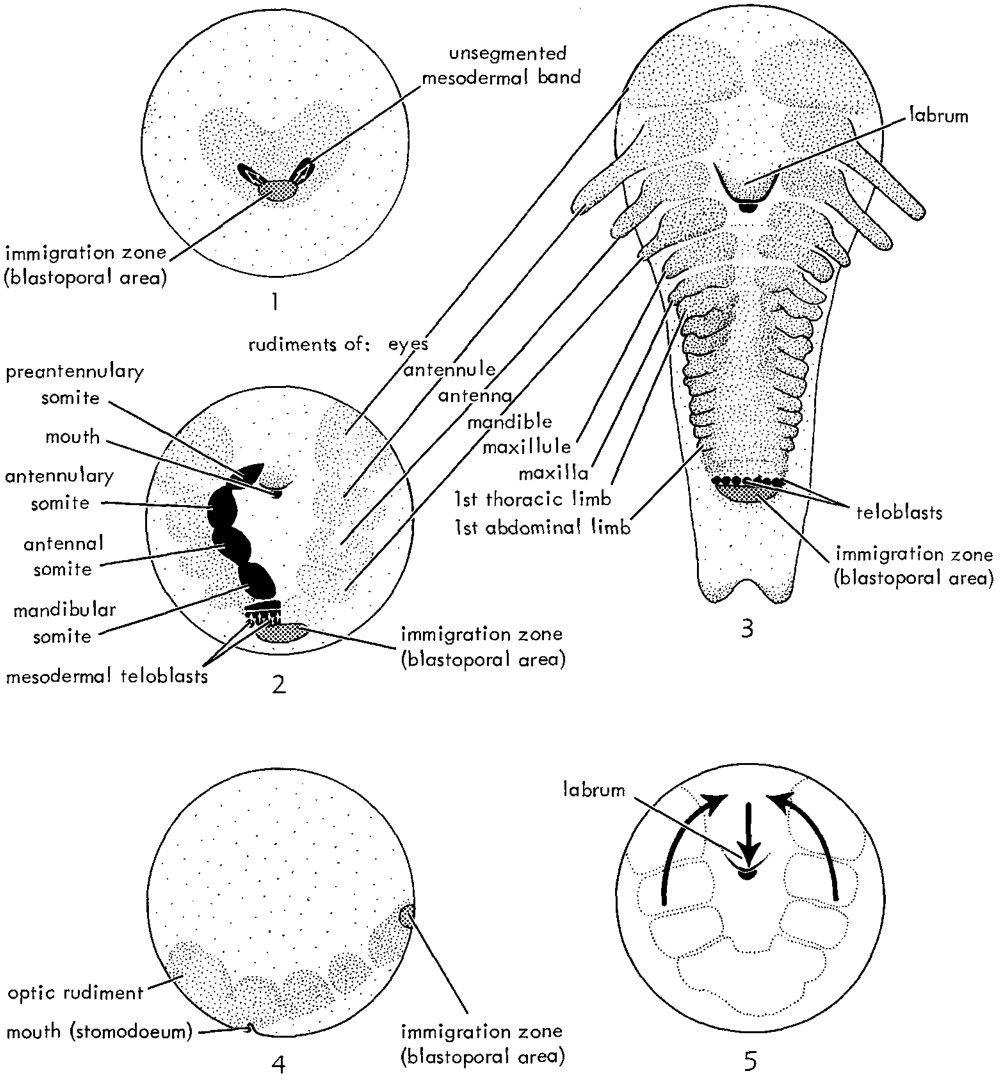


FIG. A. Diagrams illustrating manner in which a head is formed during development in an arthropod, the example being a mysid crustacean.

1-5. Progressive stages shown in *(1-3)* in ventral view, *(4)* in side view and *(5)* diagram of *(2)* showing directions in which tissues shift as they grow.

The unsegmented embryo becomes segmented only ventrally at the head end *(4)*, the dorsal surface being unsegmented. The head is formed by elaborations from this unsegmented anterodorsal tissue (acron), forming eyes, etc., and the preantennulary, antennulary, and antennal segments bend forward relative to the backgrowth of the labrum and oral aperture *(2,3)*. Stippling shows concentrations of outer ectoderm to form the optic rudiment, segmental rudiments, and upper lip (labrum). White stipple on black shows forward migration of mesoderm from its site of origin in *(1)* to form the mesodermal somites in *(2)*. The immigration zone, or blastoporal area, forms mesoderm and endoderm.

whereby segments are formed differs from class to class (4, 4a, 7, 22, 23, 24).

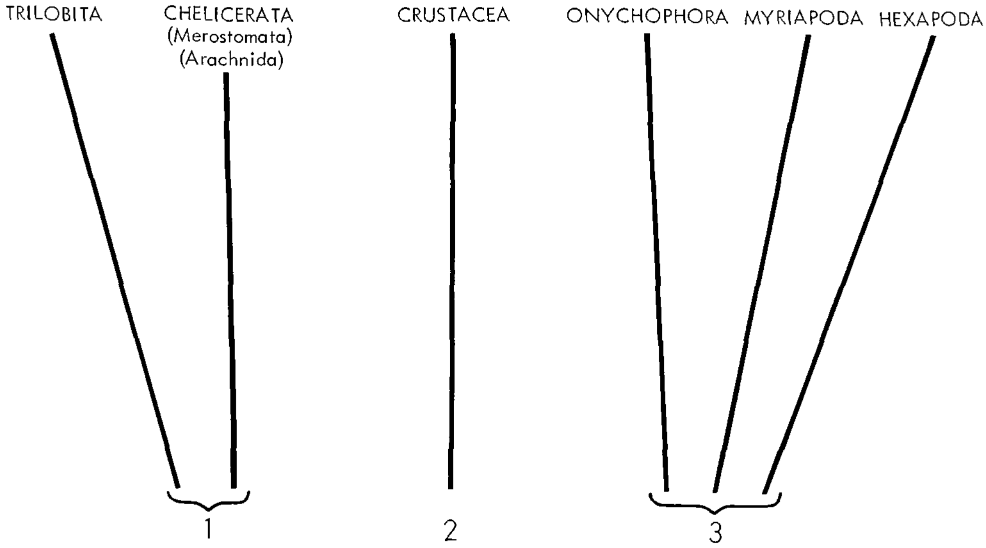
A characteristic of great evolutionary and classificatory significance concerns the limbs. Simple uniramous limbs characterize the Onychophora-Myriapoda-Hexapoda assemblage. Biramous limbs of two contrasting types occur in the primarily

FIG. B. Diagram showing conclusions reached concerning interrelationships and evolution of jaw mechanisms in classes Onychophora, Myriapoda, and Hexapoda, based upon detailed study of structure and mode of action of mandibles throughout the Arthropoda (14).

Two independent lines of evolution are shown, utilitizing an unjointed (left side) and jointed (right side) whole-limb mandible. The shaded area indicates independent evolution of entognathy and protrusible mandibles in seven groups. The left-hand branching line is not intended to mean more than the derivation of the mandible of the Pterygota whose ancestors may have passed through stages in which the mandible resembled those of *Lepisma* and *Petrobius* in certain essentials. The lower convergence of the lines denoting the several Apterygota is not meant to imply a common ancestry, but only a closer affinity between the hexapods than between them and any myriapod.

aquatic groups (Fig. B); a limb with the exopod arising distally on the protopod occurs in Crustacea, but in the Trilobita the outer ramus arises proximally on the protopod, so corresponding with the exites on the protopod of Crustacea which are situated proximal to the exopod. Reconstructions from sections of the trilobite *Olenoides* (20) show flattened respiratory filaments on the outer ramus, quite unlike the exopod setae of Crustacea so often used in swimming (25). A uniramous trunk limb in many Crustacea results from the progressive reduction of the exopod and is used for walking and not swimming. A corresponding reduction of the outer ramus is presumed to have occurred also in the Chelicerata, only a few biramous limbs remaining, such as the branchial and sixth prosomal limbs of *Limulus*. There is no indication of a biramous limb in the Onychophora, Myriapoda, or Hexapoda. The fossil record does not in any way bridge the gap between these three limb types; they all may have evolved independently from the limbs of soft-bodied ancestors. Regrettably little information of a precise nature is available concerning limb structure in fossil arthropods, and great care is needed before a limb can be assigned either to the crustacean or to the trilobite type or to something different.

The outstanding convergences among arthropods, which should be faced in any attempt at a natural classification, concern: 1) **biramous limbs,** which differ basically in structure, at least in Crustacea and Trilobita, and which are insufficiently known in most fossil Arthropoda; 2) **mandibles,** which are entirely different in derivation in Crustacea and in the Onychophora-Myriapoda-Hexapoda assemblage (14)—even in the latter group the myriapod whole limb segmented mandible, utilizing a basic adductor-abductor movement, contrasts fundamentally with the hexapod whole-limb unsegmented mandible; the basic movement of this latter mandible is a promotor-remotor roll giving a good grinding action and some cutting, and a transition from this, to mandibles which cut much more strongly in the transverse plane, takes place by morphological changes which are parallel to those Crustacea which also acquire transverse biting from a primitive rolling mandible (p. *R*25, 14); 3) **entognathy,** or boxing in of the mandibles, and in some forms of other mouth parts also, confers proximal freedom on the mandible which permits protractor and retractor movements, additional to the basic promotor-remotor roll giving grinding and cutting—entognathy has been evolved independently many times (Fig. B) and the possession of this general feature, with details differing in the several groups (15), is not indicative of close affinity, as has at times been suggested; 4) **compound eyes** do not appear to be basic in all classes—trilobite compound eyes lacked the refinements present in Hexapoda and in Crustacea which possess compound eyes, for such eyes appear to have



(1) The form of limbs and tagmata of the body perhaps suggests distant affinity between the Chelicerata and Trilobita and a lack of affinity between these classes and the other Arthropoda.

(2) The basic form of the biramous limbs and gnathobasic mandibles of Crustacea are so unlike the corresponding limbs of other Arthropoda as to preclude close affinity between them.

(3) The Onychophora, Myriapoda, and Hexapoda have similar uniramous limbs and all bite with the tips, not bases, of the mandibles. Also, similarities in the embryonic development of these groups contrast with chelicerate and crustacean developments. The three groups probably have had a roughly common origin, but the construction and mode of action of the segmented mandibles of the Myriapoda are so unlike those of the unsegmented hexapod mandibles as to indicate that the Hexapoda have not descended from any one class of the Myriapoda.

Fig. C. Diagram illustrating three major subdivisions of the Arthropoda between which there are no known connecting links.

been evolved independently in the latter classes; the eye structure in some crustacean orders and in Hexapoda, although closely similar, is not identical. Physiological requirements for this type of vision do not permit wide deviation from the most suitable mechanism, which consequently appears to have been a parallel evolution in the two groups; 5) **tracheal systems** used in air-breathing have evolved independently in Onychophora, Myriapoda, and Hexapoda, in Arachnida and certain Crustacea—the fine, almost unbranched tracheae of the Onychophora are not unique, as has often been supposed; similar tracheae are found in certain Chilopoda *(Craterostigmus)* where extensive changes in hydrostatic pressure occur in the hemocoel in association with various specialized abilities as in Onychophora (15); 6) **uric acid excretion** and the conservation of water in the excretory processes in land forms is achieved by Malpighian tubules in Arachnida and in Myriapoda and Hexapoda; uric acid secretion is done very simply by the mid-gut in Onychophora, but the presence of Malpighian tubules is not necessarily indicative of a uricotelic metabolism such as occurs in pterygote insects (Bennett & Manton, 1962); 7) **progoneate condition** of the Symphyla and Pauropoda has been shown by Tiegs (23, 24) to be secondary and probably related to anamorphosis. Further convergences could be noted, and see below for cuticular sclerotization.

No simple monophyletic scheme of arthropod classification can account for the distribution and morphology of the above features. Some measure of polyphyletic evolution within the group seems inescapable. At least three major groupings can be made, as shown diagrammatically in Figure C and distinguishable on tagmata and on the basic structure of the jaws and trunk limbs. This grouping is endorsed by Størmer (21) who can find no bridging of the gaps between them.

The Onychophora are not separable from the other classes of Arthropoda by any characteristics of fundamental importance. There is no sound evidence to justify the view that this class should be excluded from the Arthropoda. Onychophoran structure and embryology are basically arthropodan in great detail, and onychophoran peculiarities of structure and development are related to habits of life which are of survival value (5, 6, 7, 10a; Manton, 1959). Moreover, the Onychophora share many important features with the myriapod classes in contrast to all other Arthropoda (Manton, 1964; 15, 23, 24). The views to the contrary concerning the Onychophora and classification and phylogeny of the Arthropoda in general, recently put forward by Sharov (18), are not considered to be valid. They do not accord with the known evidence, they conflict with easily ascertainable new facts and rest on speculative bases. The principle advocated by Sharov that anthropod structure can only be understood by reference to the origin of the Articulata is hardly commendable since this province is unknown. A classification of the Arthropoda is not advanced by assertions that the group arose from the Ctenophora via annelids akin to the highly specialized Spintheridae. Such statements are unprovable. A reply to many of the points by Sharov is given by Manton (16 and 1967) and Anderson, 1966, together with the presentation of new data.

The factual evidence provided by the jaws is summarized in Figure D, and it divides the Arthropoda into the same three groups, separated by the heavy vertical lines, as in Figure C. The gnathobases, used for cutting and squeezing, in the Chelicerata are fundamentally different in skeletomuscular action from those of Crustacea, and the one could not have given rise to the other. The primitive rolling movement of the jaws of Crustacea and Hexapoda, described in another chapter (p. *R*49), must have arisen from the promotor-remotor swing of a walking or swimming limb, the actual mandibles in the two groups being quite different in derivation. Biting in the transverse plane is a secondary acquisition in many Crustacea and Hexapoda (shaded area), but is a primitive movement for the gnathobasic limbs of the Chelicerata and mandibles of Myriapoda. However, the limb structure in Chelicerata and Myriapoda is quite different.

The similarity in the structure and movement of the mandibles in the myria-

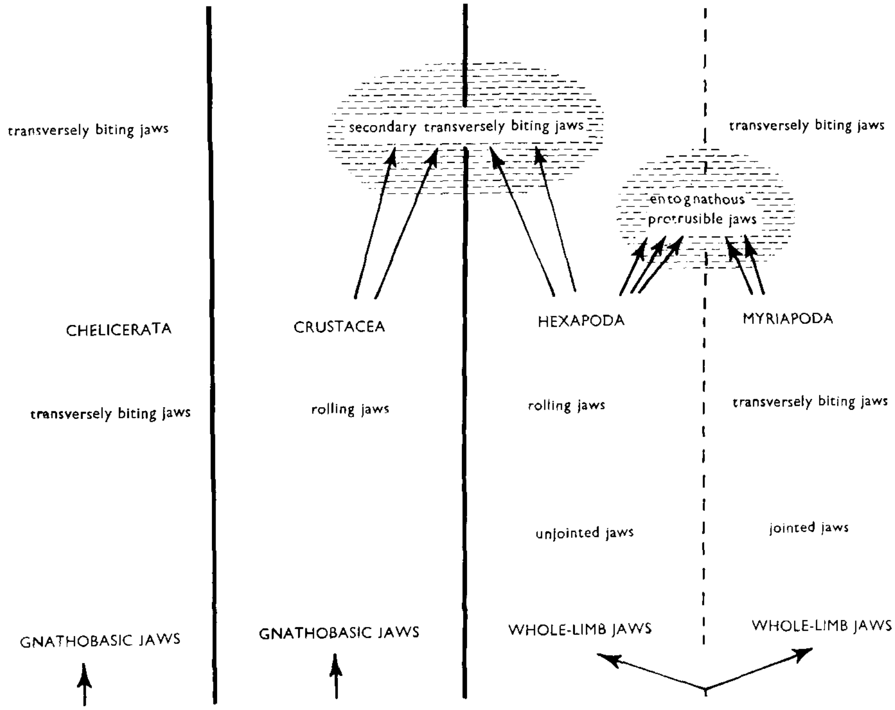


FIG. D. Diagram showing distribution of jaw types among Chelicerata, Crustacea, Hexapoda, and Myriapoda.

The heavy vertical lines indicate an entire absence of common ancestry of the jaw types, and the interrupted vertical line indicates the separate evolutions of jaw mechanisms in the classes Myriapoda and Hexapoda, although both are based on a whole-limb mandible. The shaded areas indicate convergently acquired biting in the transverse plane and convergently acquired entognathy (as in Fig. B).

pod classes, irrespective of the presence (Chilopoda, Pauropoda) or absence (Diplopoda, Symphyla) of enthognathy is of great importance (Fig. D, right side). In all, the abductor mechanism of the mandible is provided in whole or in part by the mechanical action of a swinging anterior tentorial apodeme (3, 14). No hexapod has a jointed mandible working in the myriapod manner. The hexapod anterior tentorial apodeme is rigid and is never concerned directly with causing mandibular movements. No myriapod either possesses or requires a posterior tentorial apodeme such as is present in all hexapods. Even the superficially similar maxilla *1* and maxilla *2* of Symphyla and hexapods contrast in their skeletomusculature and modes of action (14). TIEGS (23, 24) showed that the progoneate condition of Symphyla and Pauropoda is secondary and probably related to anamorphosis. There is a community in structure of the leg and of the coxa-body joint in all myriapods, which contrasts decisively with those of hexapods and the one could not have given rise to the other (16). Further, the myriapod type of coxa-body joint and its obligatory movements are not at all suitable for transition to a hexapodous state. The evolution of the myriapod type of leg base commits these animals to a multilegged condition. An opposite type of leg base in an early multilegged animal would have the potentiality of supplying the mechanical features necessary for the evolution of pterygote limbs. And it is only this type of leg base that is suitable for the further evolution of flight. The swinging pleurite, so essential to the classes of fleeter myriapods, and the associated leg base musculature, is not in the least appropriate for a further evolution of flight muscles. These are the principal reasons for the reinstatement of the once discredited Myriapoda as a natural group (14, 16). And they are the reasons for the destruction of the dream, so dear to entomologists, concerning a supposed close affinity between Symphyla and certain hexapoda. The marked differences in head and trunk anatomy between the several classes of myriapods has been shown to be associated in considerable detail with divergent habits of life (9, 10, 13, 14, 15, 16), and all could have evolved in parallel from a similar basic stock, although no one class could have given rise to any other.

The possession of only three pairs of legs borne on a thorax is functionally advantageous in that it permits the use of long legs, capable of taking a long stride, with a wide range of gait patterns, as is impossible to myriapods which possess long and many legs (MANTON, 1952b; 8, 16). The advantages of walking or running on only three pairs of legs have been acquired independently by many classes, notably certain Arachnida and Crustacea (8). It would therefore be conceivable that the six-legged state of the hexapod classes might also have been independent and parallel evolutions. Certain it is that the gulfs between the various hexapod groups are deep. But the discovery of the decisive differences between the morphology and modes of action of the head endoskeleton, the jaws and the trunk limbs of all Myriapoda, on the one hand, and of the several groups of pterygote and apterygote Hexapoda, on the other, indicates that the hexapods are indeed more akin to one another than to any other classes of arthropods. This does not mean that the hexapods had a common origin, or that the hexapodous state was acquired only once in their past history. All it suggests is that the hexapods may have had several origins from an ancestral stock of animals which was quite distinct from the ancestral myriapods. The same conclusion is indicated by a modern assessment of entognathy based upon accurate facts of morphology and function. These facts clearly demonstrate the fundamental differences between the several classs of entognathous Apterygota and the probability that their entognathy has been convergently acquired from a known basic condition, just as the entognathy of certain Crustacea and Myriapoda has been independently acquired (14).

Thus the evidence available to date suggests that the component classes of the Myriapoda and of the Hexapoda are more closely related to one another, within each of the two assemblages, than to any other Arthropoda, and that none of the hexapod classes has a claim to close relationship with any myriapod class. The common segment number shown by some hexapods and Symphyla and the possession of a labiate maxilla *2* in both are convergent similarities which do not outweigh the fundamental differences between the two groups.

The Merostomata clearly comprise the Xiphosura and the Eurypterida as major groups, and other probable merostome taxa have become extinct and are insufficiently known (19). There is evidence suggesting the derivation of the Arachnida from aquatic chelicerates, but whether the transition to land occurred once or several times is unknown (25, p. 304-307). There is no decisive evidence concerning the interrelationships of the several orders of either the Arachnida or Crustacea. The distinctions between the component orders of the Crustacea and of the Arachnida are just as profound as are those between the four myriapod classes and the several hexapod classes. But the reality of the Crustacea, Arachnida, Myriapoda, and Hexapoda as major groups seems clear.

Finally, reference must be made to the concept of grades in arthropod evolution. Such terms were first applied by TIEGS (24) to the Onychophora-Myriapoda-Hexapoda assemblage. The Monognatha (Onychophora) use one pair of postoral gnathal limbs, the Dignatha (Pauropoda and probably Diplopoda) use two pairs, the diplopod gnathochilarium probably representing but one pair of limbs, and the Trignatha (Symphyla and Hexapoda) use three pairs. These terms do not now indicate taxonomic groupings of affinity.[1] They show, on the contrary, levels of organization reached independently by various classes (Fig. E). The

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[1] The up-to-date use of the terms denoting grades in Myriapoda and Hexapoda is not appreciated in the article on the Myriapoda, where it is implied that the grades have a taxonomic sense (*Treatise*, p. *R*575).

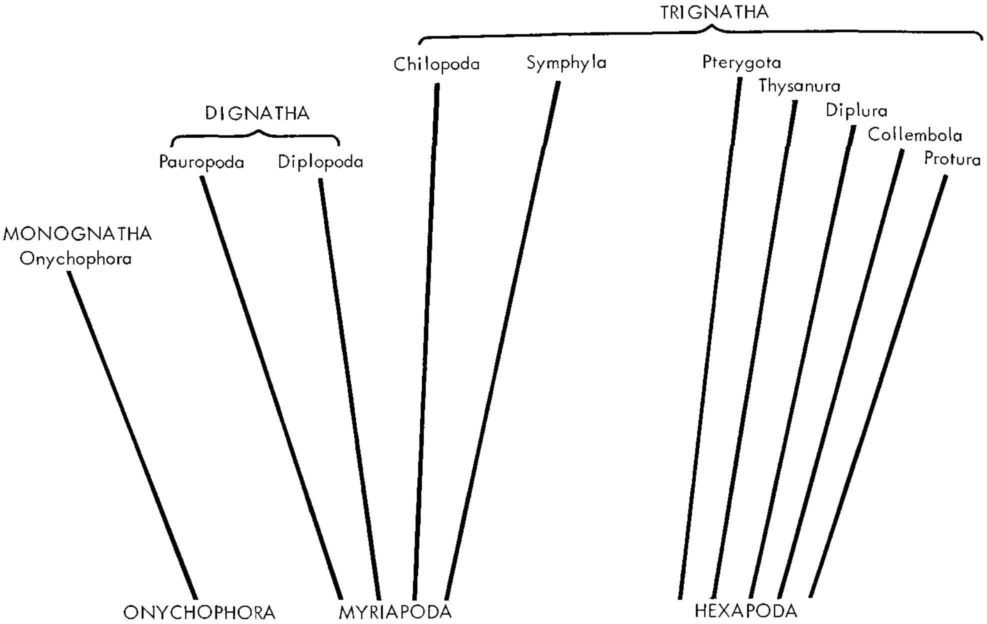

FIG. E. Diagram illustrating significance of grades in relation to taxonomy of Onychophora, Myriapoda, and Hexapoda.

The grades Monognatha, Dignatha, and Trignatha represent stages of advancement reached independently by various classes and do not represent taxa denoting close affinity. Positions of the two groups of converging lines show the related myriapod and related hexapod classes which have each evolved in parallel. For further description see text.

trignathy of the Symphyla does not separate this class from the other Myriapoda with which they have fundamental resemblances in the mandible, head endoskeleton, and structure of limbs and joints. Further, there is no reason to suppose that these grades have been acquired progressively. In any one phylogeny a monognathous state need not have preceded dignathy and the latter need not have come before a trignathous condition. These three states probably evolved directly from animals with undiversified limbs, as have the three or the one pair of maxillipeds in the eucaridan and pericaridan Crustacea. The absence of a dignathous hexapod or a monognathous myriapod probably means that no such animals ever existed. Similarly the term "Mandibulata" represents a grade of organization, of great functional importance, reached independently and by different means in Crustacea and terrestrial myriapods and hexapods.

The above outline of arthropodan classification is based rigidly upon factual evidence available in 1966, and no speculations are offered concerning the ultimate origins of the groups of arthropods set out in the figures. But one further point may be made. The Arthropoda as a whole appear to be polyphyletic at least to the extent of the three main groups shown in Figure C, but there were probably more independent taxa which are now extinct. The basic unity of the Onychophora-Myriapoda-Hexapoda assemblage has been demonstrated by TIEGS (23, 24, etc.) but this does not imply just one ancestor for all. The probability that the Onchophora are primitively soft-bodied, lacking surface sclerites, but not the ability for high levels of sclerotization, follows from the demonstration of the functional assets of onychophoran anatomy (MANTON, 1950; 10a). It is thus possible that the evolution or an armor of surface sclerities may have occurred more than once during the evolution of arthropods, taking place independently in the sea and on land, and that this most conspicuous characteristic of the phylum should be added to the list given above of major features which have arisen by convergence.

The popular mode of classification of the Arthropoda into graded hierarchies which correspond from one major group to another probably has little reality. CALMAN (2a) drew attention to the much larger series of units needed in the classification of some groups than of others. Within one major assemblage it matters little whether the hierarchies run from superclass to class and subclass or from class to subclass and order, or some other series of labels. It is a meaningless task to force one system of labeling onto all groups.

The main groups of the Arthropoda, on the evidence available to date, can be listed as shown below. Some doubt may be expressed as to the validity of the rank of class indicated for the Cephalocarida, Mystacocarida, and Branchiura among the Crustacea; these three groups may not be as separate from the Branchiopoda and Copepoda as the title of class suggests. Very little is known concerning the status of the Pentastomida and Tardigrada. Further subdivision of the listed classes is often long. For example, there is no general agreement concerning the existence of a few major groupings within the Arachnida and it is necessary to give 16 subclasses of the Arachnida if division is undertaken.

Main Divisions of Arthropoda

- ARTHROPODA *(phylum)*. *?Precam., Cam.-Rec.*
  - Trilobitomorpha *(superclass)* . *Cam.-Perm.*
    - Trilobitoidea *(class)* . *Cam.-Dev.*
    - Trilobita *(class)* . *Cam.-Perm.*
  - Chelicerata *(superclass)* . *Cam.-Rec.*
    - Merostomata *(class)* . *Cam.-Rec.*
    - Arachnida *(class)* . *Sil.-Rec.*
  - Pycnogonida *(superclass)* . *Dev.-Rec.*
  - Crustacea *(superclass)* . *Cam.-Rec.*
    - Cephalocarida *(class)* . *Rec.*
    - Branchiopoda *(class)* . *L.Dev.-Rec.*
    - Mystacocarida *(class)* . *Rec.*
    - Ostracoda *(class)* . *L.Cam.-Rec.*
    - Euthycarcinoidea *(class)* . *Trias.*
    - Copepoda *(class)* . *Mio.-Rec.*
    - Branchiura *(class)* . *Rec.*
    - Cirripedia *(class)*. *U.Sil.-Rec.*
    - Malacostraca *(class)* . *L.Cam.-Rec.*
  - Onychophora *(superclass)* . *?Precam., Cam.-Rec.*
  - Myriapoda *(superclass)* . *U.Sil.-Rec.*
    - Archipolypoda *(class)* . *U.Sil.-U.Carb.(Penn.).*
    - Diplopoda *(class)* . *U.Carb.(Penn.)-Rec.*
    - Pauropoda *(class)* . *Rec.*
    - Chilopoda *(class)* . *Cret.-Rec.*
    - Symphyla *(class)* . *Oligo.-Rec.*
  - Hexapoda *(superclass)* . *U.Carb.(Penn.)-Rec.*
    - Protura *(class)* . *Rec.*
    - Collembola *(class)* . *Rec.*
    - Diplura *(class)* . *Rec.*
    - Thysanura *(class)* . *Oligo.-Rec.*
    - Insecta *(class)* . *U.Carb.(Penn.)-Rec.*
  - Pentastomida *(superclass)* . *Rec.*
  - Tardigrada *(superclass)* . *Rec.*

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EVOLUTION AND AFFINITIES OF ONYCHOPHORA, MYRIAPODA, HEXAPODA, AND CRUSTACEA

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[Chapter submitted December, 1962; revised January, 1963]

CONTENTS

INTRODUCTION

The elucidation of phylogenetic relationships within the Arthropoda is essentially speculative, since the fossil record is noncommittal. Apart from the general thesis that the arthropod phylum has sprung from metamerically segmented coelomates, there are few points relating to its ancestry on which general agreement has been reached; indeed, it is uncertain whether the great arthropod assemblage is a "natural" group or whether it comprises more than one line of descent derived independently from segmented coelomates. Theories of arthropod evolution have been many and have formed the basis of various classifications which have been put forward since the time of Cuvier. A survey of these theories, associated with the names of von Siebold, Haeckel, Moseley, Kennel, Balfour, Sedgwick, Lankester, Woodward, Packard, Handlirsch, Snodgrass, Tiegs, and others, has been given by Tiegs & Manton (67) and will not be repeated here. It is pertinent now to consider the present position of our understanding of this subject, furthered by recent work in the fields of comparative embryology and of comparative functional morphology. The latter studies, in particular, have thrown a wealth of light upon the functional significance of conspicuous characters which are diagnostic of classes and of orders. Such knowledge shows the detailed relationships between habits of life and body design, and gives sure guides as to the modes of evolution of many of these characteristics. The appli-

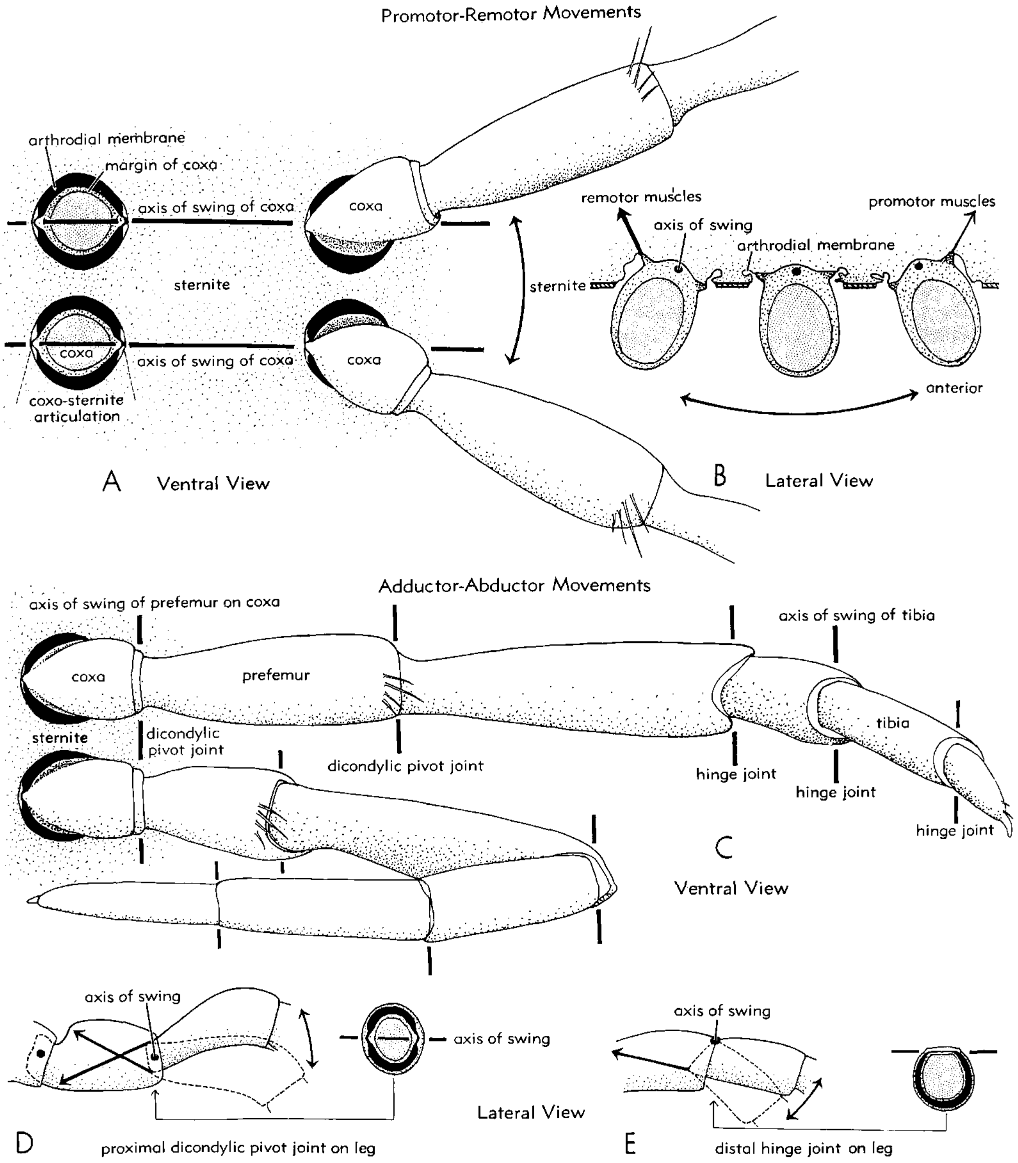

FIG. 1. Diagrams showing the two basic movements employed by many arthropodan limbs, exemplified by *Polydesmus* (Diplopoda). One or other of these movements are also used by the several types of mandibles. [Arthrodial membrane at the coxa-body joint is indicated in black.]

A. Ventral view of two successive pairs of legs, those on one side of the body being cut short close to the coxo-sternite articulation. The axis of swing, passing through the dicondylic coxo-sternite articulation, is shown by a heavy line. The legs on the right show the forward and backward positions resulting from the promotor-remoter swing of the coxa about its axis of movement on the body.

B. Lateral view of three successive coxae cut short near the coxo-sternite articulation to show the promotor-remotor swing about the axis (indicated by a black dot).

C. Ventral view of two successive legs in positions of abduction (away from) and adduction (toward) their fellows, which are not drawn. The coxae cannot participate in this movement. The

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cation of this approach to the vast assemblage of arthropods is in its infancy, but a rewarding start has been made.

Extant arthropods fall readily into at least the following distinct groups: Chelicerata, Crustacea, Onychophora, Pauropoda, Diplopoda, Chilopoda, Symphyla, Apterygota, Pterygota, Pycnogonida, and Tardigrada. The fossil record displays the long history of the Trilobita, which were the dominant arthropods of the early Paleozoic seas, becoming extinct in the Permian. Many bewildering aquatic arthropods from the Cambrian to Devonian do not fall clearly into any of the above categories. Regrettably, as yet the structure of these animals is insufficiently known for a full assessment. The name of TIEGS will be remembered for his major contribution in establishing the unity of the Onychophora, Myriapoda (Pauropoda, Diplopoda, Chilopoda, Symphyla), and Insecta, based primarily upon embryology (28, 30, 32, 61, 62, 66) and on adult form. The Chelicerata and Crustacea stand in marked contrast both to the land stem and to each other.

The differences between the structure of the head or anterior end of the body in the major groups of arthropods are alone sufficient to separate the classes. A functional consideration of the requirements at the anterior end of the body, and of the ways of meeting these needs, is particularly revealing as to the modes of head evolution. The primary anterior requirements of a bilaterally symmetrical forwardly moving animal concern the sensory equipment and the feeding organs, particularly the mandibles in the classes that possess them. Differing habits of life are associated with the evolution of the very different trunk morphologies which are diagnostic of classes and of orders.

EARLY ARTHROPOD EVOLUTION AND CONVERGENCE

The Arthropoda are bound together by very few essential characteristics: (1) metameric segmentation, coupled with modifications at the anterior end which are different from those of annelids;[1] (2) usually many paired limbs (Fig. 1, 2), which are different from those of annelids; (3) an ostiate heart and hemocoelic body cavity; and (4) a surface cuticle usually sclerotized into more or less rigid sclerites separated by flexible intersegmental arthrodial membranes at the joints on the body and limbs. Sometimes functional advantages associated with particular habits of life result from sclerotization remaining thin, giving an absence of sclerites or scutes, as in Onychophora, some insects, and the thorax and abdomen of barnacles, etc. In others, a fusion together of the sclerites of one or of several segments provides strength and rigidity.

Metamerically segmented muscles in arthropods with or without sclerites facilitate precise local actions in controlling body shape or limb movements, or both. Many

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[1] The work of ANDERSON (1) has shown that the composition of the externally simple head end of the polychaete *Scoloplos* is far from simple and its embryonic development does not follow the lines shown by simple arthropods.

FIG. 1. *(Continued from facing page.)*

axes of swing of the leg joints distal to the coxa are shown by heavy lines, the two proximal joints being dicondylic pivot joints and the three distal joints being hinge joints. The tarsal claw is hinged to the tarsus in the same plane as the other hinge joints.

D. Proximal dicondylic pivot joint on a leg showing two positions of the distal segment; the antagonistic muscles are indicated by arrows within the leg segment. A diagrammatic transverse section through the joint at the level indicated shows the lateral points of locally strengthened cuticle on the two leg segments united by very short arthrodial membrane.

E. Distal hinge joint on the leg showing two positions of the distal segment, the single flexor muscle (adductor, or depressor) being indicated by an arrow within the leg segment. A diagrammatic transverse section through the joint at the level indicated shows the dorsal point of close union between strengthened cuticle of the two leg segments which forms the hinge.

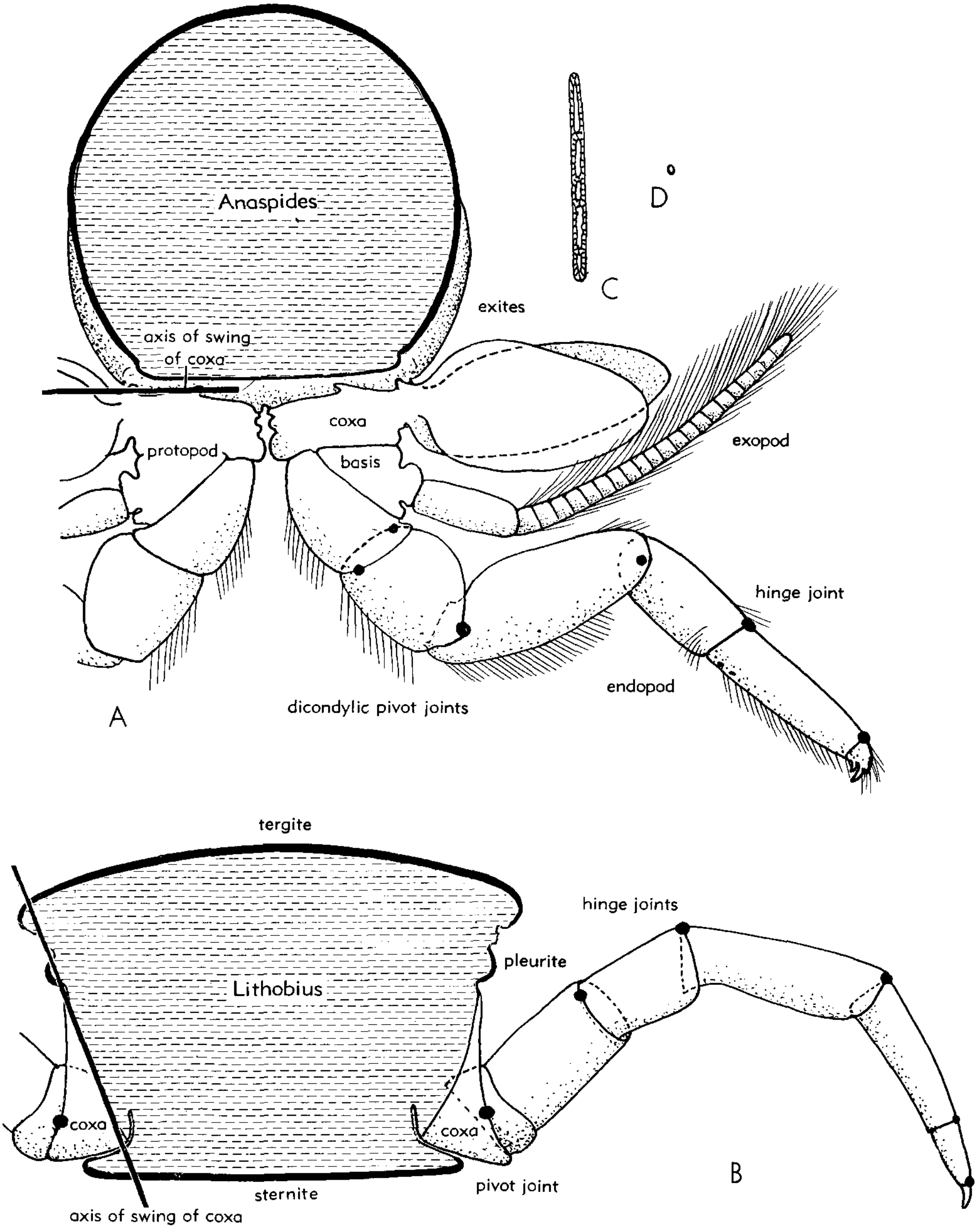

FIG. 2. Typical biramous and uniramous limbs and two types of coxa-body articulation.

A. Posterior transverse view of 6th thoracic leg of *Anaspides tasmaniae*.

B. Anterior transverse view of middle thoracic leg of *Lithobius forficatus*. A heavy line, horizontal in the crustacean and dorsoventral in the centipede, indicates the axis of swing of the coxa on the body; intermediate positions of the coxa-body axis of swing can be found among other arthropods. The crustacean coxa bears exites (also termed epipods and epipodites) laterally, and endites are present on the mesial side of certain mouth parts and on the more anterior thoracic limbs (see Fig. 13). The centipede coxa is simple. The crustacean protopod consists of two segments, the coxa and the basis, and bears two rami, the

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segmentally placed limbs make possible strong or speedy movements and give the potentiality of structural and functional differentiation along the series which is so characteristic of the more specialized Arthropoda.

The possession of a thick laminated sclerotized cuticle is not restricted to the Arthropoda. Nematodes also have such a cuticle, which is differentiated internally to a greater extent than in most Arthropoda (6, 24), and molting also takes place. The high degree of internal cuticular differentiation in nematodes is probably correlated with the maintenance of body shape and suitable flexibility under conditions of high hydrostatic pressure in the body cavity. But the absence of metameric segmentation in nematodes is coupled with the absence of joints. All arthropodan cuticles show regions where the sclerotization or calcification, or both, is minimal, so forming the flexible arthrodial membranes.

Surface sclerites do not necessarily carry muscles (see the pleural sclerites of epimorphic centipedes). The primary function of sclerites appears to be protective, and in burrowing forms they provide an armor used in pushing against the substratum (*Limulus*, Diplopoda, and geophilomorph centipedes). The possession of striated muscles inserted onto subectodermal connective tissue or basement membrane below the inner face or near to the edges of sclerites (the latter position, used by many muscles of Diplopoda, is not necessarily the more primitive) permits rapid or strong movements used in walking or swimming. Joint formation between sclerites may be elaborate and can lead to economy in certain muscles by the use of hard parts to direct movements, so permitting more musculature to be available for other purposes (38); and the sclerites themselves may be heavy, extensive, and strongly protective. On land a high degree of surface sclerotization and surface lipoids render the sclerites very hydrofuge. Thereby, internal moisture is conserved and, much more important, osmotic uptake of fresh water, rain, and dew is hindered, the latter being the greater hazard in a terrestrial habitat. PANTIN (46) has shown how the great danger to land planarians and land nemertines is osmotic uptake of water, and in consequence, these animals are found in damp niches in comparatively dry country, not in wet habitats where at first sight easier living might be anticipated.

The functional advantage of hemocoel evolution is little understood and seldom considered, apart from its physiological aspects, although the presence of the hemocoel is always regarded as an important arthropodan attribute. LANKESTER (27) suggested that a swelling of vascular spaces, or "phloebedesis," may have promoted local changes in shape in a soft-bodied arthropodan ancestor in a more advantageous manner than can be accomplished by an animal with a coelomic body cavity. The probable truth of this idea is supported by the discovery that a burrowing geophilomorph centipede can exert some four times as much force aaginst the substratum from its armored body surface as can an annelid worm of similar size (41 and MANTON, 43a). Striated muscles far from the site of application of the thrust, as well as

FIG. 2. *(Continued from facing page.)*

endopod and exopod. In the centipede the limb distal to the coxa forms a single ramus, the telopod, as in all other myriapods and in hexapods. The positions of the close articulations between the leg segments are shown by heavy dots; pivot joints allow movement in two directions about the articulation and are served by antagonistic pairs of muscles (Fig. 1,*D*); hinge joints allow movement in one direction about the articulation and are usually served by flexor muscles only (Fig. 1,*E*), hydrostatic pressure and proximal depressor muscles supplying the antagonistic force producing leg extension (Fig. 1,*A;* 1,*E*). Both types of articulation may be dicondylic or may be formed by one principal articulation. In life, the exites of *Anaspides* are forwardly directed. Only in fast-running centipedes is the tarsus divided into two segments as shown here; the distal tarsal segment possesses no muscles of its own.

C. Transverse section through an exite showing its flat shape and internal vascular spaces.

D. Transverse section through a seta from the exopod.

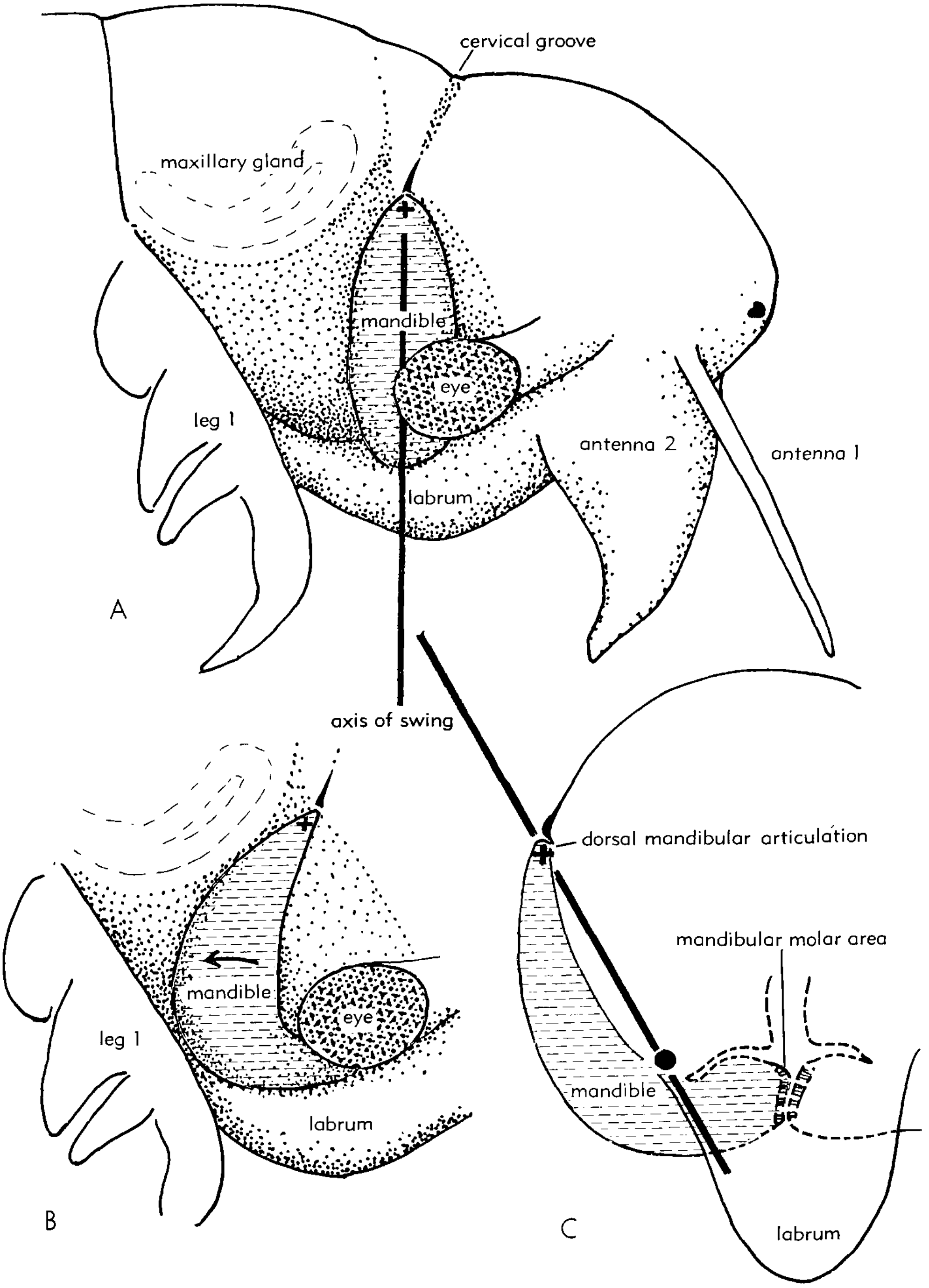

FIG. 3. A gnathobasic mandible.

A,B. Lateral views of the head of the crustacean *Chirocephalus diaphanus* showing the mandibular movements and their relationship to those of the coxa of a walking leg (Fig. 2,*B*). The movements provide a crushing or grinding mechanism, but no strong cutting in the transverse plane, and are characteristic of the less specialized mod-

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local musculature, maintain high hydrostatic pressure in the hemocoel, and assist in providing a strong local heave, which moreover can be repeated again and again. An annelid, such as *Arenicola*, cannot repeat its maximum effort without a bursting of capillaries and leakage of coelomic fluid. It is possible that the evolution of this basic attribute of all arthropods, the hemocoel, occurred along with a habit of shallow grubbing into the pre-Cambrian sea floor. Such a habit represents the simplest of escape reactions, and the evolution of a better or easier way of burrowing may have had great survival value at the dawn of arthropod evolution. It may be significant that a similar habit is envisaged for the primitive Mollusca, the hemocoel of which may have arisen in association with similar functional advantages. Later, with the acquisition of arthropodan protective armor, facilitating both shallow burrowing and surface living, the original advantage of a hemocoel largely seems to have disappeared. However, it persists in part in the frequent use of blood pressure for the extension of legs where all the musculature of the distal segments is flexor in function (14, 38, 39). Sometimes blood pressure causes leg extension in jumping, when both legs of a pair push in the same phase, as in jumping spiders (47).

Thus, evolution of the arthropodan hemocoel may have preceded the evolution of surface sclerites. It is also possible that the acquisition of surface sclerites on the trunk may have preceded those on the legs, since the force exerted by the surface of the trunk of an annelid or arthropod when burrowing is usually not generated by segmental limbs. Whether the wormlike *Anomalocaris* from the Cambrian, which has so intrigued SNODGRASS (personal communication) and which perhaps shows segmental sclerites but no leg segmentation, represents or is derived from such a stage of arthropodan evolution is uncertain. Regrettably, the fossil remains, although numerous, all lack the head end.

The Arthropoda exhibit a wealth of structural specialization suiting particular ways of life and favoring survival in particular niches. The hermit crabs inhabiting gastropod shells and the gall-forming crab *Hapalocarcinus,* living on the coral *Seriatopora,* are typical examples. The most important of the evolutionary advances of the Arthropoda, however, did not result in adaptation to particular niches, but, on the contrary, adaptation of an animal to better living in the same or in a variety of habitats. A large decaying log in South Africa or South America may harbor Onychophora, Diplopoda, Chilopoda, Symphyla, insects, arachnids, etc. The environment is roughly the same for all but the basic habits of the animals differ, and it is these habits which are associated with the trunk characters of the several groups (see below).

Where specialization of all kinds is abundant and varied, as it is within the Arthropoda, there is possibility of unlimited convergence. And, when the distinctive arthropodan characters are so few, the possibility must be faced that even these may have arisen more than once. There has been a reluctance to recognize some of the outstanding cases of convergence, although others have been readily accepted as such. There is no denying the parallel evolution of tracheae serving aerial respiration which has taken place at least four or five times. The histology or mode of embryonic origin of tracheae or both of these are not the same in land isopods, arachnids, Onychophora, and myriapods. Similarly, malpighian tubules have arisen independently and by different means in certain Arachnida and

FIG. 3. *(Continued from facing page.)*

ern Crustacea. A cross marks the dorsal articulation of the mandible with a small sclerite in the cervical groove.

C. Transverse view of head of the same showing the manner in which the mandible swings about a dorsoventral axis (cf. Fig. 2,*B*), the ventral end of the axis (black spot) not being firm. At the end of the promotor swing *(A)* the mandibles are set transversely to the body (see also Fig. 5,*C*, left-hand diagrams). At the end of the remotor swing *(B)* the lateral parts of the mandible, moving in the direction of the arrow, are backwardly directed while the molar areas are forwardly directed. The eye and trunk limb 1 are in the same position in both diagrams.

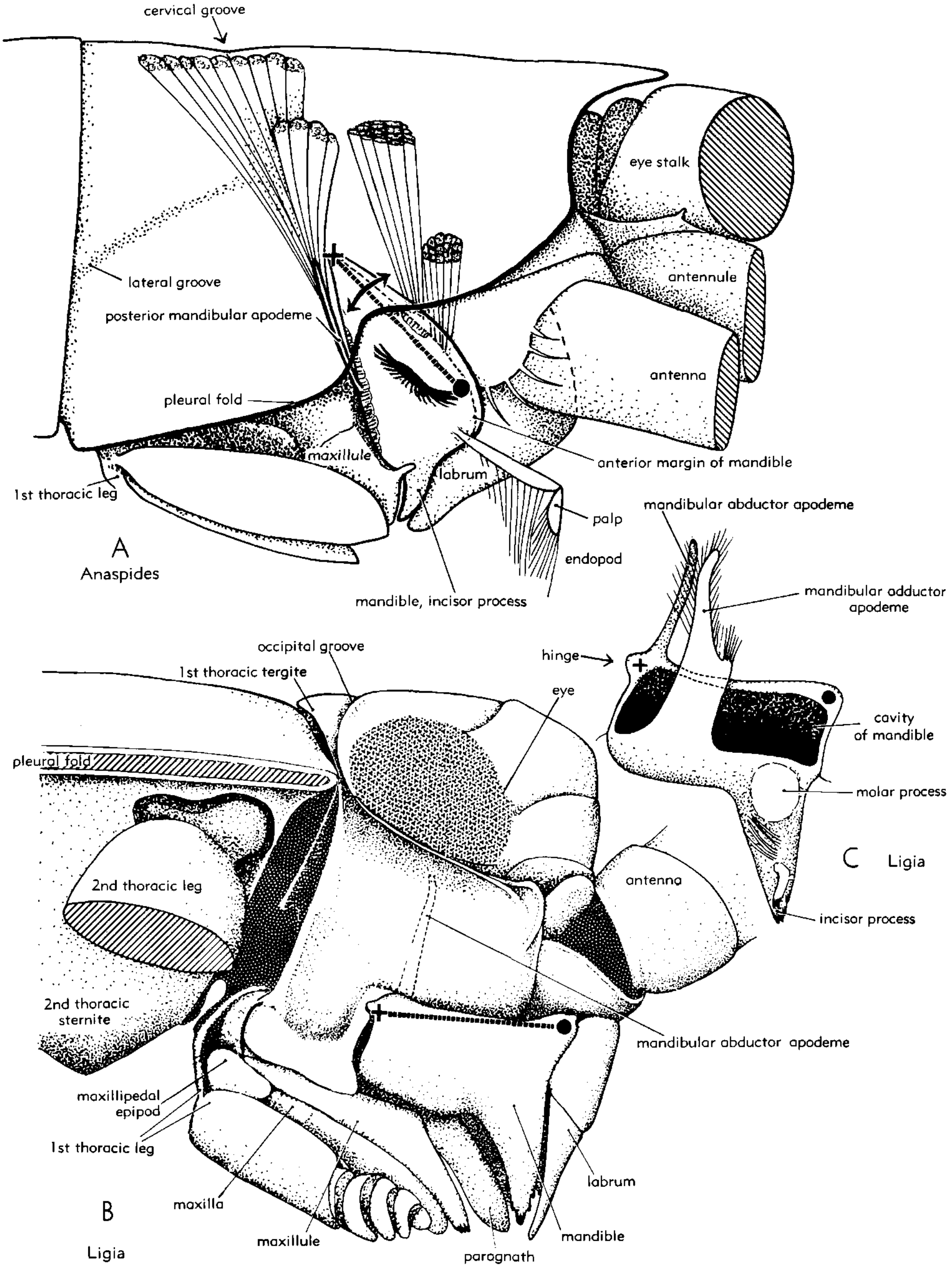

FIG. 4. Gnathobasic mandibles.

A,B. Lateral views of the heads of *Anaspides* and *Ligia* showing one mode of obtaining strong transverse biting from the simple promotor-remotor swing of a grinding mandible such as that of *Chirocephalus* (Fig. 3). Other and quite different methods of achieving transverse biting occur among some of the more specialized Crustacea. The mandibles in *A* and *B* consist of a massive gnathobasic portion with a distal palp (endopod) in *Anaspides*. The axis of mandibular movement is marked by a dotted line be-

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in Myriapoda-Insecta. These tubules often serve to eliminate dry or semidry urate excretion in place of the ammonotelic excretion by segmental organs existing in aquatic Crustacea, but the recent discovery that malpighian tubules of the centipede *Lithobius* excrete some 70 per cent of the total nitrogen as ammonia and only 8 per cent as uric acid (5) indicates how little we know of the full significance of the parallel evolution of these tubules.

That the compound eye of arthropods represents a "unique mechanism," the only practicable manner of meeting a common need, seems now inescapable. The compound eye appears to have evolved independently within the Crustacea and Insecta. Only some Crustacea possess a compound eye (Branchiopoda, Branchiura, Malacostraca) and their eyes are not exactly similar. Crustacea which lack the compound eye (Copepoda) do not appear to have secondarily lost these organs. A compound eye would not be expected to occur in the earliest ancestral Crustacea, although such eyes were possessed by the Trilobita and probably the Merostomata. Only the more advanced members of the Myriapoda (Scutigeromorpha) possess, with the hexapods, a compound eye, and again it is improbable that Onychophora and Myriapoda equipped with simpler eyes are anything but primitively so, although species living in darkness may be blind by secondary loss of eyes.

Until recently, the possession of a mandible has sometimes been regarded as a common feature linking the Myriapoda, Crustacea, and Insecta. Indeed, the conviction that all mandibles situated on the third head segment are directly homologous and indicate common inheritance has been strong enough for the erection of a taxonomic category, the Mandibulata. However, a functional, anatomical and developmental study of jaw mechanisms throughout the major groups of living arthropods shows that mandibles also have been independently acquired (43). A proximal endite or gnathobase is present on one or on many pairs of legs in Crustacea and Chelicerata and serves for manipulation or direction of food. The crustacean mandibular segment usually carries a very large pair of gnathobases, which, with the proximal part of the leg, forms a massive pair of mandibles; the distal part of the leg is reduced to a biramous or uniramous palp and may be entirely absent (Fig. 3-6). The jaws of the Onychophora, Myriapoda, and Insecta, on the contrary, develop from a whole limb, the distal part of the biting edge representing the limb tip (Fig. 8-11). The onychophoran jaw is very short, bearing a larger pair of terminal claws than do the walking legs (Fig. 9,*B*). The jaws of myriapods and hexapods are often longer than those of Onychophora, and, as in Crustacea, may extend up the "cheeks."

The onychophoran jaws slice anteroposteriorly, the pair moving in opposite phase essentially like the walking legs (Fig. 9,*B*). The movements of gnathobases or jaws of other arthropods are derivatives of one or other of two types of movement characteristic of ambulatory limbs, (1) the promotor-remotor swing of the coxa on the body about a more or less transversely placed axis, and (2) direct adductor-abductor movements in the transverse plane such as shown by a pair of telopods (Fig. 1, 2). Direct biting in the transverse plane is usually not a primitive arthropodan attribute owing to the difficulty of providing an abductor mechanism which will part mandibles so large that they form the most

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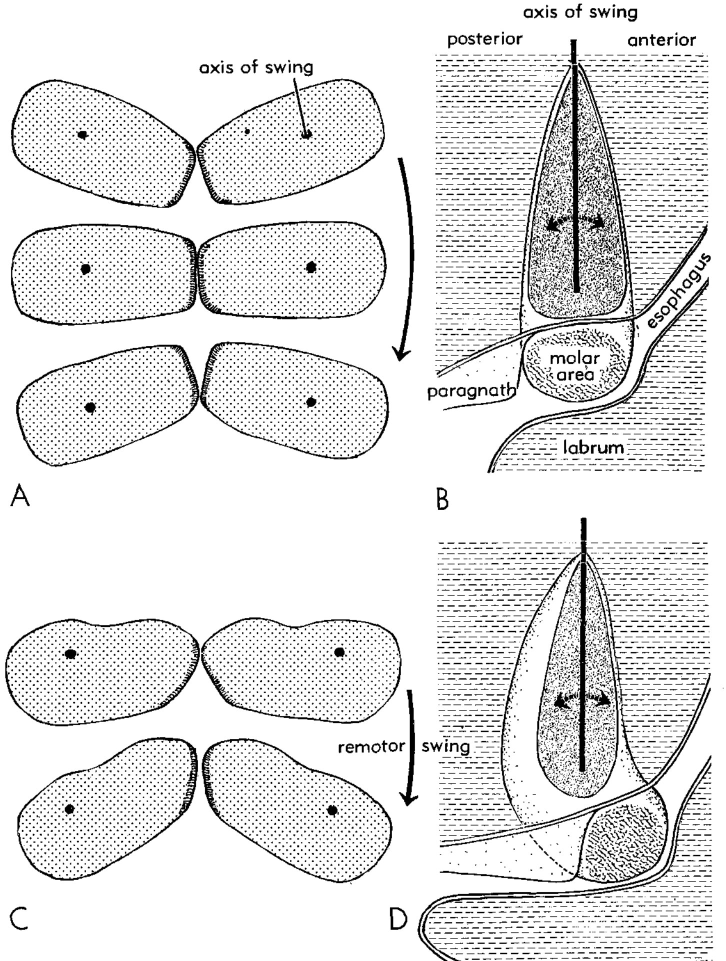
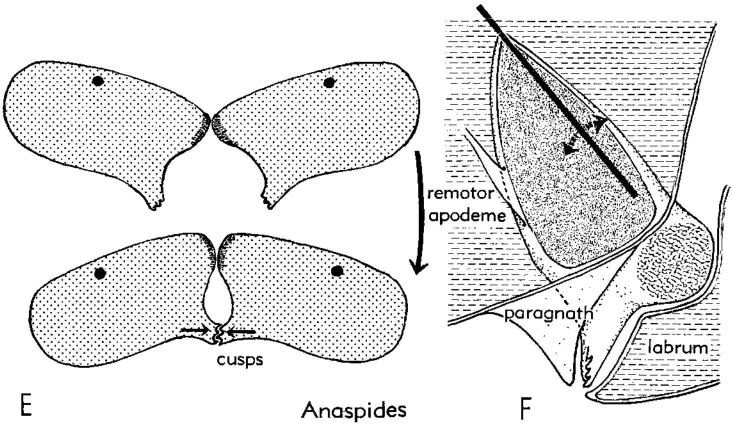
FIG. 4. *(Continued from facing page.)*

tween the cross and spot, corresponding with the points similarly marked on Fig. 3. The pre-axial part of the mandible is progressively reduced as the dorsal articulation (cross) becomes more posterior in position (Fig. 5, right-hand side). An incisor process, situated far from the axis, gives effective transverse biting in *Anaspides* (Fig. 6), combined with some grinding by the molar areas, as a result of the promotor-remotor swing. In *Ligia* the promotor-remotor swing becomes a strong direct biting movement in the transverse plane and only a little grinding by the edges of the molar process is possible. A firm anteroposterior hinge forms the axis of movement in *Ligia*.

C. Mandible of *Ligia* (devoid of muscles) viewed from the sagittal plane, the esophagus passing directly upward above the molar process.



Chirocephalus



Anaspides

Fig. 5. Gnathobasic mandibles.

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lateral parts of the head. In Crustacea (gnathobasic mandible) and in the hexapods (whole-limb mandible) the more primitive living forms show a promotor-remotor swing of the mandible about an axis on which the lateral end slopes upward toward the dorsal head extremity (Fig. 3, 4,*A*, 5,*A*). Frequently a firm dorsal articulation is seen, but the mandible does not swing toward the middle line from this point to any great extent.

When the axis of the promotor-remotor swing slopes neither forward nor backward, the molar faces of the mandibles roll across one another on the promotor, as well as the remotor swing of the mandible, and there is very little direct abduction (many Branchiopoda and the thysanuran *Petrobius*) (Fig. 3, 5,*A,B*). The strong remotor movements roll the molar processes forward and together at the same time as the lateral bulge of the mandibles rolls backward. Adduction of incisor processes and grinding by molar processes both take place on the remotor roll as a consequence of the shape of the mandible and a backward-upward slope of the axis of swing (e.g., *Anaspides, Mysis*, etc.); abduction of the incisor processes and a parting of the molar processes occur on the promotor swing of the mandible as a whole (Fig. 4,*A*, 5, 6). Biting by incisor processes and grinding by molar processes are implemented by massive remotor musculature, inserted on to the head wall and on to a transverse mandibular tendon; the promotor muscles insert on the same sites but are much weaker.

The farther back the dorsal end of the axis of swing is situated, the greater is the adductor-abductor movement of the incisor processes and the less is the grinding movement of the molar areas. When the position of the axis approaches the horizontal, as in isopods, some Thysanura, and pterygote insects, the preaxial part of the mandible becomes much reduced and the axis forms a strong hinge line (Fig. 4,*B*, 8,*B-D*). Variety in mandibular movements is lost, grinding is impossible, but very much stronger adductor movements through a wide angle take place. The disappearance of the transverse mandibular tendon permits the wide gape, and direct adductor and abductor muscles, often pulling on very well-formed tendons and apodemes set at advantageous angles, result in a large mandible which can cut very strongly in the transverse plane. This end term in the evolution of mandibles has been reached independently many times from different initial conditions and by different means. For example, the nature of the mandible and the principles of its movement in the woodlouse and the crab are the same, but the details are entirely different and transverse biting has been convergently acquired. Also, it happens that mandibles of unlike nature in Crustacea and in Thysanura-

Fig. 5. *(Continued from facing page.)*

Diagrams showing the movements of simple crustacean mandibles that provide grinding only or grinding combined with some biting. Figures on the right show the median aspect of each mandible as seen in the left half of the body (muscles omitted and mandible drawn as if body is transparent, mechanical tint indicating the open concavity of the mandible that in life is filled by muscles). Figures on the left show frontal sections across the mandibles at successive moments during the remotor roll (axis of movement shown by black spots corresponding to heavy lines in right-hand figures, with arrows indicating direction of movements about the axis).

A,B. An ideally simple crustacean mandible which serves only for grinding. The axis is vertical (as in *Chirocephalus*, Fig. 3) and the symmetrical promotor-remotor swing about this axis rolls the molar areas across each other. The mandibles of *Daphnia* and of many other Cladocera closely approach this type.

C,D. Mandible of *Chirocephalus diaphanus* showing a forwardly bent molar lobe with range of the promotor-remotor swing enabling the mandibles not only to grind food but to push it forward toward the esophagus.

E,F. Mandible of *Anaspides tasmaniae* showing an oblique axis of swing placed near the anterior border of the mandible and a cusped incisor process lying far from this axis of swing. The promotor-remotor movement causes grinding by the molar areas and also biting by the incisor processes in approximately the transverse plane (see also Fig. 6). The above are the principal movements of these mandibles, but the looseness of the ventral end of the axis of movement permits other small movements to occur at times.

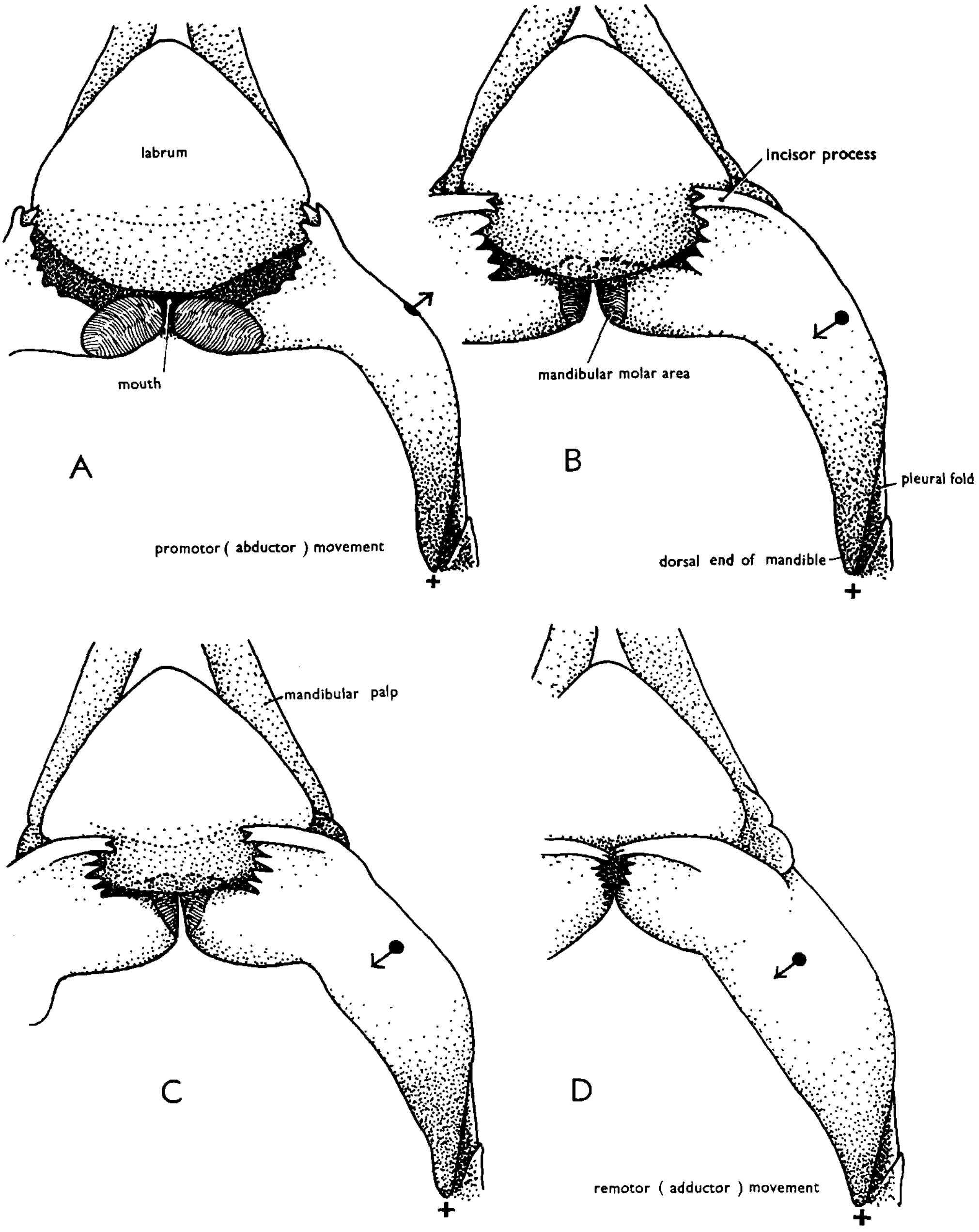


FIG. 6. Gnathobasic mandible.

Ventral views of the mandibles of *Anaspides tasmaniae* to show grinding by the molar processes and biting in the transverse plane by the incisor processes, both due to the shape of the mandible and the oblique position of the axis of movement. ——*A* shows the extreme end of a promotor swing (a little more extreme than in life), which opens a space between the molar lobes and parts the incisor processes as far as the labral margins.——*B,C,D* show the remotor (backward) roll of the lateral part of the mandibles, the black spot moving in the direction of the arrow, which brings the incisor processes together, moving along a hollow in the labrum. A further displacement of the axis of movement results in a predominantly biting mandible such as that of *Ligia* (Fig. 4,*B*). Other small movements occur at times.

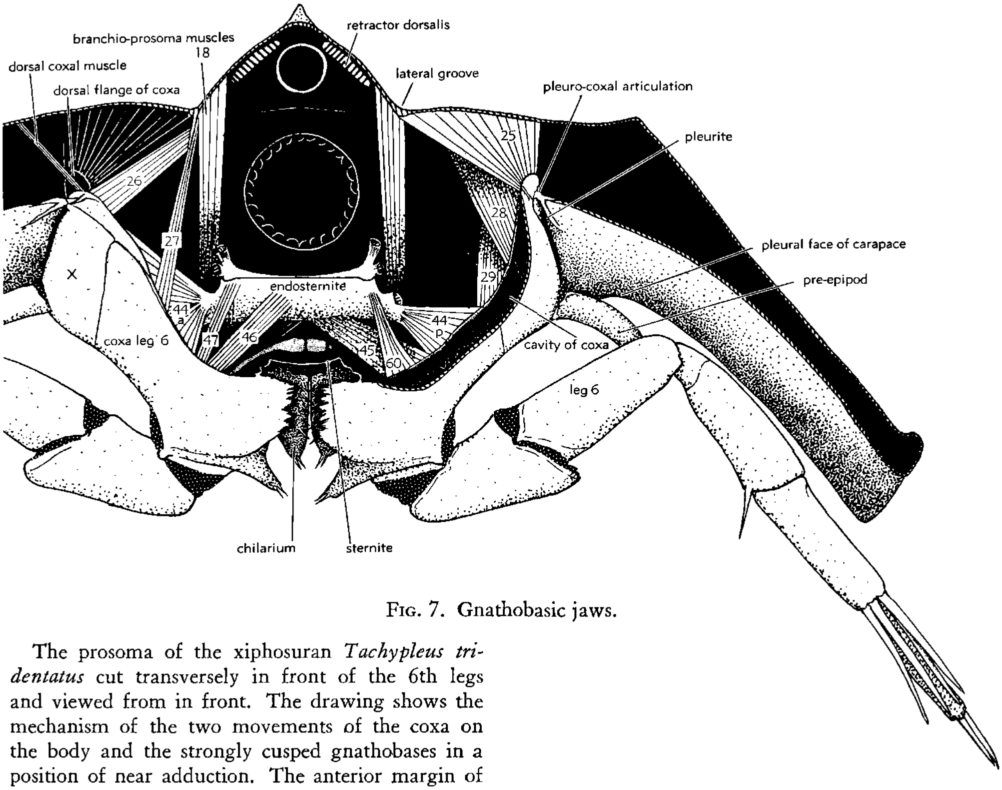


FIG. 7. Gnathobasic jaws.

The prosoma of the xiphosuran *Tachypleus tridentatus* cut transversely in front of the 6th legs and viewed from in front. The drawing shows the mechanism of the two movements of the coxa on the body and the strongly cusped gnathobases in a position of near adduction. The anterior margin of the 6th coxa is cut away on the right in order to display the posterior margin. The tight pleurocoxal articulation is marked. Elsewhere there is ample arthrodial membrane between coxa and body. Adductor-abductor movements in the transverse plane about the pleuro-coxal articulation cause direct biting by the gnathobasic cusps. Adductor muscles 44a, 46, 44p, and 45 are opposed by abductors 25 and 26 pulling on short levers dorsal to the pleurocoxal articulation. The walking movement takes place at right angles to the biting movement and is a promotor-remotor swing about a dorsoventral axis (cf. Fig. 2,*B*). Promotor muscles 27 and remotors 28 and 29 are probably aided by the dorsal parts of muscles 44a and 44p (muscles 28, 47, and 60 have other functions). The area X has been claimed to represent part of a precoxal segment but the evidence is considered to have doubtful validity, since the structures in question are directly related to the adductor-abductor mechanism and may not have a segmental significance (43a). The pre-epipod arises from this region and serves to keep sand away from the branchial filaments during the digging movements of the 6th telopods. The pre-epipod corresponds in position of origin with the outer ramus of the trilobite limb (see Fig. 12) and with the proximal exite of the crustacean *Anaspides* (Fig.2,*A*) and of *Chirocephalus* (see Fig. 13,*C*).

Pterygota have independently evolved very similar solutions to the problem of obtaining strongly cutting mandibles (Fig. 4,*B*, 8,*D*).

Two groups of arthropods (Myriapoda, Xiphosura), have achieved transverse biting without a preliminary promotor-remotor swing, and they have done so quite independently. The segmented mandibles of the Myriapoda essentially adduct like a pair of gripping telopods (Fig. 1,*C*). Their musculature is entirely or largely adductor in effect and there is little or no abductor mechanism appertaining to the mandibles themselves. In Chilopoda, Diplopoda, and Symphyla the tentorium is not a rigid endoskeletal system, as in the Pterygota, but has the form of internal bars which swing from the cranium. A downward-forward movement of the tentorium presses on the mandibles and causes abduction of the gnathal lobes. This mechanism is seen in its sim-

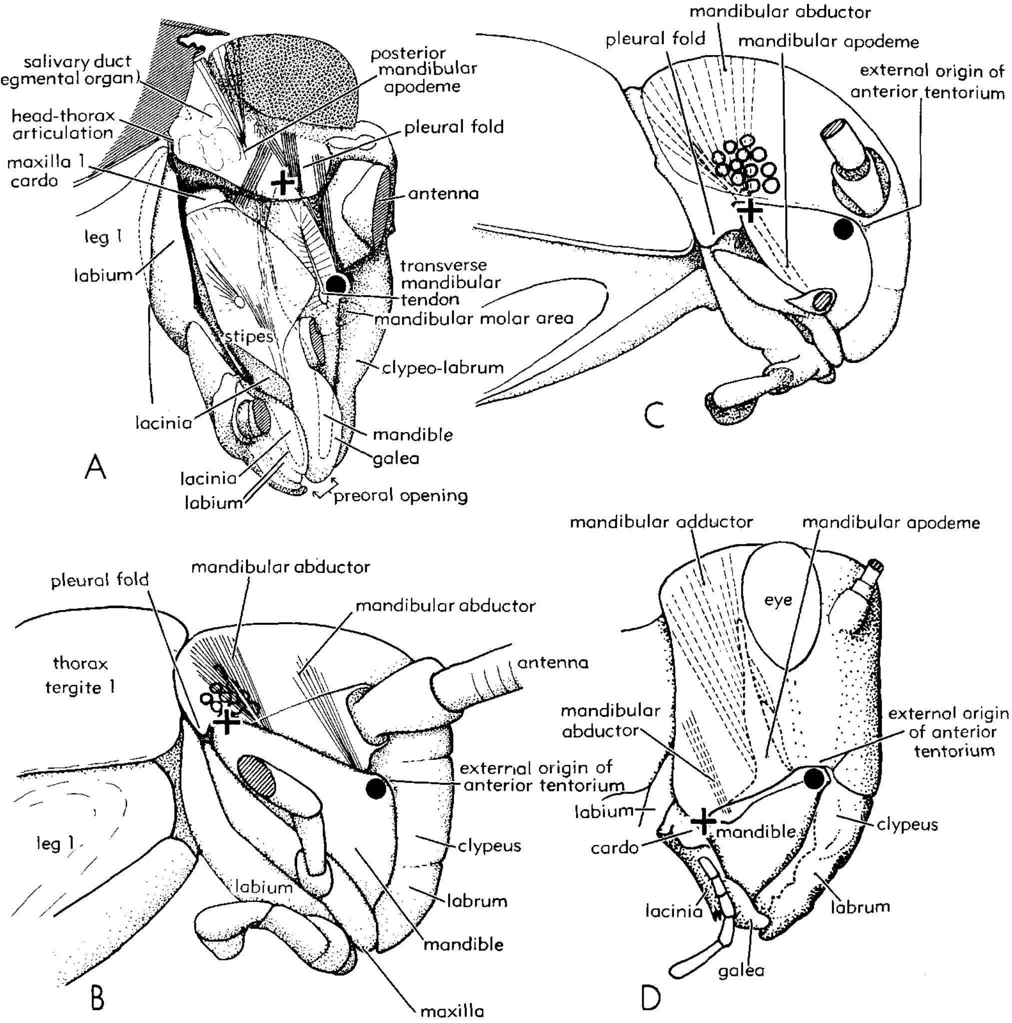


FIG. 8. Unsegmented whole-limb mandibles.

Side views of the heads of the thysanurans *(A) Petrobius brevistylis, (B) Ctenolepisma longicaudata,* and *(C) Thermobia domestica* and *(D)* of the migratory locust. The series shows a mode of obtaining strong transverse biting similar to that seen in the crustaceans *Anaspides* and *Ligia* (Fig. 3-6), but the mandible is formed from a whole limb and not from a gnathobase. The axis of movement passes through the cross and black spot of the diagrams.

In *Petrobius (A)* a tight articulation lies at the cross, and promotor-remotor movements cause grinding by the molar areas as in the branchiopod Crustacea (Fig. 3, 5). Scraping of the food surface by the distal points of the mandibles loosens particles which are then sucked up a food channel, owing to the boxing in of the mandible by the other mouth parts and superlinguae. No biting is possible.

In *Ctenolepisma (B),* as in *Anaspides,* the dorsal articulation of the mandible is displaced posteriorly, the pre-axial part of the mandible is reduced, and a firm hinge (between the cross and black spot) forms the axis of movement. There are no molar areas and strong transverse cutting and scraping by the distal mandibular cusps are now possible. The gape is small because many of the mandibular muscles still arise from the internal face of the mandible.

In *Thermobia (C)* the axis of movement is more horizontal and approaches the condition of *Ligia* (Fig. 4,*B*), but for the same reason the gape is small.

In the locust *(D)* the dorsal articulation of the mandible (cross) lies a little below the black spot. Strong articulations lie at these points and the pre-axial part of the mandible is small. The absence

(Continued on facing page.)

plest form in the Diplopoda (Fig. 11). The base of the mandible is strongly articulated with the head by an anteroposterior hinge line permitting adductor-abductor movements only. Very strong biting in the transverse plane is used by the diplopods in eating the large quantities of humus, leaf mold, decaying timber, etc., of low food value on which they feed. The symphylan mandible is more complex, being linked to the head by a single point of close union. This articulation allows a little promotor-remotor swing of the mandible to be combined with greater direct adductor-abductor movements, and some remotor mandibular muscles contribute to the biting effect. An additional extraneous abductor mechanism is provided by maxilla 1 which assists the tentorium in pushing the mandibles apart. The Chilopoda possess an even more elaborate mandibular mechanism in which, in contrast to the Diplopoda, proximal freedom and mobility in many directions of the mandible on the head is a conspicuous feature. This freedom is associated with the development of entognathy (see below) and is not primitive. The tentorial muscles again provide an abductor mechanism.

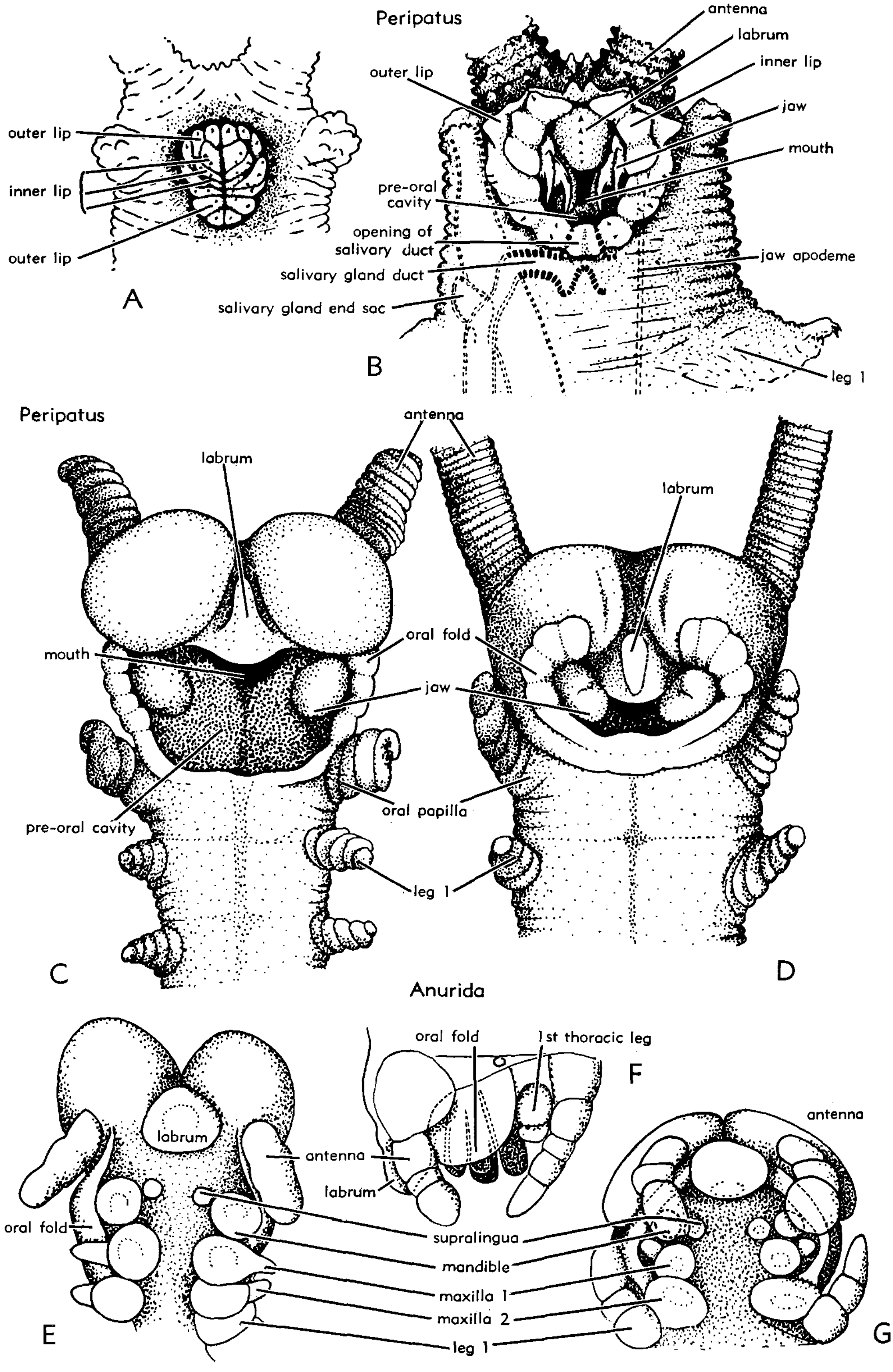
The segmented mandible of the myriapod classes represents an entire limb, as does the unsegmented mandible of the hexapods, but the principles and detail of the mechanisms of movement are entirely different in the two groups, and the one could not have given rise to the other. These groups show quite independent lines of jaw evolution, although based upon the use of a whole limb. An understanding of these jaw mechanisms makes the symphylan theory of insect origin untenable. The jaw and head evolution of the myriapod classes, although sharing a common basis, must have evolved independently. The mandibles of each class are much too specialized along their own lines to have been able to give rise to the types shown by the other myriapod classes.

Limulus also bites in the transverse plane, the gnathobases of prosomal limbs 3 to 5 chewing food by direct transverse biting, the phase difference between each pair being about half a cycle. The massive cusped gnathobases of legs 6 are used as "nutcrackers" to break the shells of lamellibranchs and cut up tough molluscan tissue (Fig. 7). The endopodites of these legs are used for walking and digging. The coxae are very wide at their attachment to the body, flattened anteroposteriorly and spread far up the flanks of the animal.

The basic walking movement in *Limulus* is the usual arthropodan promotor-remotor swing of the coxa on the body, implemented by extrinsic muscles pulling on the anterior and posterior margins of the coxa (Fig. 7, muscles 27, 28, 29). The biting movement takes place at right angles to this and is alternative to it. The dorsolateral coxal extremity forms a ball-and-socket joint with the pleurite. In front and behind this joint, two short cuticular expansions extend dorsally from the coxa and bear very stout but short abductor muscles (Fig. 7, muscles 25, 26). These levers, working at poor mechanical advantage, can pull the extreme dorsal part of the coxa inward a little and this results in much greater outward movement of the gnathobases. Massive adductor muscles pass from the coxa to the endosternite (Fig. 7, muscles 44a, 44p, 45, 46), a structure comparable with the partially fused transverse segmental tendons of postoral segments in Crustacea (30, 43a). No crustacean mandible or gnathobase has been found to possess a dorsal lever system causing direct abduction. Since the gnathobases of *Limulus* and crustaceans bite in such fundamentally different ways it seems unlikely that their limb evolution can have followed a common path.

Fig. 8. *(Continued from facing page.)*

of muscles arising from the internal face of the mandible and the mechanically advantageous disposition of the mandibular adductor and abductor muscles permit the use both of a wide gape and of a very large cutting edge which bites strongly in the transverse plane. This end term in jaw evolution parallels that of the crustacean *Ligia,* in general principles, but all the details are different, as is the nature of the jaw itself. [For further details see Manton (43a).]


Peripatus
outer lip
inner lip
outer lip
A
antenna
labrum
inner lip
outer lip
jaw
mouth
pre-oral cavity
opening of salivary duct
salivary gland duct
jaw apodeme
salivary gland end sac
leg 1
B
Peripatus
antenna
labrum
labrum
mouth
oral fold
jaw
pre-oral cavity
oral papilla
leg 1
C
D
Anurida
oral fold
1st thoracic leg
F
antenna
labrum
antenna
labrum
oral fold
supralingua
mandible
maxilla 1
maxilla 2
leg 1
E
G

The survey which has recently been made of arthropodan jaw mechanisms (43) has disclosed yet another parallel evolution, that of entognathy or the formation of a pouch around the mandible so that only the tip can be protruded. Maxilla 1 sometimes is found to be lodged in the same pouch (Fig. 10). This character, in the absence of full morphological and functional details, has been put forward as one of taxonomic value (68) indicating close affinity between animals possessing it (Diplura, Collembola, Protura). But the jaws of Onychophora (Fig. 9) and the mandibles of Chilopoda are essentially entognathous and the mandibles of the Pauropoda also are functionally so, the boxing in being differently accomplished. Many parasitic Crustacea with stylet-like mandibles are entognathous, but no information is available as to how their stylets move. The principal advantage of the entognathous condition resides in the great freedom which is permissible at the mandibular union with the head, so that the mandible can become protrusible and very mobile; in many it shows rapid rotator and counter-rotator movements. The different ways in which mandibular protraction is achieved in Diplura and Collembola (and other differences) suggest that entognathy in these two groups has been independently acquired. Both could readily have been derived from an archi-*Petrobius*-like thysanuran state by enlargement of the small pleural fold, seen in *Petrobius* (Fig. 8,*A*), to form the side walls of the gnathal pouch. The preoral gnathal space of the Onychophora is developed embryologically in a very similar manner by the enlargement of lateral "oral" folds (Fig. 9,*C-G*).

The last important case of probable convergence which should be considered in any discussion of arthropodan interrelationships concerns the trunk limbs themselves. A biramous limb occurs in Trilobita, Merostomata, Chelicerata, and Crustacea (Fig. 2,*A*, 12, 13). No onychophoran, myriapod, or hexapod shows a trace of a true biramous condition in the leg; the walking legs of these animals represent the whole limb (Fig. 1, 2,*B*, 9,*B*; see Fig. 15, 16). The walking legs of Crustacea, trilobites, and *Limulus* (Fig. 2,*A*, 7, 12) are formed by the endopodite only, an exopodite being present or absent. This limb difference, combined with the jaw difference between the Crustacea and the myriapod-insect stem, is important and an indication of a fundamental lack of affinity between these groups.

Størmer (59, 60) and others have stressed the differences between the proximal exite or pre-epipod of the trilobite limb and the more distal single exopod of the crustacean limb. The Crustacea protopod may possess one or two proximal exites as well as the distal exopod, as in *Anaspides* (Fig. 2,*A*), but among the vast and varied assemblage of crustacean limbs none show a proximal exite or pre-epipod possessing a comb of respiratory plates as on the trilobite pre-epipod or the outer part of the branchial limbs of *Limulus*. The 6th prosomal limb of *Limulus* possesses a nonbranchial pre-epipod or exite (Fig. 7) resembling the pre-epipod of the trilobites and the proximal exite of *Anaspides* (Fig. 2,*A*), but not the crustacean exopod. These fundamentally different leg patterns suggest independence in their evolution.

Fig. 9. Form and development of gnathal pouch in arthropods *(on facing page)*.

A,B. Ventral views of the oral region of *Peripatopsis sedgwicki* showing (in *A*) the round lip (outer and inner lips) closed over the jaws and pre-oral cavity, and (in *B*) the position of the mouth behind the labrum with jaw blades (two to each jaw) slicing widely from front to back at sides of the mouth (jaw apodemes indicated by dotted lines). The circular lip is composed of inner-lip and outer-lip folds.

C,D. Oral views of embryos of *Peripatus edwardsii* (younger one in *C*, and older one in *D*, redrawn from Kennel, 1886). Paired oral folds at sides of the jaws in young embryos *(C)* unite with each other behind the jaws in older embryos *(D)* so as to enclose the pre-oral cavity, later joining also in front of the labrum.

E-G. Oral views of embryos of the collembolan *Anurida maritima* showing oral folds in early stage (*E*, redrawn from Folsom, 1900) lateral to both mandibles and maxillules but at later stage (*F*, lateral, *G*, ventral) with labrum and labium (maxillae) united to form walls of the gnathal pouch.

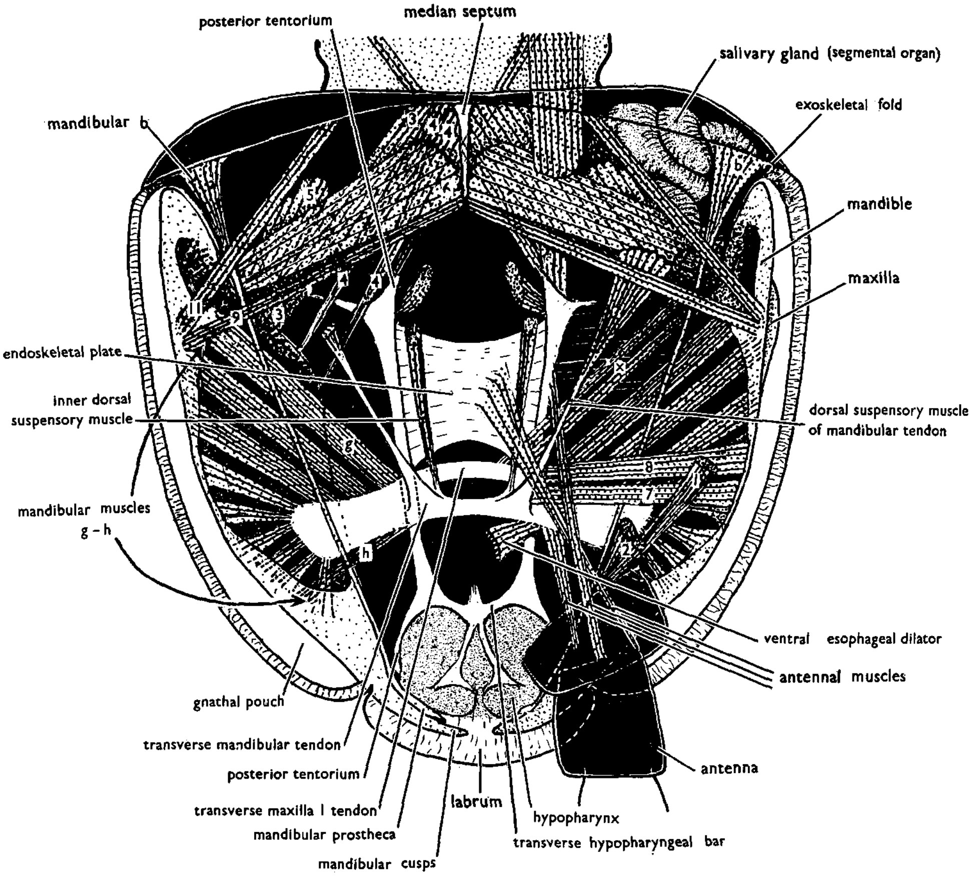


FIG. 10. Unsegmented whole-limb entognathous mandible.

Anterodorsal reconstruction of the head of the dipluran *Campodea staphylinus,* drawn as a transparent object, to show the entognathous mandible enclosed in a gnathal pouch. The antenna is omitted on the left. The mandible is not articulated with the head but is attached by loose arthrodial membrane and moves against cuticular bearings which permit a great variety of movements, including protraction and retraction. A promotor-remotor rolling movement about the long axis of the mandible essentially resembles that of *Petrobius.*

The positions of origin (Fig. 2) and the movements of arthropodan coxae are various, both being bound up with the leg mechanisms. Evolution along one path of coxal advancement may be just as effective a one-way street as are some of the types of mandibles or the basic forms of the trunk. There does not appear to be adequate support for the view (56, 58) that arthropod limbs are primitively pleural in position and basically associated with or articulated with pleural sclerites, as in insects. A ventral or ventrolateral origin of the legs exists in Onychophora, Diplopoda, and Crustacea, the legs arising on or against the sternite unless the leg base is so wide, as in some Branchiopoda, as to need no particular articulation and to leave no space for a sternite. The flanks of Diplopoda and Crustacea are well armored in contrast to those of *Limulus*, Arachnida, Chilopoda, and Symphyla. In the latter classes the legs are set in flexible pleuron, except at one point, and the coxae perform multiple movements. Here there is a ventral point of close union between the coxa and some major sclerite, usually the sternite, but with a pleurite in insects. There is no justification for explaining away these differences in leg insertion by feats of terminology, such as calling the diplopod sternite a pleurite (58).

The reconstruction in the transverse plane of trilobite limbs (59) shows a wide base to the coxa, as in *Limulus* (Fig. 7, 12), and there must have been ample flexible cuticle around most of the coxa-body union. One would like to know whether the trilobite coxal insertions were really as ventrally directed as suggested by the reconstructions. Enrolment was possible at least to some trilobites, and this implies considerable ventral flexibility in association with the stiff dorsal cuticle. Possibly ventrally directed coxae and an approximation of the body proper to a half cylindrical shape facilitated enrolment, as in modern arthropods (36, 41). But it is also possible that dorsoventral flattening of a trilobite occurred after death, producing the apparently ventrally directed fossil coxae which in life mav not have been unlike those of the prosomal limbs of *Limulus.* Thus it is clear that the Crustacea contrast with the Xiphosura and Trilobita in the pattern of their biramous limbs; and that the Crustacea contrast with the Xiphosura, and perhaps with the Trilobita also in the absence of the flexible pleuron which allows the various types of coxal movements seen in *Limulus.*

In view of basic differences in the types of coxal insertions and of outer ramus, and the complete absence of this ramus in the Onychophora-Myriapoda-Insecta group, the general similarities in some details of a leg and of a walking endopod are likely to be explicable on a basis of similar functional needs (Fig. 2). No evidence supports the suggestion (58) that a particular number of leg segments existed in an archiarthropodan leg, and that present numbers in the various groups have arisen by reduction or multiplication of leg segments from this archetype.[1] It is more probable that a single ancestral type of leg never existed. The more we are able to comprehend the mechanics of leg movement and the variety of ways in which legs are used, the clearer it becomes that segment number, type of jointing, position of a "knee," etc., are intimately bound up with function (38). But there are differences, such as the coxa-body articulations of myriapods and insects, which indicate a fundamental and early divergence of two groups along independent and mutually exclusive evolutionary lines.

In myriapods the principal proximal coxal articulation is ventral and with the sternite, but in insects it is lateral and with a pleurite, the latter being firmly fixed to both tergite and sternite. In all myriapods a promotor-remotor swing of the coxa on the body takes place, as in Crustacea, but in Symphyla, Chilopoda, and Pauropoda mechanical usefulness results from a simultaneous rock of the coxa about its sternal articulation, so that the dorsal surface of the leg becomes a little anterior during the propulsive backstroke, rocking in the opposite direction on the recovery forward swing. Mobile pleurites and special musculature causes this movement. In insects such a rocking movement is impossible because of the rigidity of the pleurite to which the coxa is articulated. The myriapod type of coxal movement carries with it the suitability and usefulness of a series of hinge joints between the more distal leg segments, each joint lacking extensor muscles. The insect type of coxal articulation permits far more varied movements of the coxa on the body than in myriapods, promotor-remotor, adductor-abductor and twisting about the pleurite, but a series of pivot joints worked by antagonistic pairs of muscles is needed all along the leg. No myriapod leg could be considered as a mechanically suitable forerunner of insect legs. In the pursuit of speedy running in myriapods many specializations have occurred in leg and joint construction: long intrinsic and extrinsic muscles give large displacements of the segments they move; leg joints are weak but allow wide angles of flexure; and mobile pleurites support the leg base in progressive measure as leg length and speed of running increases, culminating in *Scutigera.* In strongly burrowing centipedes four pleurites encircle the coxa and support the strong slow leg move-

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[1] There are, however, examples of arthropods in which certain leg segments have divided and others which have fused in association well-known functional needs. The tarsus of fast-running Diplopoda (Lysiopetaloidea) and Chilopoda (some Scolopendromorpha and Anamorpha) has divided into two or more segments, and the trochanter in certain myriapods has fused with the next distal or proximal segment (38).

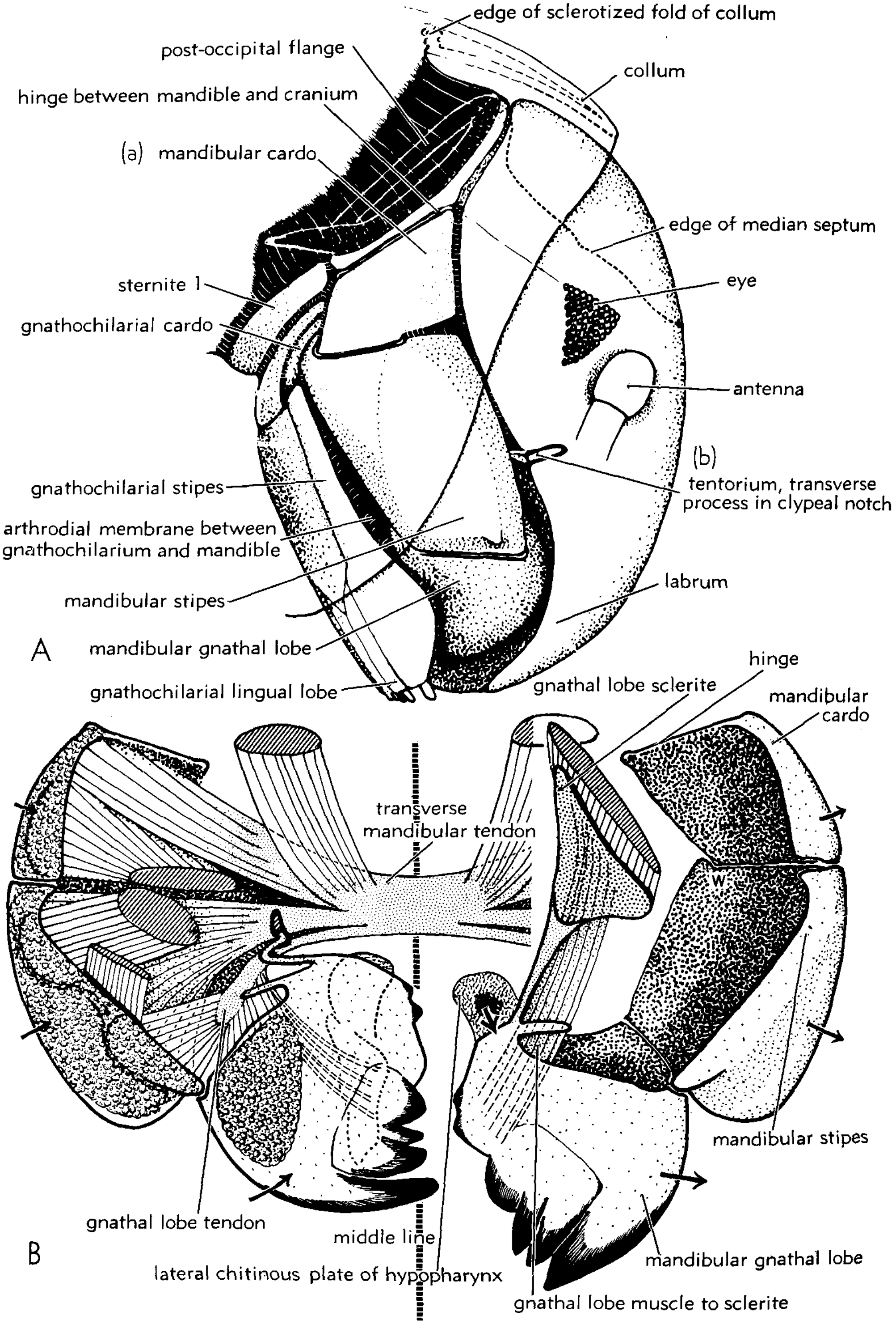

FIG. 11. Three-segmented whole-limb mandible of a iuliform diplopod *(Poratophilus punctatus).*

ments, another advancement of pleurite evolution. The myriapod type of leg is suitable for a many-legged animal, and an end term in respect of speedy running appears already to have been reached. This type of leg does not have the potentiality of leading to few pairs of relatively larger, stronger, longer legs as in insects. And myriapod extrinsic and leg-base muscles are not suitable for evolution into flight muscles, as are the comparably placed muscles in insects (44).

The brief references made here to mandibular mechanisms and to limb movements in living arthropods need amplification for their full comprehension (38, 43, 43a, 44, and future publications). It is clear that all available data concerning details of joints, possible axes of movement, etc., in fossil forms, besides the morphology of leg rami, respiratory filaments, etc., will be most valuable in building up a fuller picture of arthropod evolution and interrelationships.

In view of the strong probability of a parallel evolution of uniramous legs and of more than one type of biramous leg, as well as several types of jaws and compound eyes, and a variety of respiratory and excretory organs, we may ask, what surety have we that surface sclerites and a hemocoel have been evolved once only in metamerically segmented animals? It must be remembered that Mollusca also have a hemocoel, that the Annelida comprise animals (e.g., *Hermione*) which can stand up on very leglike parapodia and walk without any ventral contact with the ground; the mechanism of movement, however, is annelidan and not arthropodan in that to a considerable extent the annelids use the motive force of trunk muscles in walking, and an acicular mechanism provides essential parapodial length changes during stepping. The Annelida, as well as Arthropoda, possess a surface cuticle, and the arthropodan cuticles do not fall into a simple unified scheme in their fine structure and chemical composition. It will be shown below how the absence of surface sclerites in the Onychophora is bound up with the manner of survival of these animals and does not constitute a reason for regarding the group as subarthropodan in status. It should also be

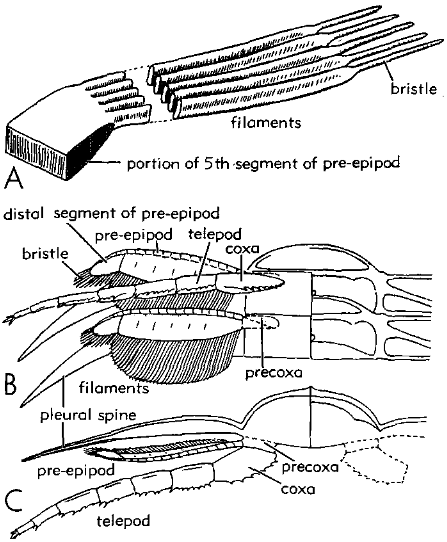

FIG. 12. Limbs of trilobites.

A. Diagrammatic reconstruction of the filaments of the outer branch of a limb of *Ceraurus pleurexanthemus* (Ordovician).

B,C. Reconstruction of limbs of *Olenoides* [*Neolenus*] *serratus* (Middle Cambrian) (after 59).

FIG. 11. *(Continued from facing page.)*

This mandible, which bites directly in the transverse plane, cannot have been derived from one that utilizes a promotor-remotor swing such as is seen in hexapods (cf. Fig. 8, 10).

A. Lateral view of head with the antenna cut short and the collum drawn as if it were transparent. The mandibular cardo *(a)* articulates with the head along the marked hinge line. The tentorium *(b)*, which provides the abductor force used to part the mandibles, swings from the clypeal notch.

B. Anterior view of isolated mandibles showing musculature and articulations. All mandibular muscles are adductor in function. On the left the mandible is in a position of maximum adduction. On the right most of the muscles have been removed to display the three mandibular segments, and the gnathal lobe is in a position of extreme abduction. The contrasting positions of the lateral hypopharyngeal scutes on either side are shown. The heavy arrow on the right indicates the direction of thrust by the anterior tentorial apodeme aaginst the gnathal lobe which abducts the mandibles.

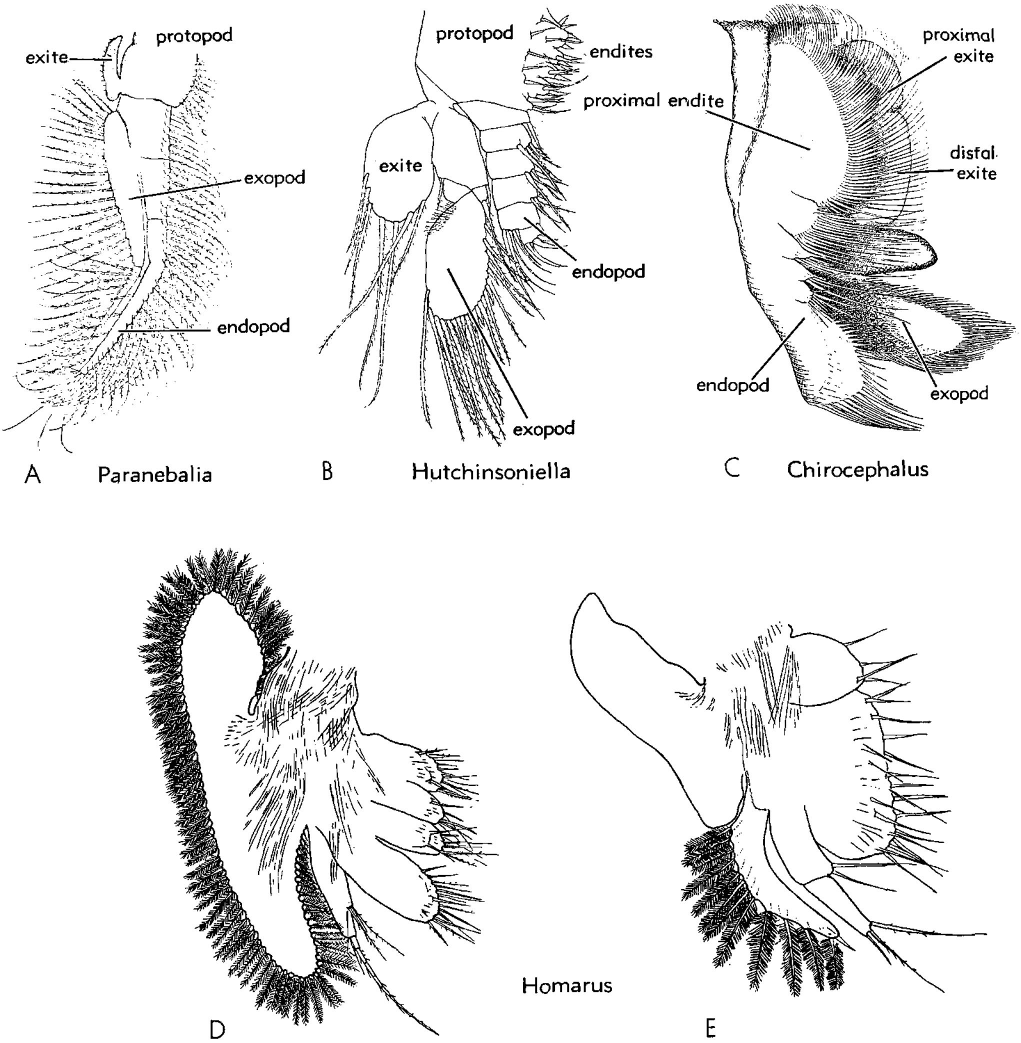

FIG. 13. Crustacean limbs which possess most of the basic parts—protopod, endopod, exopod, endites, and exites.

A. Fifth thoracic leg of *Paranebalia longipes* (after Calman, 1909).

B. Fifth thoracic leg of *Hutchinsoniella macracantha* (after 50).

C. Median view of trunk limb of *Chirocephalus diaphanus* in its natural position with backwardly directed exites and endites (after 8).

D. Second maxilla of first larva of *Homarus americanus* (after Herrick, 1895).

E. First maxilliped of first larva of *Homarus americanus* (after Herrick, 1895).

The limbs shown in *C-E* are markedly flattened (phyllopodia).

The limb of *Anaspides tasmaniae* (Fig. 2,*A*) is a typical stenopodium and also possesses most of the basic parts. Many stenopodia are reduced to the protopod and a walking endopod, thus superficially resembling the uniramous limbs of myriapods and hexapods (Fig. 2,*B*).

noted how clearly the polyphyletic origin of mammals (26) and of reptiles has been demonstrated by the fossil record. Quite independently, a number of separate lines of vertebrates have reached these grades of organization. The threshhold of a new grade depends on definitions and is essentially arbitrary. It would be surprising indeed to find no polyphyly in the origin of so vast and varied a group as the Arthropoda.

Many questions remain to be answered. As yet, we can give no precise functional interpretation of the formation of the arthropodan procephalon. A preoral cavity is more marked in most myriapods and hexapods than in Crustacea, and is formed by ventrolateral bending of anterior segmental components relative to the mouth, so that three segments become apparently preoral. The preoral cavity surrounding the mouth usually opens subterminally. At first sight, this similarity in head composition, in spite of the disparity in number of sensory limbs (antennules and antennae), appears so striking as to preclude explanation by convergence. But with the evidence concerning eyes, limbs, jaws, etc., before us, together with present ignorance of the factors which have led to head formation, the matter of segmentation of the procephalon must await further functional study. Meanwhile, the possession of three preoral segments cannot be taken as sound evidence of affinity between Crustacea and the land types.

HABITS CORRELATED WITH EVOLUTION OF LARGE TAXONOMIC UNITS

Specializations which fit animals to live in particular ecological niches are easily recognized, but this type of structural modification has usually not led to the evolution of classes or orders. Structural features which facilitate habits of life, such as running, pushing or squeezing through cracks, have hitherto been little appreciated and are of great importance. Recent work (34, 36, 37, 38, 41, 42, 43a, 44 and future publications) on the locomotory mechanisms and other habits of terrestrial arthropods has shown how conspicuous characters, which are diagnostic of classes and of orders, are correlated with some all-important habit or habits. These may be one or two of many habits exhibited by the animal, and if exercised frequently are easily recognized (e.g., diplopod bulldozer-like burrowing and characteristic feeding), but if the habit becomes of selective value only occasionally it may be less easy to apprehend. For example, the amazing structure of the Pselaphognatha is bound up with the ability to live, molt, and reproduce on the ceilings of small crevices, even on glass-smooth rock, together with an ability to run fast, which takes these tiny creatures out to alga-covered surfaces for feeding and back again to the same hiding place. These animals can survive in this manner under adverse conditions which would exterminate them from the many less favorable habitats they adopt when survival pressure permits.

Characters such as overall shape of the animal, number of segments, details of the skeleton and joints on the body and legs, form of the sclerites, together with their reduction or multiplication in number, detail of the musculature, formation of a thorax, etc., are correlated with habits such as (1) the diplopod ability to burrow by bulldozer-like pushing, the motive force being supplied by the legs; (2) the geophilomorph centipede habit of burrowing by an earthworm-like technique, the body surface applying the thrust; (3) the fast running and carnivorous habits of Chilopoda; the Scolopendromorpha and Lithobiomorpha strongly adapted for crevice living and catching and eating prey in confined places no deeper than the tergite-sternite span, while the Scutigeromorpha show end terms in structural modifications of trunk and legs which permit these fleetest of all centipedes to lead a more open life, catching flies, etc.; (4) the symphylan habit of seeking shelter deeply in soil, litter, or logs, but without pushing, the great flexibility of the body permitting sufficient twisting and turning for these little creatures to pass through small channels without extreme deformation; (5) the onychophoran habit of seeking refuge by extreme body deformation, again without pushing, so passing through narrow crevices which give access to larger cavities in decaying logs, under stones, etc., into which sizable

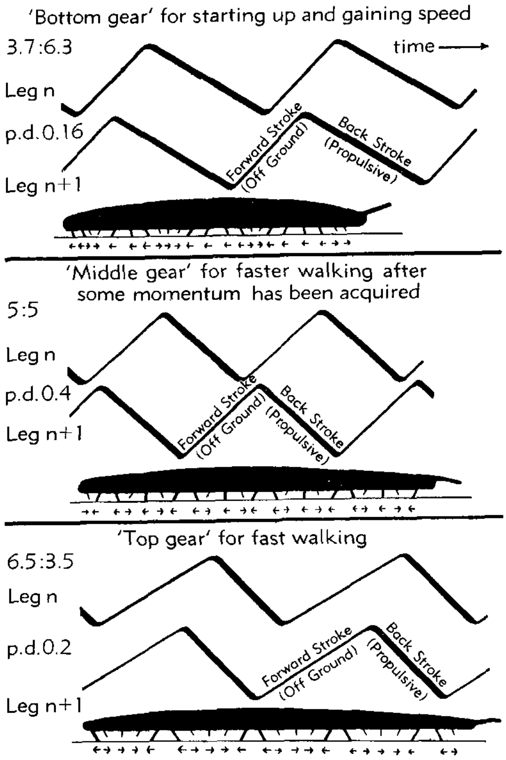

FIG. 14. Diagrammatic representation of the gaits most frequently employed by the Onychophora, *Peripatopsis*; intermediates between the gaits shown are also used. For each gait the movements relative to the body of two successive legs are shown by thin and thick lines in respect of time. Legs executing the propulsive backstroke are indicated by heavy lines and those in the recovery swing by thin lines; arrows below each leg show the direction of movement. The durations of the forward and backward strokes are as (3.7:6.3), (5:5), and (6.5:3.5) in *A, B,* and *C,* respectively, *p.d.* indicating the phase difference between successive legs (see legend to Fig. 15). A further advancement of the type of gait shown in *A* has led to the gaits and diagnostic trunk features of the Diplopoda (Fig. 15,*A-C*); an exploitation of the type of gait shown in *B* has led to the gaits of the epimorphic Chilopoda and the associated trunk characters (Fig. 15,*D-F*); the type of gait shown in *C* has been elaborated by the anamorphic Chilopoda again in association with the evolution of conspicuous trunk morphology. The type of gait shown in *B* is seen also in the slower gaits of the Pauropoda and in the faster gaits of Symphyla, but with an improvement in the stepping made possible by the presence of pointed sclerotized limb tips. The utilization of the latter type of gait by the ancestors of hexapods has avoided the morphological specializations referred to above and paved the way for hexapod evolution.

predators cannot follow; (6) the habit of hexapods in running on three pairs of legs and of arachnids in running on three or four pairs represents a way of achieving speedy movement which does not limit the choice and variety of practicable gaits, as is imposed on some centipedes and isopods by the evolution of many pairs of long legs. [This list could be lengthened but it suffices to indicate the type of habits that are important in the evolution of the structural features which are diagnostic of large terrestrial taxonomic groups, features which facilitate the attainment of the various proficiencies.] There are also interesting secondary habit reversals, such as lysiopetaloidean diplopods which have given up the ability to push strongly and have achieved a measure of fleetness and carnivorous feeding. Here, chilopod-like modifications of structure are superimposed upon the basic diplopodan anatomy of these animals, but they are neither primitive diplopods nor related to centipedes.

When the relationship between structure and habits is understood it is possible to assess the significance of much hitherto meaningless body structure. Real affinity can be distinguished from convergence, and one can decide with surety which end of a morphological series is the less advanced. There has been much doubt and controversy about such matters in the Myriapoda. The Scutigeromorpha, for example, in the absence of any functional understanding of the conspicuous characteristics of their trunk and limbs, have been considered to be the most primitive and not the most advanced of all centipedes. No doubt now arises as to the trunk and limbs of *Scutigera* being end terms in centipede advancement correlated with speedy running. Only the heads lacks the extreme flattening seen in burrowing and crevice-living centipedes, and these specializations are not needed by the Scutigeromorpha. The eyes of these animals are fittingly the most advanced of all Myriapoda, as are the mandibles (43a).

Similarly, opinions have been divided as to the probable primitive length of body in myriapods. In the absence of a functional appraisal of these features, some persons have suggested that short bodies, and others that long bodies, are the more primitive. An analysis of locomotory mechanisms (5, 34, 36) shows that a moderate or small number of trunk segments favors speedy running; many segments, forceful burrowing. As with a machine, even loading contributes to smooth running, and an even load on each leg of *Lithobius* during its propulsive backstroke can be achieved during the fastest gaits if 13 pairs of legs are employed; a smaller or a larger number leads to uneven loading. The early instar with 8 pairs of legs cannot employ so speedy a pattern of gait as can the adult if the mechanical advantage of even loading is maintained. Mechanical advantages are associated with the presence of 14 pairs of ambulatory limbs in *Lithobius*, the 14th pair being ambulatory only during slow running, and on occasion provide a gripping posterior holdfast. The functionally optimum number of trunk segments is bound up with other matters also, such as the potentialities of muscle physiology.

This brief outline roughly indicates the scope of morphological interpretation of trunk characters which has so far been reached, and, as with the jaw mechanisms, reference must be made to the full accounts for details. The bearing of this type of investigation on elucidation of the evolution and affinities of some of the major classes of arthropods may now be considered.

EVOLUTION AND RELATIONSHIPS OF ONYCHOPHORA

The Onychophora, which frequent damp environments in logs, crevices, under stones, etc., mainly in the southern hemisphere, have variously been interpreted as primitive, intermediate between annelids and arthropods, and even nonarthropodan. A reasoned argument for alignment of the Onychophora with the progenitors of myriapods has been given by Tiegs (66). An arthropodan heart, hemocoel, and cuticle are present, confirming their arthropodan status. A simple head, comprising three segments, is followed by a trunk not demarcated into regions and bearing many pairs of uniramous limbs. A simple alimentary canal performs excretory functions, as well as digestion and storage, and segmental organs are well developed, those on the third segment forming the enormous salivary glands which correspond with the premandibular salivary glands of Pauropoda and Symphyla.

Onychophoran embryonic development is of myriapodan type, not of crustacean or chelicerate type. Coelomic sacs are strongly developed, with large initial cavities, and the long series of coelomoducts even includes those of the antennal somites. The penultimate coelomoduct forms a genital duct directly comparable to the primitive opisthogoneate ducts of myriapods. The progoneate myriapods appear to be secondarily so (62, 65, 66). The teloblastic manner of laying down the embryonic trunk, which characterizes the Malacostraca with long embryonic developments (Manton, 28, 30, and the many subsequent workers on other species), is entirely absent in Onychophora, Myriapoda, and Insecta.

In *Peripatopsis capensis*, among the Onychophora, and in *Pauropus silvaticus*, among the Myriapoda, a recognizable gastrula is present. In *P. balfouri* the blastopore is virtual and the primitive endodermal cells degenerate, never forming an epithelium. In *P. sedgwicki* and in *P. moseleyi* these cells are never formed, the apparent blastula being really a gastrula devoid of endoderm, the definitive adult endoderm arising later and in another manner (32). Tiegs (62, 66) has pointed out essentially the same sort of series in the Myriapoda-Hexapoda. In *Pauropus* only one, or at most two, primitive endodermal cells lie within the gastrula epithelium, and give rise to the endoderm. The symphylan gastrula is composed of a superficial blastoderm covering a mass of yolk cells, a large proportion of which degenerate but some form the mid-gut. In most myriapods and insects the primitive endoderm disappears and the "blastoderm stage" is a postgastrula, not a blastula stage as had commonly been believed. It is remarkable to find such close correspondence in gastrula modifications

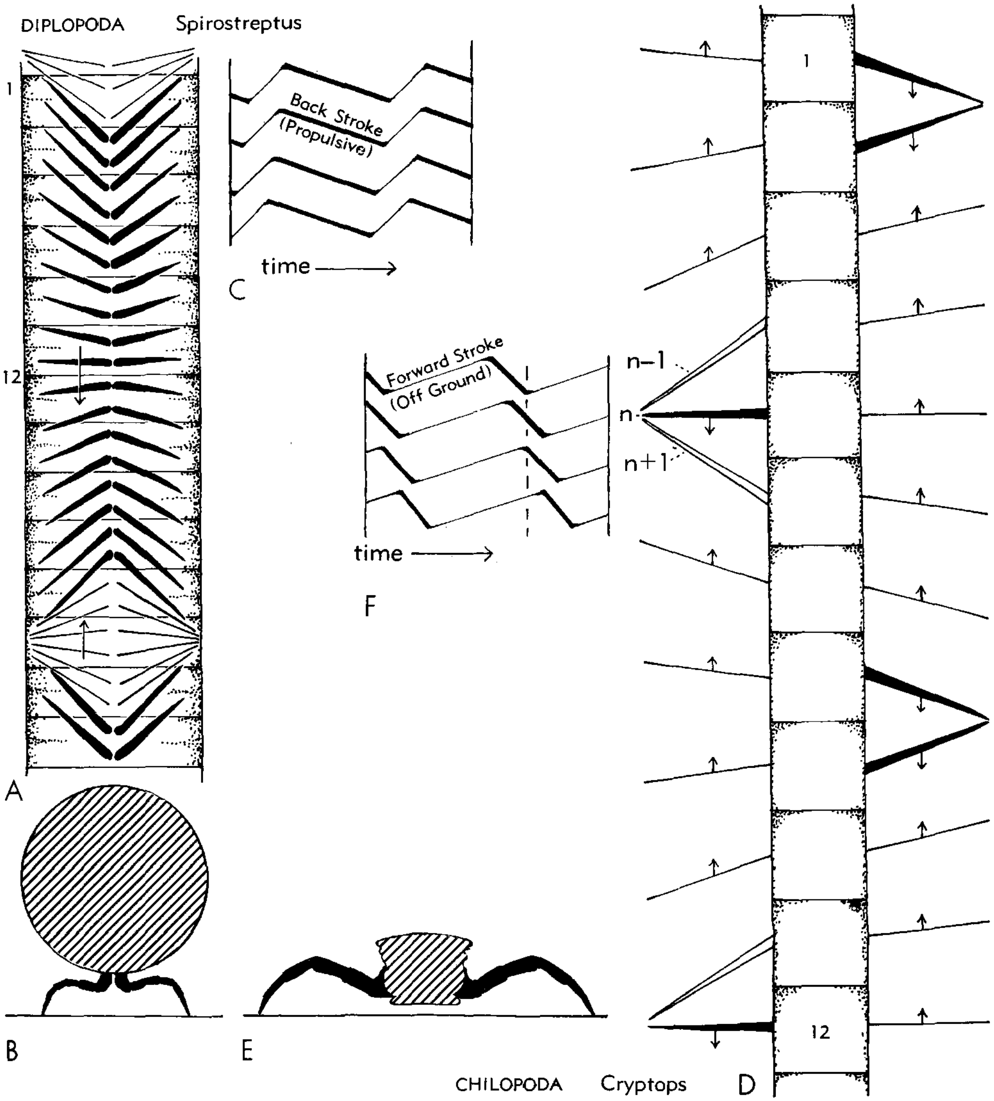

Fig. 15. Diagrams representing types of gait used in pursuance of the contrasting habits of Diplopoda and Chilopoda, together with some of the characteristic trunk morphology of these two classes which is correlated with the execution of these gaits.

The segment volumes of the diplopod *(A, B)* and of the chilopod *(D, E)* are similar and the figures show the very different shapes of the segments and the position of origin of the legs. The 12 trunk segments of the chilopod *(D)* correspond with the 6 marked diplosegments, each with two pairs of legs of the diplopod *(A)*.

In *C* the movements of four successive legs illustrate one of the slow strong gaits of a diplopod which are used in burrowing, and *F* shows a fast gait of an epimorphic chilopod used in running. The forward swing of a leg is indicated by a thin line and the propulsive backstroke by a thick line, as in Fig. 14. The relative durations of the forward and backward strokes are (2.5:7.5) in *C* and (7.5:2.5) in *F*. The phase difference between successive legs, expressed as that proportion of a pace by which leg n+1 is in advance of leg n, is 0.042 in *C* and 0.857 in *F*. Thus many legs are in the propulsive phase at one moment in the diplopod *(A)*, resulting in strong pushing, and few legs are in contact with the ground at one moment in the chilopod *(D)*, resulting in speed. Limb tips n—1

(Continued on facing page.)

proceeding in parallel manner within the Onychophora and the Myriapoda-Insecta, in contrast to the Crustacea.

Lastly, the nerve ganglia of Onychophora develop in association with "ventral organs," as they do in myriapods but in no other arthropod. These embryonic features provide very strong evidence of onychophoran-myriapodan affinity, which, although outside the scope of paleontology, should be generally recognized.

The superficial similarity between the mid-Cambrian *Aysheaia* and extant Onychophora is very great and appears to indicate antiquity of the onychophoran stem. Whether *Aysheaia* was sea-living or littoral is uncertain. If this type of animal "has set in train the evolution of the great terrestrial groups of myriapods and insects . . . it will have been one of the most momentous events in the whole Palaeozoic age" (66).[1] Further data concerning this important matter emerge from a study of habits.

Peripatopsis can pass through a hole in a card which is but one-ninth of the transverse sectional area of the resting animal. Slowly, by locally deforming the body and one leg at a time, the animal voluntarily traverses such a space, and Onychophora habitually squeeze through narrow passages before coming to rest (39a, 43a). The advantages of gaining protection from predators in this manner appears to have been over-riding, and the whole morphology, slow movements, and primitive undifferentiated gaits (Fig. 14) are associated with it. Correlated features are (1) the furrowed cuticle, which consequently can expand in all directions, though the surface layer of sclerotization is unstretchable; (2) the velvety appearance, due to the presence of papillae bearing sensory spines; (3) the fibrous subcutaneous connective tissue "skeleton" on to which the muscles are inserted, expandable in all directions though its fibers are probably unstretchable (cf. coelenterate mesogloea); (4) the lack of surface sclerites, although the capacity to form sclerotized plates is present (see jaw blades, claws, and long jaw apodeme extending through several segments figured by MANTON, 31); (5) the primitive jaws, made very effective by entognathy, with ability to cut a hole in a sizable arthropod, so that the contents can be sucked out or portions cut up and swallowed (31); (6) unstriated muscle fibers capable of great length changes, such as are impossible to striated but more quickly moving fibers, and the slow movements which keep changes in hydrostatic pressure minimal, as in Actiniaria (2, 3); (7) the defensive weapons in the form of slime ejection from oral papillae, the slime setting at once and entangling a predator at a distance of some inches; (8) the gaits employed in walking are amazingly primitive (33, 34, 42, and a future publication), but an animal depending for its survival on the habits already described has no need of speedy running or strong pushing, etc.; (9) Onychophora do not need acute vision for their crevice-living and walking abroad at night, or (10) an ability to hinder water loss from their innumerable spiracles supplying unbranched tracheae, a ureotetic metabolism effecting considerable conservation of water (31). Dry places do not easily provide food and are no attraction. (11) The extremely hydrofuge cuticular surface serves to keep water out. (12) Internal fertilization, with oviparity in some species and a variety of very efficient modes of viviparous development, constitute reproductive advances which are second to none among the Arthropoda.

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[1] TIEGS' (66) admirable discussion of this subject contains erroneous references to and deductions from the embryology of Onychophora because a modern account (32) was not then available to him and he based his remarks upon the work of the last century.

FIG. 15. *(Continued from facing page.)*

and n+1 in *D* are stationary; these legs are being lifted up and put down respectively at the moment shown by the vertical dotted line in *F*. Legs of a pair are in similar phase in *A* and in opposite phase in *D*. The pace duration of the chilopod can be very much less than that of the diplopod. The diplopod gait is a derivative of the type shown in Fig. 14,*A*, and the epimorphic chilopod gait is a derivative of the type shown in Fig. 14,*B*. For further description see text and the original accounts (33, 34, 35, 36, 43a, etc.).

A functional account can thus be given of all the major features of the Onychophora. The head segmentation stands at a lower level of advancement than that of all myriapods, hexapods, and crustaceans, and possibly indicates a very early adoption of the over-riding habit of life. Archiarthropods of this general type, but with less specialized heads (appendages and preoral cavity), could have become pauropods, diplopods, chilopods, symphylans, and hexapods by progressive evolution of the head and the pursuit of other habits of life, but no community exists with arthropods possessing biramous legs and gnathobasic jaws. An independence of early arthropods with uniramous limbs from other lines with biramous limbs is probable, and the acquisition of such limbs probably preceded the development of sclerites in the onychophoran-like line or lines which led to the dominant land types.

EVOLUTION AND RELATIONSHIPS OF MYRIAPODA AND HEXAPODA

These groups have in common a three-segmented procephalon with antennae borne on the second segment and in some species evanescent limb rudiments on the third or premandibular segment. This entails the formation of an antenna on the second segment, instead of a jaw, as seen in the Onychophora. Many examples of a shift of the segmental origin of jawlike or grasping organs in Arthropoda can be cited, and an early separation of the onychophoran and myriapodan types of procephalon might not be extraordinary in a related stock of terrestrial arthropods. Some crustaceans bite with a mandible-like antennal gnathobase and not with the mandible (e.g., nauplius of *Thalestris rodameniae*); male claspers arise on the antennal or on the first and second thoracic segment in Branchiopoda. A two-jointed gripping claw is present on the antenna in the naupliar stages and on the maxilliped in the copepodites and adult of the harpacticid *Thisbe,* both claws being exactly similar in shape and size.

The sclerotized head capsule presumably arose by the incorporation of the three-segmented procephalon with two (*Dignatha,* comprising Pauropoda and perhaps Diplopoda) or three (*Trignatha,* comprising Chilopoda, Symphyla, and hexapods) trunk segments, the limbs of these segments serving feeding purposes.[1] A preoral cavity is formed by a bending of segments and not by a progressive backward shift of the mouth out of one segment into the next. This cavity primarily conserves fluid and digestive juices around the mandible, and around other mouth parts in some arthropods.

All myriapod and hexapod classes typically possess a partial or complete armor of sclerites. The evolution of sclerites has permitted the formation of more quickly moving striated muscle fibers, and an abundance of joints is needed for speedier ways of life and a differentiation of habits. The initial function of sclerites was probably protective and useful in pushing against the substratum, but, as in present-day Geophilomorpha and some Scolopendromorpha, the sclerites probably did not form an inflexible armor. The presence of tiny cones of sclerotization set in the flexible unsclerotized endocuticle of the margins of certain sclerites (6) enables these sclerites to change shape considerably by rolling the margins inward to various extents. This capacity is much specialized in present-day epimorphic centipedes, but a less perfect version may have been a first step in habit divergence from seeking shelter by body deformability without pushing (as in Onychophora) to shallow burrowing by actively pressing on the

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[1] The table showing arthropod segmentation given in *Treatise Part O,* Arthropoda 1, p. O11, and the accompanying account of arthropod segmentation needs emendation. The embryology of no chelicerate shows more than one precheliceral segment (see DAWYDOFF, 15, and the original accounts). The fallacy of interpreting an arthropod head as composed of a series of modified cylindrical segmental components has been considered (40). Much of the dorsal part of the head has no primary segmental origin because it is derived from unsegmented blastoderm taken over from an unsegmented ontogenetic stage. The diagrams in text-fig. 7*A-C* of *Treatise* Part O, have no reality in living arthropods. The reference to the concept of primary and secondary segmentation (put forward originally by IVANOV, 25), does not represent the views of embryologists in general on this subject (32).

soil. Once sclerites were present, unlimited possibilities in habit divergence were opened up, culminating in the ability to lead an exposed life in dry places and to fly.

PAUROPODA

TIEGS' (66) studies of *Pauropus* led him to regard it as "a dwarfed, simplified, but also in some respects very specialized, survivor of a primitive stock of myriapods, in which only two segments have been added to the procephalon; and it is probable that when their development is better known, the diplopods also will be found to be members of this group. . . . The presence of a limbless collum segment in Diplopoda and Pauropoda even suggests a community of origin for these two groups."

Both the feeding arrangements and the locomotory mechanism of *Pauropus* are specialized. The elimination of alternate tergites gives stability to the body and limbs in executing fast gaits. A similar tendency is seen progressively in the Chilopoda (35, 43a). The limbless collum segment with its great dorsal shield in the Diplopoda is correlated both with bull-dozer-like burrowing and with the ability to enroll in a spiral. *Pauropus* is much too wide to roll up and too small to push effectively. If its ancestors had been larger, less fleet, and less specialized, it might be possible to guess from the general morphology of fossil finds the original usefulness of the collum in this class. The mobile, protrusible entognathous jaws and the tentorium (hypopharyngeal apophysis) are clearly specialized along lines of their own, although giving the same general advantages of entognathy seen in other groups (43, 43a).

DIPLOPODA

The longitudinally incompressible strongly calcified armor and the formation of diplosegments are the most conspicuous features of this group, together with the usual smooth strong outlines of the head and the manner in which the antennae can be tucked away. Both these and a host of other details are correlated with the ability to burrow by strong head-on pushing using the motive force of the legs (36, 37, 39, 42). Many legs provide a strong anterior thrust on the soil (See Fig. 15,*A*,*C*), but a very long body must be firmly held by intersegmental musculature and in any curvature dictated by the soil contents, in order that the force exerted by the legs may be transmitted to the head end. A shortening and deepening of segments will mitigate the evil, but much greater shortening and deepening can be effected if segments are fused together in pairs because the space needed by every other joint is eliminated. Propulsive legs cannot project far without causing interference in soil burrowing, and their mid-ventral origin gives maximum protection by the flanks, in contrast to chilopod legs which arise laterally and are fully exposed (see Fig. 15,*B*,*E*). The parallel-sided Iuliformia probably show the closest approach to an ancestral diplopodan method of burrowing, but there are many divergencies. An anteriorly tapered body and the long laterally projecting legs of the Polydesmoidea favor the splitting open of layers of decaying leaves. The thrust is exerted by the whole dorsal surface and a progressive forward movement of the wedge-shaped front end widens the crevice. Such animals cannot burrow into compact material.

It seems probable that diplosegments and a burrowing habit may have evolved before the perfection of an ability to enroll. The manner of formation of diplosegments is uniform, but the modifications facilitating enrollment at the anterior end are very different in the various orders (36, 42) suggesting independent acquisition. The modifications include the limblessness of the collum segment, its large tergite extending no more than halfway down the flanks. The three following segments carry only one pair of legs and commonly possess free sternites; these segments are less deep than the main part of the body and have a variety of muscular specializations, and permit space being found for the intucked head on enrolment and a spreading out of the legs on walking. The exactly cylindrical shape of the body or joints is associated with spiraling, for the segments need to twist on one another as the animal walks away from the spiral position (a total rotation of 90 degrees may be needed). Further specializations for enrolment into a sphere and not a spiral are shown by the short-bodied Oniscomorpha; their capacity for burrowing is poor, since they possess fewer limbs. As yet, the diplopod fossil material does not show clearly whether the anterior segments had only one pair of legs, but the general form of the anterior segments in fresh finds of early diplopodan fossils may indicate whether enrolment was practiced or not. There is nothing in common functionally between the three single-legged segments of a diplopod and the thorax of a hexapod; the two are in no way comparable, as has sometimes been supposed.

The Colobognatha have, on quite inadequate grounds, been regarded as the most primitive of living diplopods. In fact, they show a perfection of "wedge"-burrowing carried further than by the Nematophora (42). A propulsive thrust for burrowing is enhanced by the utilization of trunk as well as limb musculature. *Dolistenus savii* can exert a pushing force some three times greater than that of any other diplopod of comparable size which has so far been recorded. The segmental sclerites can telescope into one another, unlike the longitudinally incompressible Iuliformia and Polydesmoidea. Segments of progressively larger diameter at the anterior end are dragged forward by the trunk muscles, so widening a crevice. That this represents a secondary and not a primitive condition is shown by the very great muscular changes which make this habit possible. The progressive development of suctorial feeding within the Colobognatha entails profound modifications of mandible and tentorium and represents a major divergence from the feeding apparatus of typical diplopods.

It is probable that in myriapods several sclerites per segment preceded a welding of the sclerites into a rigid whole (cf. Crustacea; see below). The latter condition facilitates strong burrowing. But the usual presence of free sternites and frequently free pleurites also in the Colobognatha cannot, in their present form, be regarded as primitive. These sclerites are invisible or hardly visible in side view, and they contribute to the reduction of the body to a dorsal half cylinder with a flat ventral surface. This shape facilitates enrolment; the transverse axis of movement between the tergal arches is maintained at the ventral diameter of the cylinder, so eliminating a need for considerable ventral compression on enrollment. The axis of movement is sometimes maintained in this position by sternites which overlap from behind forward and pleurites which overlap in the reverse direction (36, 42). These features suggest specialization and are not at all like the probably primitively free pleurites of the Permian *Pleuroiulus* (17). Some Colobognatha (e.g., *Siphonophora hartii*) are even capable of enrolment in the lateral plane upon the ceilings of hides, an ability not found in other orders, and certainly not primitive.

The strong slow movements of diplopod legs when moving against a resistance show, at any one moment, very many legs in the slow propulsive backstroke and few legs performing a rapid recovery forward swing. This type of gait is a direct derivative of the onychophoran "bottom gear" gaits, and the greater the number of simultaneously pushing legs, the greater will be the total momentary output of force (Fig. 14, 15).

Reference has already been made to the diplopod mandibular mechanism composed of a very strong three-segmented mandible biting in the transverse plane (Fig. 11), and a mobile tentorium providing the abductor force. Such a mandible could have been derived from a simple whole-limb mandible, presumably characteristic of early unknown terrestrial arthropods.

Thus the primary habits of life which have acted as determinants of the evolution of diplopod characteristics relate to strong pushing, protective enrolment, and the eating of large quantities of vegetable matter of low food value.

CHILOPODA

Centipedes possess a trignathan grade of head development and the evolution of their outstanding features is associated with carnivorous feeding and more speedy running than practiced by Diplopoda and Onychophora. Primitive fossil chilopods, should they be discovered showing more detail than those recorded by Scudder (53), would be expected to possess a moderate number of segments (perhaps 25-35), each segment armored by a principal and an intercalary tergite and sternite and a few pleural sclerites set in ample flexible lateral body cuticle. No further tergite heteronomy would be expected. Moderate powers of burrowing would have been exercised by the body, locally becoming alternately thicker and thinner, the dorsal and ventral surfaces pressing on the soil. The legs would be short and freely projecting from a lateral origin; the coxae would be wide and short.

Among living centipedes well-formed intercalary sclerites are present in Geophilomorpha and the less advanced of the Scolopendromorpha. Here the intercalary and principal sclerites slide over one another dorsally and also become convex on body, shortening under the influence of the stout longitudinal trunk musculature. A thickening of a few segments travels tailward, the segments in front of the thickened zone, which is stationary to the ground, becoming thin and advancing forward. Speedy running is accomplished by swinging of the legs through a wide angle and the utilization of fast patterns of gait in which the duration of the propulsive backstroke may be only one hundredth of a second *(Cryptops)* and few legs (1 in 10 to 1 in 20) are in the propulsive phase at any one moment.

An early parting of the ways of centipedes in two directions has led to (1) the perfection of an earthworm-like burrowing technique (Geophilomorpha), and (2) speedy running, and at night a more surface-living habit (Scolopendromorpha and Lithobiomorpha), culminating in the very fleet Scutigeromorpha, which hunt flies by day. Worm burrows, soil cracks, and stones, particularly in warm countries, provide deep shelter for inexpert burrowers that can run. The requirements for these two habits are in many ways opposed. For burrowing, short wide segments and many of them, a pavement of pleural armor, and short legs are required, the legs on the anterior third of the body being stouter than the rest. Extrinsic leg muscles are not bulky, but the dorsal, lateral, and ventral longitudinal muscles need and use all the space they can obtain. For speedy running a flexible pleuron with isolated sclerites is required so that the coxa can swing tangentially to the surface about a ventral fulcrum. The coxae need to be short but dorsoventrally deep and well emarginated posteriorly. These coxal modifications, found also in Pauropoda and Symphyla, are bound up with fast movements.

Acceleration is obtained in Scolopendromorpha by the use of gaits with progressively fewer legs in contact with the ground at any one moment, until a minimum of two to three points of support on each side of the body is reached, legs of a pair being used in opposite phase (Fig. 16,*D*). During slow running, when the points of support along each side are close together and more numerous, the body can be held straight, but as the points of support become farther apart, the body tends to undulate in a horizontal plane. Such undulations are undesirable for mechanical reasons, and devices providing a progressive measure of control are found in the fleeter members of the Scolopendromorpha and in the Anamorpha. Intercalary tergites become smaller, less mobile and disappear, tergites become alternately long and short, the short ones finally being so small as to be invisible in dorsal view (Scutigeromorpha); extrinsic leg muscles and dorsoventral and oblique trunk muscles shift their insertions from the short to the long tergites, and the dorsal musculature becomes heteronomous. Each long tergite becomes strongly tied by muscles, directly and indirectly to five successive sternites. These features progressively reduce the mobility of the joint between the anterior end of each long tergite and the posterior end of the short tergite in front during fast running. The most stable part of the body lies at the seventh and eighth tergites, both of which are long, and fused together in Scutigeromorpha. The head and antennae of *Peripatus*, centipedes and some diplopods are alternately turned from side to side as the animal walks, the antennae touching the ground and sensing a path wide enough to take the leg track. In fast-running centipedes these movements start the anterior body undulations which are damped out or reduced at the seventh or eighth tergite region. *Scutigera* possesses

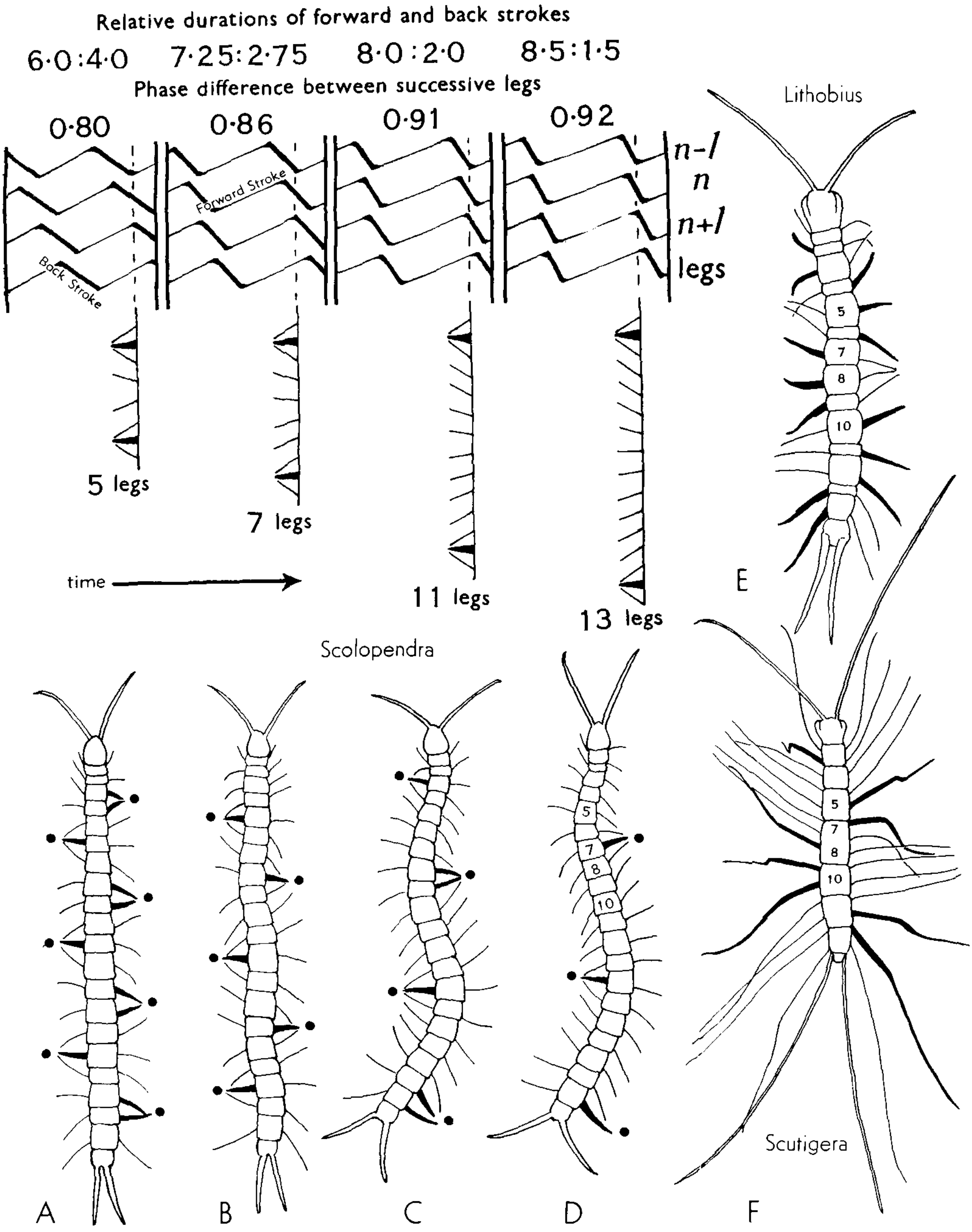

FIG. 16. Data illustrating some of the correlations between the habit of fast running of centipedes and their trunk morphology.

The lower diagrams *(A-D)* are tracings of photographs of *Scolopendra cingulata* running progressively faster. Legs with their tips in contact with the ground and performing the propulsive backstroke are shown in heavy lines; legs off the ground performing the recovery forward swing are shown by thin lines. The points of support of the body against the ground are indicated by black spots. The distances between the black spots show the stride lengths. Legs 1 and 21 are not used in fast running.

(Continued on facing page.)

the longest and most elaborate of centipede legs, each operated by 33 extrinsic muscles as compared with 13 pairs in a geophilomorph and two in a iulid. If the antiundulation mechanism here were less perfect, undulations would make the use of a large angle of swing by so many long legs set close together quite impossible and slower speeds would result. Sclerite perfection has, in fact, led to an economy in longitudinal trunk musculature, so making space for the abundance of extrinsic leg muscles. These locomotory perfections, together with the greater control of water loss by the formation of only eight median respiratory openings, the utilization of the blood for the transport of respiratory gases, and the compound eyes have made possible the more open habits of Scutigeromorpha. Centipedes do not run fast all the time, they run their fastest with reluctance, but it is the ability to make a supremely speedy effort occasionally which secures a meal or escape from a predator and is of selective value.

The specialized poison claws, the entognathous whole limb, but segmented, mandibles and the first and second maxillae suit flesh-eating but not the cutting up and swallowing of hard parts. The extreme head-flattening in all but the Scutigeromorpha is related to hunting and manipulating food in narrow places. This type of head evolution is entirely opposed to that of the Diplopoda, although both could have come from a common archimyriapodan type, and both use the mobility of the tentorium to obtain mandibular abduction.

Thus, the Chilopoda clearly represent an evolutionary line parallel to that of the Diplopoda, neither being the more primitive nor specialized in similar ways. Chilopodan evolution shows a dichotomy in life cycle, the Epimorpha hatching with many segments and the Anamorpha with few; but these groups differ also in their basic manner of hunting and in the use and structure of their poison claws and mandibles. Both have gone in for speed but in rather different manners, and they have solved their common antiundulation

FIG. 16. *(Continued from facing page.)*

Above are shown the gaits employed by the animals drawn below. The movements of four successive legs are given from left to right (arrow), the forward swing being indicated by a thin line and the propulsive backstroke by a thick line. The vertical dotted lines show the moment in time when leg n is halfway through the backstroke legs n—1 and n+1 converging on to the same footprint as they are picked up and put down respectively. The phase difference between successive legs is defined in the legend to Fig. 15.

As the faster patterns of gait are employed *(A-D)* so the relative duration of the backstroke decreases, and it is obligatory for the phase difference between successive legs to increase simultaneously (in order that the body always be supported over the common footprint and very long stretches of unsupported body be avoided). The points of support of the body on each side become farther apart in *A-D*, the metachronal waves comprising 5, 7, 11, and 13 legs respectively. Body undulations are absent in *A*, and are present in progressive measure in *B-D*; in *D* the animal is supported by three points in all.

The body length and segment number allow slight, but advantageous, anterior and posterior fanning out of the fields of movement of the legs; a shorter body could not accommodate the fastest gaits of *F*; the lateral origin of the legs and their length ensure a wide angle of swing and a long stride; the alternate-sized tergites, and the successive long tergites corresponding with legs 7 and 8, by their morphology and muscular connections, provide a measure of control of the deleterious body undulations.

Figures *E* and *F* are tracings of photographs of *Lithobius forficatus* and *Scutigera coleoptrata,* respectively, running fast (conventions as in *A-D*). Compared with *Scolopendra (D)*, the legs of *Lithobius* and *Scutigera* are progressively longer, yet the undulations of the body are progressively smaller, owing to the increase in heteronomy of tergite lengths. The short tergites 2, 4, 6, 9, 11, and 13 are minute and covered by the long tergites in *Scutigera,* where 7 and 8 are fused at the zone of maximum stability. *Scutigera* is the fleetest of all centipedes and a lack of control of body undulations would make speedy running by long legs an impossibility. The exact number of trunk segments, tergite shapes, and leg lengths in these anamorphic centipedes are correlated with fast-running habits, but the gaits employed differ from those of *Scolopendra* (for further details see MANTON, 35, 43a).

needs in the same way but to different degrees. The Epimorpha alone have perfected the primitive method of burrowing (Geophilomorpha), and without doubt the Scutigeromorpha represent the most advanced of all Chilopoda (43a).

SYMPHYLA

This small class of myriapods is of great interest because it appears to resemble the hexapods more closely than does any other myriapodan class. The Symphyla possess 14 trunk segments as in some insects (62, 65), with cerci on the 13th (62) as in Campodea (69). The trignathan head bears a labiate second maxilla, the progoneate condition secondarily superseding the primitive opisthogoneate state, probably as a consequence of anamorphic development. Many curious resemblances exist, such as the presence of a similar embryonic dorsal organ in Symphyla, Collembola, and *Campodea.* A range of gaits such as seen in Symphyla could have given rise to those of hexapods simply by reduction of leg number. The gaits of diplopods, chilopods, and pauropods are much too specialized along their own lines to form a basis for hexapod movements. The easy conclusion that Symphyla stand nearer to the insects than any other group of myriapods is not, however, substantiated by a further understanding of the head and trunk.

The mobile anterior tentorium of Symphyla resembles that of the myriapods and does not resemble that of insects where a posterior as well as an anterior tentorial apodeme is present (43). The two-segmented mandible, performing direct adductor-abductor movements, contrasts with that of the hexapods and could not have been a forerunner of the latter. As in other myriapods, an abductor mechanism extraneous to the mandible is present. This is partly provided by the swinging tentorium, in principle, but not in details resembling other myriapods, and in part by maxilla 1 in a unique manner. The adult head segmental organ lies on the maxilla 1 segment in Symphyla, whereas it is labial in Thysanura. The coxa is of the myriapod type and unlike that of insects. These facts are not reconcilable with a supposed symphylan origin of insects.

The outstanding habits of the Symphyla are an ability to penetrate deeply into soil, decaying logs, etc., and to dart about on an exposed surface, changing direction repeatedly and sharply. Symphyla cannot push their way into soil, neither can they deform their bodies in the manner of the Onychophora, but they are adept at twisting and turning, so utilizing minute spaces. This habit is made possible by: the presence of intercalary tergites all along the body, as well as divided ones on segments 4, 6 and 8, giving added flexibility to the middle part of the body; by the flexible chilopod-like pleura; and by the ventral surface being capable of longitudinal folding like a concertina. The gaits employed are of the chilopod type, but form the slower end of this series, and speed is obtained by very short pace durations. The ability to change direction, and suddenly run in the opposite or another direction, may be of survival value against small arachnid predators which cannot turn so easily. The trunk anatomy, including musculature, and antennal movements are bound up with these habits (44).

One can but conclude that the hexapods and Symphyla cannot have shared an immediate common ancestor,[1] even an archisymphylan (21), perhaps lacking the progoneate condition and possessing eyes, would be clearly a myriapodan line parallel to those of Diplopoda and Chilopoda, with the same basic type of myriapodan anatomy but modified for different habits. A similarity in sensory organs of Tomosvary in Diplopoda, Symphyla, and Collembola is probably related to needs, but the function of these organs is not yet clearly known.

HEXAPODA

Six-legged arthropods with a thorax more or less demarcated from the abdomen, and often with a much more elaborate exoskeleton, possess some functional advantages for certain habits over most myriapods. A re-

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[1] This view is contrary to that expressed by TIEGS & MANTON (67) when the relevant data concerning mandibles, tentorium, and trunk (43, 43a) were not available.

duction in leg number permits longer legs, these can give longer strides which contribute to faster running, suitable for more open habits; the three pairs of legs are always fanned out so that their fields of movement overlap little or not at all (34). Changes in speed can be effected by wide changes in pattern of gait, besides changes in pace duration. Walking or running on six legs has been evolved many times in unrelated classes. It is seen in some prawns and spider crabs, *Galeodes* and sometimes in spiders. Thus, the possibility of a hexapodous state having arisen more than once in the radiation of terrestrial groups persisting today as the myriapods and hexapods cannot be set aside, and the mere possession of three pairs of legs is not in itself sufficient justification for a supposed unity of pterygote and apterygote insects.

Insect ancestry has often been discussed (CALMAN, 1936; IMMS, 21, 22, 23; TIEGS & MANTON, 67). WILLE (70) has listed the resemblances and differences between the various hexapods and considered the implications. But adequate knowledge of existing jaw and tentorial systems in hexapods and myriapods has only just become available, and these data, together with an appreciation of the functional significance of entognathy and its probable parallel evolution, give clear pointers to affinities (43).

In considering the tentorium and mandibles it is necessary to make reference to the more generalized types found in the larger hexapod groups, since the extreme and varied specializations existing among some insects are not primitive and not relevant to the general question. The remarks which follow without further qualification apply to the more generalized known examples. The hexapod mandible is primitively a whole limb and unsegmented (as in Thysanura, e.g., *Petrobius*). Its movement is a basic promotor-remotor swing about a more or less dorsoventral axis, as in Crustacea, but presumably independently acquired. Dorsal close articulation exists, and some freedom about the axis of swing is conferred by the absence of a ventral or anterior articulation. This is useful as it is in the more primitive Crustacea performing the same basic movement. A primary effect of this movement is grinding by molar areas, as in *Petrobius*. The Thysanura and Pterygota show a series of mandibles (not phylogenetically connected) indicating the course of evolution which has led to strong biting in the transverse plane as seen in a cockroach or locust. The course is similar to that employed by the Peracarida culminating in the Isopoda. A backward shift of the dorsal end of the axis of swing, and a reduction in the preaxial part of the mandible leads to a more or less horizontal hinge between two principal condyles. Molar grinding becomes impossible, strong cutting by the distal edge increases, and a wide angle of swing is obtained by dissolution of the transverse mandibular tendon. Muscle modifications lead ultimately to a very simple but strong system of adductor and abductor muscles, tendons, and apodemes which work a very large mandible with relatively enormous cutting surfaces. These are parallel evolutions to certain Crustacea, and the details are different.

The mandible of *Petrobius*, although in some ways strongly suggestive of what the archihexapodan mandible may have been like, is itself specialized for a particular mode of feeding. The mandible is not exposed, as drawn in the textbooks. It is shut in, working in an enclosed space formed by the overlapping lateral parts of the labium, galea, labrum, and superlingua. The scratching activities of the tips of the mandibles and laciniae within enclosed spaces allow particles and salivary juice to be sucked up. There is no biting by the pair of mandibles. The hydraulic efficiency round the oral cone of *Petrobius* may not have been present in the thysanuran anestors where the mandible may have been less long and thin.

The mandibles of the other apterygote classes may have had a common or similar origin with that of the Thysanura, but thereafter their evolution has been totally opposed, precluding any supposed origin of the Pterygota from an apterygote group other than the Thysanura. An enlargement of the small pleural fold of *Petrobius* could have led to the entognathous condition of the Collembola and Diplura. The development of entognathy permits of the evolution of proximal freedom and protrusibility of the mandible, and is an entirely opposite trend to that seen in the Thysanura (Machilidae)-Pterygota group. The rotator-counter-rotator movements of the mandible in Collembola and Diplura has resulted in certain general similarities in musculature, but the many differences in detail suggest that entognathy has been independently acquired in these two classes. Anterior and posterior tentorial apodemes are present in Collembola, but they possess some mobility and are modified to suit mandibular protrusibility and entognathy. Posterior tentorial apodemes are present alone in Diplura (for functional and spacial reasons), while the Myriapoda all possess an anterior pair of tentorial apodemes only. The trend in tentorial evolution in the Thysanura-Pterygota line is one of progressive fusion, rigidity and massiveness. This is associated with transversely biting mandibles moving from a rigid hinge line and with strongly moving maxillae, an entirely opposite trend to that of the entognathous classes.

A functional and anatomical study of the head region does not support a phylogenetic unity of entognathous apterygotes[1] (68). It is more probable that entognathy, and all that goes with it, the details far exceeding those mentioned above (43), have been evolved several times within the Hexapoda. The Collembola and Diplura may have had a common origin in an archithysanuran stem, but thereafter their evolution has been independent and convergent in some ways. The Protura are clearly specialized minute crawlers into soil, litter, and crevices. The antennae presumably are secondarily absent, and the entognathous stylet-like mandibles and the tentorium are highly specialized. The prothoracic legs are used for intermittent hauling by movements requiring no lateral "elbow room." The meso- and metathoracic legs are together ambulatory, performing cart horselike walking gaits. These characters cannot be primitive in spite of the presence of an apparently primitive number of 14 abdominal trunk segments.

That the apterygote and pterygote groups all share the same type of mandible with the same movements and also show basically similar anterior and posterior tentorial apodemes (43) and a similar type of coxa-body articulation suggests that the pterygotes and apterygotes may have had a common origin. Their many-legged ancestors probably used the simple range of gaits found also in the Symphyla. These gaits are directly related to those of the Onychophora and avoid the specializations displayed by the Diplopoda and Chilopoda and the faster gaits of the Pauropoda. Whether the number of 14 trunk segments of Symphyla, the Permian Monura (55), and Protura, a number also recognizable in the Pterygota, is related to locomotion has not yet been ascertained. Since chilopod segment numbers, particularly in the Anamorpha, are so closely related to locomotory needs, possibly a similar number of trunk segments in some hexapods and in Symphyla may be the result of convergence, but the details are not yet ascertained. Such a number does not suit the jumping mechanism of the Collembola, in which a smaller number of segments is more favorable; this small number was already established in the Middle Devonian (52).

At what stage the hexapodous state appeared is uncertain. There are not many ways of using only three pairs of legs (MANTON, future publication), so that the same usage may have been independently acquired. The less specialized Pterygota, and *Petrobius* under some circumstances, exhibit the same type of leg movements, but different methods are employed by some other apterygotes. Thus, there seems to be as strong an indication of distant unity between the hexapod groups as there is between the several myriapod groups, but the former cannot have arisen from the primitive members of any extant class of myriapods. Such a conclusion is not surprising. Had a modern group possessed the genetic potentiality of giving rise to the most dominant of present-day land arthropods, some of its members would not be expected to remain arrested at imperfect stages of such a momentous evolutionary advance. Rather must we endorse the view of SEDGWICK (1909), who considered the present myria-

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[1] As suggested by TUXEN.

pod and insect fauna to represent the isolated descendants of a once widespread early radiation of terrestrial arthropods.

The recent work by SHAROV (54, 55) on the Lower Permian Monura shows animals which are close to the Thysanura, but more primitive in some respects. In *Dasyleptus* we have the 14 thoracic and abdominal segments but forming an even series with a large 14th segment, and nine pairs of short abdominal limbs following the three thoracic legs. The head capsule of *Dasyleptus* shows separate tergite rudiments of the mandibular to labial segments, and large maxillary palps are present much as in *Petrobius*. SHAROV (54) has shown that the nymphs and life cycle of various Lower Permian insects were more primitive than those of modern Hemimetabola. On all counts we can agree with SHAROV in looking to this type of animal as the forerunner of the winged insects.

EVOLUTION AND RELATIONSHIPS OF CRUSTACEA

Little can be added with certainty to the many previous considerations of phylogeny of the crustacean subclasses. We have no direct or indirect conclusive evidence concerning interrelationships of the Branchiopoda, Copepoda, Cirripedia, Ostracoda, and Malacostraca. The Leptostraca, although possessing a caudal furca in the adult, are clearly malacostracan in limb construction, feeding mechanism (7, 10), abdominal segmentation, and embryonic development (28, 30). Leptostraca retain the seventh abdominal segment in the adult, seven being the apparently primitive number for the Malacostraca (28, 29, 30). Leptostraca can no longer be regarded as a possible link between the Malacostraca and the "lower" Crustacea. A modern tendency to add taxonomic units to the existing system, in order to accommodate the newer finds as Mystacocarida, Cephalocarida, and additional taxa within the Malacostraca, has not given trustworthy indications of the relationships of the larger crustacean groups. The Cephalocarida show certain primitive features, such as the leglike second maxilla in series with undifferentiated trunk limbs each showing a generalized form (49, 50). Food collection of suspended material by many limbs without true filtration is probably another primitive attribute. The common pattern of maxilla 2 and the trunk limbs of *Hutchinsoniella* is as generalized as can be found among living Crustacea, but there are other examples (Fig. 13*A,B*). Limbs roughly of this form could have given rise to the various types of phyllopodium and stenopodium (Fig. 2, 13*C,D*); but a consideration of the modes of evolution of crustacean limbs put forward by CANNON (7, 8, 10, 11, 13, etc.) based on observation and detailed functional analysis are far more plausible than the theoretical suggestions of SANDERS (50).

Almost every class of Crustacea contains members which swim and others which crawl over the substratum. But we cannot as yet associate the more obvious of the diagnostic features of each class (apart from Cirripedia and Ostracoda) with particular habits or functions, and therefore we cannot appreciate the needs for these characters or the circumstances of their evolution. The ever-growing body of information concerning suspension and other feeding (summarized by TIEGS & MANTON, 67) serves to emphasize how different are the mechanisms in the several classes. Similar principles may be used, but the details are so unlike as to preclude the filter- and suspension-feeding mechanisms of any one class from having had the capacity to give rise to that of any other (see in particular the work of CANNON, 7, 8, 9, 10, 11, 12, etc.). Similarly the ability to tackle large food is correlated with the same general changes and specializations in mouth parts and anterior trunk limbs, but the details differ from group to group. Further comparative anatomical studies have produced no clear picture, although there are certain discoveries, such as the life cycle of *Hutchinsoniella,* which may help to bridge the gaps between Malacostraca and other classes. Since we have no primitive Ostracoda, Cirripedia, or Branchiura alive today, we are left with a consideration of Branchiopoda, Copepoda, Malacostraca, and the small new groups.

With no clear evidence concerning the interrelationships of the main crustacean classes, a consideration of the possible morphology of ancestral types of Crustacea becomes very speculative. It appears necessary at the present time to reaffirm the fallacy of considering a nauplius larva to represent a modified adult crustacean ancestor, as has recently been claimed (50, 51). GARSTANG (18), DE BEER (4) and others have given ample reasons for regarding the nauplius as representing only the larva of ancestral Crustacea. Metamerically segmented wormlike coelomates with short-bodied larvae may have given rise to arthropods, but it is unjustifiable to suppose that such an ancestor shortened its adult body to naupliar dimensions, elongated the adult again to the lengths found in the less advanced of modern Crustacea, and then embarked upon the shortening and posterior modifications seen in the most advanced of living species.

Presumably Crustacea arose from coelomate ancestors, at first as more open living bottom-dwellers whose exoskeleton gave better protection. Little differentiation into separate sclerites would be expected on each segment. A walking habit may have preceded a swimming one, although the possession of a biramous leg may have favored swimming as an alternative method of progression at an early stage. There have doubtless been many habit reversals and changes in the ways of life of Crustacea, and often it is not clear which habits are the secondary ones within a class. On functional grounds it is difficult to see how the differentiation of the malacostracan thorax and abdomen could have taken place in other than predominantly bottom-living animals. A reduction in leg number and an increase in length of endopodite would give the locomotory advantage of a walking thorax. A persistence of abdominal limbs may initially have been of service in swimming, and might have disappeared had the Malacostraca remained entirely bottom-living, as have the posterior limbs of arachnids and hexapods. Thereafter, there may have been several parallel evolutions of the shrimplike form and pelagic habit, each with a perfection of filtratory feeding. The latter cannot be an absolutely primitive method of food collection. Something less localized than a single pair of maxillary filters probably preceded it and may have been practiced on the bottom. CANNON (7, 8, 10) has suggested how a maxillary filtering mechanism may have arisen initially to assist a primitive trunk-limb-feeding mechanism. Perfection of the former in the Leptostraca and other Malacostraca would then allow many changes to take place in the form and usage of the carapace and trunk limbs. If the caridoid facies is a parallel evolution in Peracarida, Syncarida, and Eucarida, although comprising in many ways the more primitive living types in these divisions, the more specialized adaptive radiations within each division need not be regarded as having been derived from pelagic filter-feeding ancestors. The benthic forms may have come directly from the bottom-living stocks which also gave rise to the pelagic mysids, syncarids, euphausiids, and penaeids within the several divisions. The benthic adaptive radiations have also led to secondary pelagic types such as swimming crabs and secondary filter-feeders such as *Porcellana* (45), *Haustorius* (16), and *Nebaliopsis* (10). The Branchiopoda and Copepoda also show habit reversals, but the direction of interpreting the series is not always clear. A further functional study of pelagic and bottom-living members of these groups would be most welcome.

Some apparently simple conditions, when properly investigated, are seen to be anything but simple or primitive. The coupler of *Calanus,* one of the most primitive copepods, linking each pair of thoracic swimming legs, is characteristic of the subclass. The structure of the coupler is highly complex and related to an elaborate sternal system of sclerites. The coupler enables these legs to swing through a large angle—some 105 degrees (48)—thus facilitating the (almost synchronous) backstroke of these legs which gives the sudden copepod dart through the water. A complex system such as the coupler ranks as a very great and unique specialization which could not have been present in primitive types.

What has already been said about the fundamental difference between the mandibles of crustaceans and hexapods, the differences in head endoskeleton, sense organs, and sensory limbs, the differences in embryonic development and the persistence of segmental organs on different segments, suggests that there can be no close relationship between Crustacea and the Onychophora-Myriapoda-Insecta stem, and that there is no such taxon as the "Mandibulata." This conclusion implies a parallel evolution here of two types of limbs and mandibles, and a parallel development of exoskeleton, if, as seems probable, the early onychophoran line lacked surface sclerites.

The structure of the biramous crustacean limb and the contrasting manner in which the gnathobases of Crustacea and of *Limulus* are formed and used, the pleural origin of the limbs in chelicerates and their basically ventral origin in Crustacea (Fig. 2-4, 7, 12, 13) suggests a wide gap between Crustacea, Merostomata, and Trilobita. The head shields and limbs of the Merostomata and Trilobita have more in common than either has with the heads and limbs of Crustacea.

In considering the possible mode of evolution of the arthropodan armor, the chilopodan disposition of sclerites has sometimes been taken as representing a common primitive stage (Snodgrass, 56, 58; Størmer, p. *O*11, Vol. O, Arthropoda 1, and various modern textbooks). The probability of this is far from clear. Chilopoda need a flexible lateral body wall both for their technique in burrowing and for their coxal movements. A diplopod and a crustacean, by contrast, need a rigid lateral body wall, no matter whether this is provided by fused pleurites or by a pleural extension of the tergal arch. The diplopod and crustacean types of skeleton need not have passed through a chilopod-like evolutionary stage.

The more we appreciate the functional significance of structure, the clearer can we see how evolution can have proceeded, and the better will we be able to interpret structure in fossil arthropods where no direct study of function can be made. Even the details whereby tight enrolment is achieved by living animals, together with an appreciation of the mechanical difficulties which have had to be faced, is one of many examples of data derived from living animals which may be very useful to paleontologists.

Thus, as far as the evidence at present available goes, a supposed polyphyletic evolution of Arthropoda seems inescapable in the sense that the Onychophora-Myriapoda-Insecta and the Crustacea have evolved independently from each other and from the Merostomata and Trilobita. But the evidence does not indicate the state of advancement reached at the dawn of differentiation of these great groups. We should, however, be less dogmatic in upholding a supposed annelidan origin of the Arthropoda, if the term Annelida implies the Polychaeta, Oligochaeta, Hirudinea, and Archiannelida.

A metamerically segmented coelomate is as far as can justifiably be envisaged, a grade of animal perhaps very different from any modern annelid. Spiral cleavage characterizes the less yolky embryos of both annelids and molluscs, the cell lineages being extraordinarily similar in the two phyla, but arthropods show little of these features. As yet we know too little about the Tardigrada to decide whether they are more closely related to the Onychophora than to any other class, and the affinities of the Pycnogonida are also debatable (19, 20).

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GENERAL FEATURES OF CRUSTACEA

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CONTENTS

INTRODUCTION

The purpose of this chapter is to scan the general nature of crustaceans, mainly based on extant forms. Such a survey is desirable as an approach to detailed descriptions of the numerous major and minor crustacean groups, with emphasis on their fossil records, which follow. Though intended to be generalized and comprehensive, the initial review must be confined to relatively small space and cannot be allowed to duplicate discussions given at greater length by authors of systematic chapters included in this volume. Various generalizations may be expressed at known risk of ignoring exceptions (though hopefully none very important). Examples of morphological and other features are chosen on the basis of judgment that they are representative and illustrative, thus lending some degree of specificity to general statements.

The Crustacea are prevailingly aquatic arthropods distinguished basically from others by the presence of two pairs of antennary appendages on the **head,** for in other groups only a single pair of these structures is found or none at all. Behind the region of the antennae are three head somites which bear appendages functioning as jaws (mandibles) and for handling food (maxillules, maxillae). These components

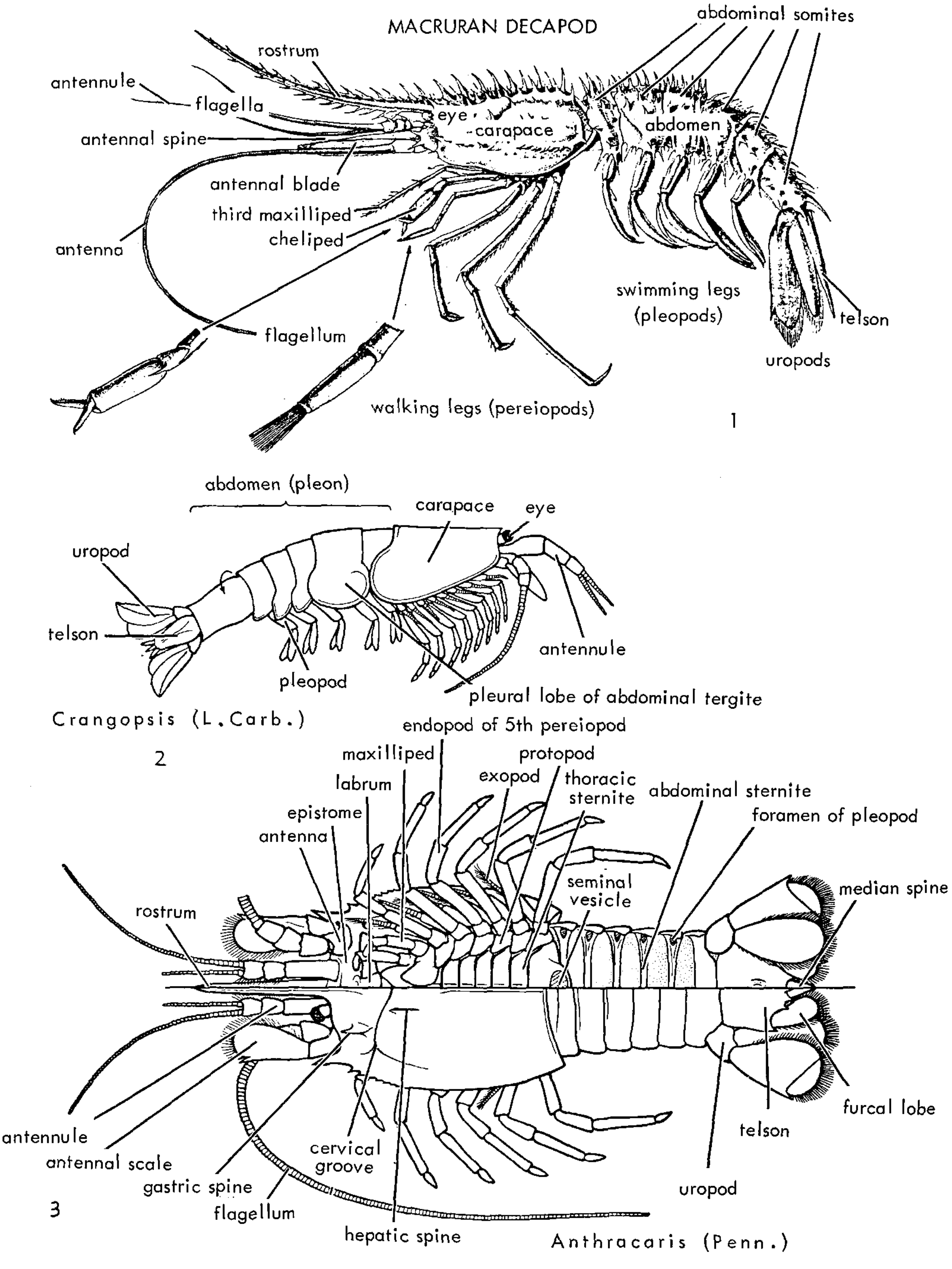

FIG. 17. Malacostracan crustaceans showing features of exoskeleton enclosing body and variously differentiated appendages.

1. Spinose living caridean, *Psalidopus spiniventris,* from Indian Ocean with unusually elongate rostrum projecting forward from carapace which covers head and thorax, with six abdominal somites. Appendages of the cephalothoracic region include antennules, antennae, a visible maxilliped, and dissimilar sorts of pereiopods, among which the frontmost pair is unusual in of the head region are reasonably consistent and diagnostic, whereas other parts of the body may vary considerably. Generally, parts of the crustacean body behind the head are differentiated in two major groups or tagmata of somites, anterior ones forming a **thorax** and posterior ones an **abdomen** (Fig. 17).

An **exoskeleton** consisting of hardened cuticle (L., *crusta,* hard shell) covers the soft parts of most crustaceans, including their appendages, and it even lines front and rear parts of the alimentary canal. This external integument is generally chitinoid but may be chitinous (Branchiopoda). Almost universally it is strengthened by calcareous deposits, sufficiently in some to develop extreme rigidity. Commonly, parts of the exoskeleton covering the body include in the anterior region a unified dorsal shield **(carapace)** with lateral extensions over the sides or developed as a hinged bivalve structure, and jointed segments covering rear parts of the body. The jointed appendages are encased in exoskeletal covers.

The vast majority of crustaceans are marine, ranging from near-shore shallow waters to the open ocean, where their distribution ranges from the surface to abyssal depths. Many are free-swimmers but some are planktonic floaters; others crawl about on the bottom or burrow in sediment, and a few (barnacles) live in fixed locations after attaining the adult stage. These sessile forms may be attached to almost any foreign object, including the shells of other marine invertebrates. Crustaceans also have invaded fresh waters of the land where they are found in streams, lakes, ponds, swamps, and even hot springs. A few have become air-breathers and thus adapted to terrestrial habitats (generally moist) far inland.

Only insects exceed crustaceans in numbers of individuals—at least this is generally considered to be so. Actually, crustaceans may considerably surpass insects in aggregate numbers, in view of the incredibly large populations of tiny marine copepods ("insects of the sea") and ostracodes with ocean habitat, for the oceans are vastly greater in spatial extent than all land areas combined. Additional are similarly stupendous hordes of branchiopods and other crustaceans of continental waters and less abundant air-breathing terrestrial forms. Crustaceans do not remotely compete with insects in variety, however, since the estimated number of known species of crustaceans (40,000) (GRUNER & HOLTHUIS, 1967, p. iii, iv) is only 1/25 (0.04) of the approximate total of described species of insects (900,000) (ROSS, 1965, p. 45) (nearly 1,000,000) (WIGGLESWORTH, 1964, p. 1).

In comparing crustaceans with other main divisions (superclasses) of the Arthropoda some far-reaching resemblances are easily discernible, foremost of which are the jointed nature of nearly all body appendages, encasement of soft parts prevailingly by an exoskeleton, division of the body into a series of more or less similar parts (somites) following one another in succession longitudinally but highly variable in number and distinctness (Table 1), and generally by well-developed articulations between segments of appendages and exoskeletal coverings of contiguous somites. As known to almost everyone, the name of the whole arthropod assemblage, signifying jointed foot, indicates a common denominator, though it must be admitted that some representatives hardly seem to qualify for membership.

FIG. 17. *(Continued from facing page.)*

having chelae with two movable fingers, and the second in bearing terminal brushes for work as cleaners of skeletal parts. The abdomen carries five pairs of biramous swimming appendages and a tail fan composed of uropods and telson. (Mod. from W. T. Calman in E. R. Lankester, *Treatise on Zoology,* by permission A. & C. Black, publ.)

2. Side view (reconstr.) of eocaridacean eocarid, *Crangopsis socialis* (SALTER), from Lower Carboniferous of Scotland, ×3. The head and thorax are concealed by a carapace unmarked by projections or grooves. Beneath the stalked eyes are robust antennules and antennae. The pereiopods and pleopods are all biramous and very similar to one another within each group. Tail fan well developed (Brooks, 1962).
3. Ventral (upper part of figure) and dorsal (lower part) views of exoskeleton of pygocephalomorph eocarid, *Anthracaris gracilis* (MEEK & WORTHEN), from Pennsylvanian of Illinois, ×1.7. The abdominal somites lack pleopods (Brooks, 1962).

Only a few distinguishing differences in arthropodan superclasses can be enumerated here. 1) Whereas crustaceans are characterized by biramous limbs and possession of two pairs of antennary appendages in front of the mouth, only trilobitomorphs also have biramous limbs and no noncrustacean arthropods are known to have more than a single pair of antennae. 2) Chelicerates are distinguished by the presence of one or more pairs of preoral pincer-bearing appendages (chelicerae). Many crustaceans also possess chelate limbs, but invariably these are located postorally. Chelicerates lack antennae. 3) Onychophores and myriapods are elongate wormlike arthropods characterized by very numerous almost identical somites. Both have a single pair of antennae, and both lack biramous limbs, thus differing from crustaceans. 4) Hexapods possess one pair of antennae and six pairs of uniramous limbs. Many of them differ from all other arthropods in having wings and thus in being able to fly. 5) Pycnogonids (sea spiders) and the primitive aberrant ill-known Tardigrada and Pentastomida are so unlike Crustacea as to need no statement of distinctions.

As recorded by MANTON (p. *R*5), diagnostic distinctions among the main groups of arthropods relate to the number of paired postoral limbs used in feeding and the manner in which these operate. Crustaceans correspond to myriapods and hexapods in having the first three pairs of these limbs (mandibles, maxillules, maxillae) largely or entirely employed for feeding, and additional limbs may be used similarly in Crustacea and certain Myriapoda. Crustaceans have gnathobasic jaws, biting with bases of the mandibles, whereas all myriapods and hexapods bite with the tips of the mandibles. In Trilobitomorpha homologous limbs are biramous appendages which appear to have served no function for aid in feeding. Chelicerates generally utilize the gnathobases of one or more pairs of postoral limbs for cutting and chewing food, but in manner quite unlike that of operating the crustacean gnathobases.

Observations of the habitats of arthropodan groups are worthy of mention in comparing crustaceans with other superclasses. Trilobitomorpha and Pycnogonida are exclusively marine. Crustacea are prevailingly marine but include a minority of fresh-, brackish-, and hypersaline-water forms, as well as a few air-breathing terrestrial species. Hexapoda are overwhelmingly terrestrial arthropods, including fliers and burrowers, but some are fresh-water aquatic and a small number are adapted for life in the sea. Chelicerates are found in all environments, except the air. Myriapods and onychophores are mainly terrestrial, but taking account of the fossil record, some kinds appear to have been aquatic. Pentastomids and tardigrades, of insignificant importance, may not belong to Arthropoda.

DIVERSITY OF GROUPS

GENERAL STATEMENT

Antecedent to consideration of appropriate subjects of general scope relating to the Crustacea—comparative morphology of the body, nature and function of appendages, features of internal anatomy, various physiological systems, modes of reproduction, ontogenetic development, life habits, ecologic adaptations, distribution in time and space, and classification—it is desirable to survey briefly main attributes of the several distinct groups that are recognized. These are enumerated in a preceding chapter by MANTON in her tabulation of main divisions of Arthropoda (p. *R*13). The groups are considered in the order there given, which is followed also in the arrangement of systematic descriptions in subsequent pages of this volume.

Nineteenth-century students of the Crustacea prevailingly divided them into two major assemblages, respectively named Entomostraca (insect-shelled) and Malacostraca (soft-shelled). From several viewpoints both are misnomers.

In the first group little more than average diminutive size and considerable range

Table 1. *Somites of Some Crustacean Groups and Appendages Borne by Them.*
[Somites are serially numbered from front to back (limbless eye-bearing anterior one of head region omitted). Data from Borradaile, *The Invertebrata* (4th edit.), 1963, and other sources.]

somite	CEPHALOCARIDA - Hutchinsoniella	NOTOSTRACA - Triops	MYSTACOCARIDA - Derocheilocaris	OSTRACODA - Cythere	COPEPODA - Cyclops	CIRRIPEDIA - Lepas	PHYLLOCARIDA - Nebalia	EOCARIDA - Eocaris	SYNCARIDA - Palaeocaris	MYSIDACEA - Mysis	CUMACEA - Diastylis	TANAIDACEA - Apseudes	ISOPODA - Ligidium	AMPHIPODA - Gammarus	DECAPODA - Astacus
2	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
3	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
4	m	m	m	m	m	m	m	m	m	m	m	m	m	m	m
5	mx	mx	mx	mx	mx	mx	mx	?	mx	mx	mx	mx	mx	mx	mx
6	Mx	Mx	Mx	Mx	Mx	Mx	Mx	?	Mx	Mx	Mx	Mx	Mx	Mx	Mx
7	th	th	Mxp	th	Mxp	c ♀	th	Mxp	th	Mxp	Mxp	Mxp	Mxp	Mxp	Mxp
8	th	th	th	th	th	c	th	Mxp	th	th	Mxp	th*	th	th*	Mxp
9	th	th	th	g ♂♀	th	c	th	th	th	th	Mxp	th	th	th*	Mxp
10	th	th	th ♂♀	0	th	c	th	th	th	th	th	th	th	th	th*
11	th	th	th	f f	th	c	th	th	th	th	th	th	th	th	th
12	th ♂♀	th	0		th(g)	c ♂	th ♀	th ♀	th ♀	th ♀	th ♀	th ♀	th ♀	th ♀	th ♀
13	th	th	0		g ♂♀		th	th	th	th	th	th	th	th	th
14	th	th	0		0		th ♂	th ♂	th ♂	th ♂	th ♂	th ♂	th ♂	th ♂	th ♂
15	g	th	0		0		p	p	p	p	0	p	p	p	p
16	0	th	0		0		p	p	p	p	0	p	p	p	p
17	0	th ♂♀	T		0		p	p	p	p	0	p	p	p	p
18	0	p	f f		f f		p	p	p	p	0	p	p	u	p
19	0	p					p	p	p	p	p	p	p	u	p
20	0	p					p	u	u	u	u	u	u	u	u
21	0	p					0	T	T	T	T	(1)	T	T	T
22	0	p					T	f f	f f		(1)				
23	0	p					f f		?						
24	0	p													
25	0	p													
26	T	p													
27	f f	p													
28		p													
29		p													
30		p													
31		p													
32		p													
33		p													
34		p													
35 to 39 (variable)		0													
		T													
		f f													

EXPLANATION

a = antennules
A = antennae
m = mandibles
mx = maxillules
Mx = maxillae
Mxp = maxillipeds (thoracopods)
th = thoracopods
p = pleopods (or natatory limbs)
u = uropods

c = cirri (thoracopods of Cirripedia)
0 = limbless somite
g = genital appendage
T = telson (not true somite)
f f = caudal furca
♂ = male genital aperture
♀ = female genital aperture
* = chelate or subchelate

(1) Note. Abdominal somites of female commonly lacking pleopods, those of male having variable number.

in form, besides the segmented body and generally similar appendages, remotely suggest the insects. The entomostracans, which include the branchiopods, ostracodes, copepods, and a few other kinds of crustaceans, collectively display characteristics less specialized or highly developed than those observed in the malacostracans and hence they have been considered to be low-rank divisions of Crustacea. Including extinct forms, their diversity furnishes basis for present-day differentiation of them into eight independent classes (or subclasses as ranked by many zoologists).

Oppositely, the Malacostraca remain as a morphologically somewhat closely related assemblage having more complex structures and more advanced specializations than in other crustaceans, but except at times of molting they cannot qualify for designation

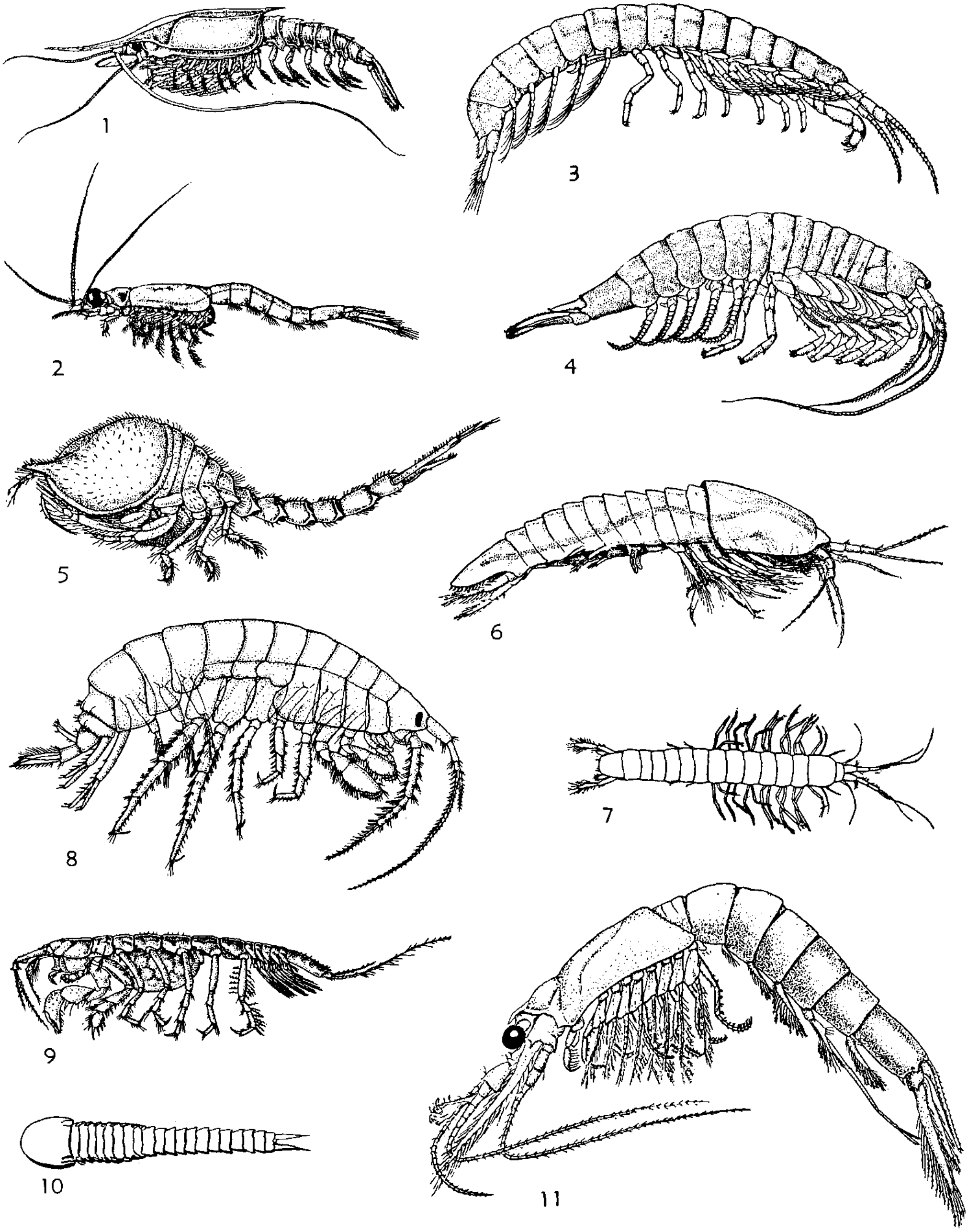

FIG. 18. Types of crustaceans illustrating diversity of groups, all extant.

1-2, 11. Mysidacean peracarids (Malacostraca).——*1. Gnathophausia zoea,* marine form from Atlantic off east coast of North America, characterized by possession of branched gills on some thoracopods, ×0.3.——*2. Mysis relicta,* fresh-water form lacking gills, from North American Great Lakes, ×2.——*11. Neomysis integer,* marine form with smooth somites behind carapace, male from English Channel, ×3.7.

3-4. Syncarids (Malacostraca), fresh-water.——*3. Koonunga cursor,* female from small stream near Melbourne, Australia, ×7.——*4. Anaspides tasmaniae,* mountain shrimp from pool 3,500 feet above sea level in Tasmania, male, ×2.

as soft-shelled. Many develop rock-hard exoskeletons or at least have a tough cuticle covering the body somites and appendages. The host of decapods, including lobsters, crabs, shrimps, and the like, together with less well-known groups (amphipods, isopods, mysidaceans, and others) belong to the Malacostraca.

SIZE AND MODE OF LIFE

Adult crustaceans range in size from less than 0.25 mm. (0.01 inch), measured as miximum length or width, to a "wing spread" of outstretched appendages amounting to 12 feet (3.6 m.) in the giant spider crab *(Macrocheira kaempferi)* of Japan. If account is taken of the hugely preponderant number of diminutive crustaceans, as compared with species having maximum dimensions of 25 mm. (1 inch) or more, a conservative estimate indicates that the average size of all crustaceans cannot exceed 1 mm. Further, if weight is given to the uncountable trillions of tiny copepods, ostracodes, and branchiopods having adult sizes of 0.5 mm. or less to 1 mm. the grand average must be in the neighborhood of 0.7 mm. This is a relevant guess for the crustacean world as a whole, emphasizing the quantitative importance of diminutive forms which are unrivaled as direct or indirect food sources for most aquatic animal life, but otherwise it is unrealistic to compute averages of the many different kinds of crustaceans in terms of size.

Consideration of the mode of life and ecologic adaptations of different groups of crustaceans is reserved for a subsequent section of this chapter. Here it is sufficient to note that the vast majority of these arthropods live in the sea, that they are most abundant in shallow waters of neritic belts and surface or near-surface waters of open oceans, that a few range to abyssal depths, and that crustaceans of land areas are predominantly aquatic forms found in fresh-water bodies or in saline lakes and ponds, as well as coastal lagoons. The temperature of crustacean-inhabited waters on land ranges from hot springs and spring-fed pools to icy cold, and levels at which crustaceans have been collected reach from more than 30,000 feet below sea level to at least 12,000 feet above sea level. A modest number of crustaceans are air-breathers which have acquired ability to travel about on land (e.g., numerous isopods, some amphipods), generally seeking out moist environments.

CEPHALOCARIDS

Cephalocarids are diminutive crustaceans (length of adults 2 to 3.7 mm.) which live as burrowers in fine sediment distributed from slightly below low-tide level to 1,000 feet or more below sea level (SCHMITT, 1965, p. 42). They are blind and colorless. Since only four species are known, differentiation of them as a separate class may seem surprising. This is based on their extremely primitive nature, which precludes placement of them in any already-recognized crustacean group. Behind a horseshoe-shaped cephalon formed by five fused somites (in addition to an embryonic, partly hypothetical preantennary first somite with

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FIG. 18. *(Continued from facing page.)*

5. Cumacean peracarid (Malacostraca); *Diastylis goodsiri,* female from Arctic Ocean showing head and thorax sharply marked off from abdomen, ×3.

6-7. Thermosbaenacean peracarids (Malacostraca).——*6. Thermosbaena mirabilis,* male from hot-water pool in Tunisia, ×20.——*7. Monodella halophila,* male from subterranean pool in Yugoslavia, ×13.

8 Amphipod peracarid (Malacostraca); *Gammarus locusta,* fresh-water form from northern Europe, male, ×3.

9. Tanaidacean peracarid (Malacostraca); *Apseudes spinosus,* female from North Atlantic, ×7.5.

10. Cephalocarid; *Hutchinsoniella macracantha,* primitive shallow-water marine crustacean from Long Island Sound, showing rounded cephalon and subequal body somites, ×11.

[*1-5, 8-9,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission A. & C. Black, publ.; *6,* from T. Monod in H. G. Bronn, *Klassen und Ordnungen des Tierreichs,* by permission Akademische Verlagsgesellschaft, publ.; *7, 10 11,* from T. Monod, H. L. Sanders, and K. Lang in Encyclopedia of Science and Technology, by permission, McGraw-Hill, publ., copyright 1960.]

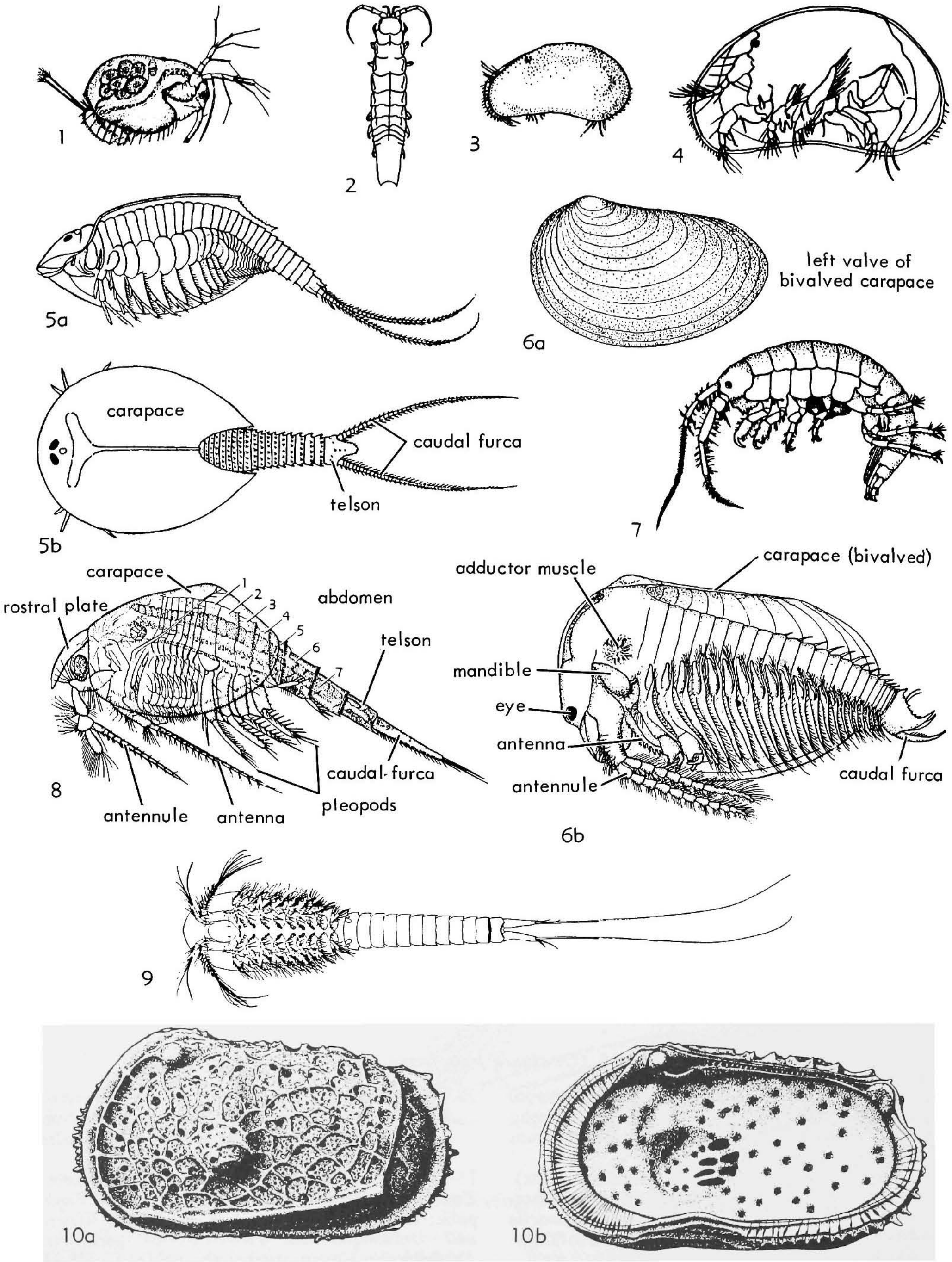

Fig. 19. Types of crustaceans illustrating diversity of groups, all extant.

1, 5-6. Branchiopoda.——*1.* Cladoceran, *Maerothrix rosea,* fresh-water, USA, enl.——*5.* Notostracan, *Lepidurus glacialis,* fresh-water, northern Europe; *5a,b,* lateral with left part of carapace removed, and dorsal views, ×1.7.——*6.* Conchostracan, *Cyzicus obliquus,* fresh-water, northern eye rudiments—Fig. A of MANTON) are eight thoracic somites and 12 abdominal ones, each identical in all essential features to others (Fig. 18,*10;* 19,*9*) (Table 1). The maxillules and maxillae are nearly the same in structural pattern as the thoracic limbs (thoracopods), which display nearly complete lack of serial specialization. Simplicity of the digestive tube, ladder-like ventral nerve cord, and homology of musculature from somite to somite mark the cephalocarids as uniquely generalized crustaceans, interpretable as approaching morphological attributes of ancestors of the Crustacea.

BRANCHIOPODS

Next to the cephalocarids, branchiopods are considered to be the most primitive living crustaceans, marked by morphological similarities of their numerous somites and multifilamentous limbs, and (commonly but not exclusively) by their filter-feeding mode of obtaining nourishment (Fig. 19,*1,5-6*). They swim about freely, mainly in continental waters ranging from fresh to hypersaline. Branchiopods (gill-feet), also known as phyllopods (leaf-feet), use their limbs for locomotion in swimming, for respiration, and for sieving water to extract food particles. They are mostly tiny, with length of adults 3 mm. or less, but in some groups (e.g., Notostraca) 15 to 30 mm. and exceptionally up to 90 mm. (LINDER, 1952). The head bears compound eyes, generally reduced and unsegmented antennules, biramous antennae, which may be relatively large or reduced to rudiments, mandibles usually lacking palps, maxillules and maxillae varyingly reduced in most. Thoracic and abdominal somites are highly variable in number but commonly are numerous. The front part of the body usually is protected by a carapace (Fig. 19,*5b-6a*), but anostracan branchiopods lack this covering. Paired limbs range from as few as four pairs (Cladocera) to 70 (Notostraca) (Table 1). In all branchiopods the posterior part of the abdomen is limbless, and posterior somites of the thorax also may lack limbs. A caudal furca is present in nearly all forms, and the multiarticulate rami of this may be very long (Fig. 19,*5a,b*).

MYSTACOCARIDS

Mystacocarids resemble cephalocarids in small size (length of adult 0.5 mm.), colorless subcylindrical slender body composed of similar somites, mode of life interstitial in near-shore sediment, and in being represented by only three known species. They also are primitive but have fewer and more specialized cephalic and thoracic appendages than the cephalocarids, in some respects suggesting those of copepods. The three known species all live in the interstitial environment of sand beaches.

OSTRACODES

Ostracodes are ubiquitous, mainly marine crustaceans which are characterized mainly by their few somites (distinctly less numerous than in other classes, Table 1) and by

FIG. 19. *(Continued from facing page.)*

Europe; *6a,* left valve of female, enl.; *6b,* side view of male with left valve removed, enl.

2. Isopod peracarid (Malacostraca); *Pentidotea resecata,* intertidal marine, off California, dorsal view, ×0.6.

3-4, 10. Ostracoda.——*3-4. Cylindroleberis* sp., fresh-water, northern Europe; *3,* left valve exterior, enl.; *4,* left side of animal with left valve removed, female, enl.——*10. Australicythere polylyca,* shallow-water marine form of southwestern Pacific, hemicytherid podocopid; *10a,b,* left valve exterior and right valve interior, latter showing subcentral adductor muscle scars (clustered elongate black areas), ×53.

7. Amphipod peracarid (Malacostraca); *Ampithoe* sp., intertidal marine form, Pacific off California coast, ×0.7.

8. Leptostracan phyllocarid (Malacostraca); *Nebalia bipes,* marine, left side of female from north Atlantic, with carapace shown as though transparent, ×6.

9. Cephalocarid, *Hutchinsoniella macracantha,* from Long Island Sound, ventral side showing thoracic appendages and caudal furca with very elongate rami, ×14.

[*1-4, 7,* from S. F. Light *et al., Intertidal invertebrates of the central California coast,* by permission, University of California Press; *5-6, 8,* from W.T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *9,* from H. L. Sanders, 1963; *10,* from R. H. Benson, 1966.]

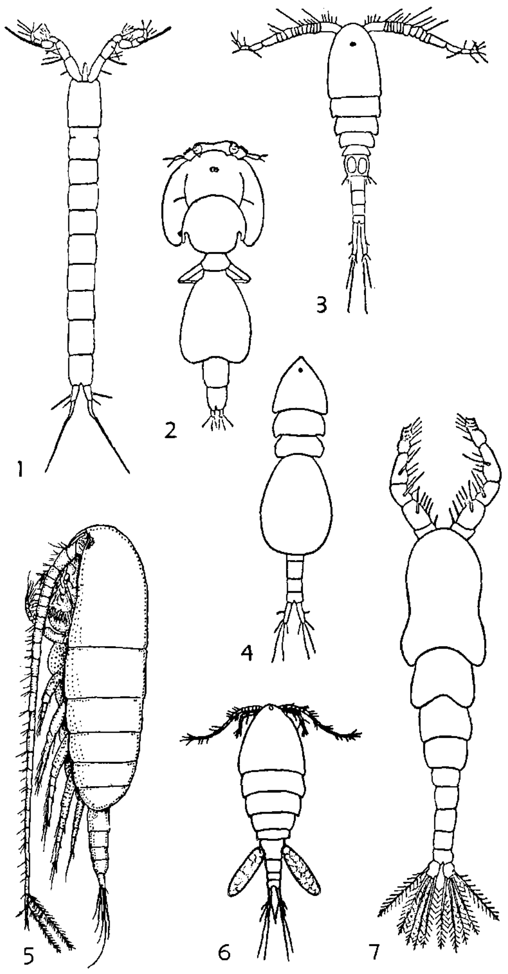

Fig. 20. Types of copepod crustaceans, all extant and chiefly marine.

1. Harpacticoid, *Evansula incerta,* characterized by elongate slender body, male, ×53.
2. Caligoid, *Caligus mirabilis,* widely distributed external parasite on fishes, ×33.
3, 6. Cyclopoids, *Cyclops bicuspidatus* and *Cyclops* sp., representing diminutive one-eyed fresh-water and marine group important as food source for fishes and other animals, ×33, ×20.
4. Notodelphyoid, *Notodelphys agilis,* belonging to estuarine and marine environments, generally found in body cavity of sedentary tunicates, ×10.
5. Calanoid, *Calanus finmarchicus,* among largest and most abundant pelagic copepods, this form characteristic of boreal waters, side view of female, ×11.
7. Monstrilloid, *Monstrilla dudica,* diminutive planktonic copepod, free-swimming as adult but with immature form parasitic on marine invertebrates, ×10.

enclosure of the head, entire body, and most of the appendages within a bivalved carapace (Fig. 19,*3,4,10*). Their extremely long geologic record (L.Cam.-Rec.) is rivaled only by the bivalved primitive malacostracans known as Phyllocarida. Ostracodes are much smaller than phyllocarids, having average length of adults barely more than 1 mm. (maximum 34 mm.) as compared with an average of approximately 10 mm. in modern phyllocarids (maximum 40 mm.) and nearly 200 mm. in some fossil forms. Both in ostracodes and most phyllocarids the carapace is hinged along the dorsal margin of the valves (Fig. 19,*10*). More than 1,000 genera of ostracodes have been described, among which extant ones only slightly exceed 10 percent.

The head region of ostracodes bears well-developed eyes, antennules, antennae, mandibles, maxillules, and maxillae. Two or three pairs of thoracic limbs are present and the posterior extremity of the abdomen is modified as a bilobed furca. The arrangement of antennary, mandibular, and adductor muscle scars on valve interiors and nature of the dorsal hingement are important for classification (Fig. 19,*10b*), as in different groups are other morphological features of the carapace (radial and pore canals, duplicature, surface ornament).

Ostracodes are mostly swimmers and they thrive on almost any kind of food. Some subsist by sucking juices of marine plants, some by feeding largely on diatoms. Copepods and other small organisms may be consumed in considerable quantities, and many ostracodes are scavengers which feed on any available dead tissue.

EUTHYCARCINOIDS

Interesting but numerically insignificant crustaceans known only as fossils (Trias.) from central Europe and Australia are named euthycarcinoids. In peculiar manner

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[*1-4, 7,* from Wilson, 1932; *5,* from W. T. Calman in E. R. Lankester, *Treatise on zoology;* by permission, A. & C. Black, publ.; *6,* from S. F. Light *et al., Intertidal invertebrates of the central California coast,* by permission, University of California Press.]

they appear to combine some characteristics of merostome chelicerates and diplopod myriapods, both of which are distantly related at best to crustaceans. Even so, the euthycarcinoids are thought to have closest affinities with the Crustacea.

Moderately large arthropods (average length of adults 40 mm., maximum 65 mm.), somites of the head region are fused together. Preoral appendages identified as antennules and antennae are crustacean attributes. The first thoracic somite, attached to the head, bears appendages considered to have functioned as maxillipeds. Pairs of thoracopods borne by 11 somites of the thorax behind the first one are uniramous, multijointed, and equipped with long setae adapted for swimming. The five abdominal somites are limbless, the posterior one being followed by a long *Limulus*-like telson.

COPEPODS

Much the most abundant of all marine animals are crustaceans belonging to the class Copepoda (Table 1, Fig. 20). A majority are benthonic free-swimmers, or planktonic floaters, but very numerous kinds are parasites as adults which infest fishes, such mammals as whales, and many invertebrates, including other crustaceans. Free-living copepods usually range in size from less than 0.5 mm. to about 10 mm. in length. One of the largest parasitic forms *(Penella)* may be more than 300 mm. long, with trailing egg sacs approximately equal in length (overall some 2 feet).

Copepods lack compound eyes and have no carapace. Typically, they possess long antennules and short antennae, six pairs of thoracic limbs, and a limbless abdomen. The thoracopods are biramous, except for the first pair which invariably is uniramous and the last pair which also may be uniramous.

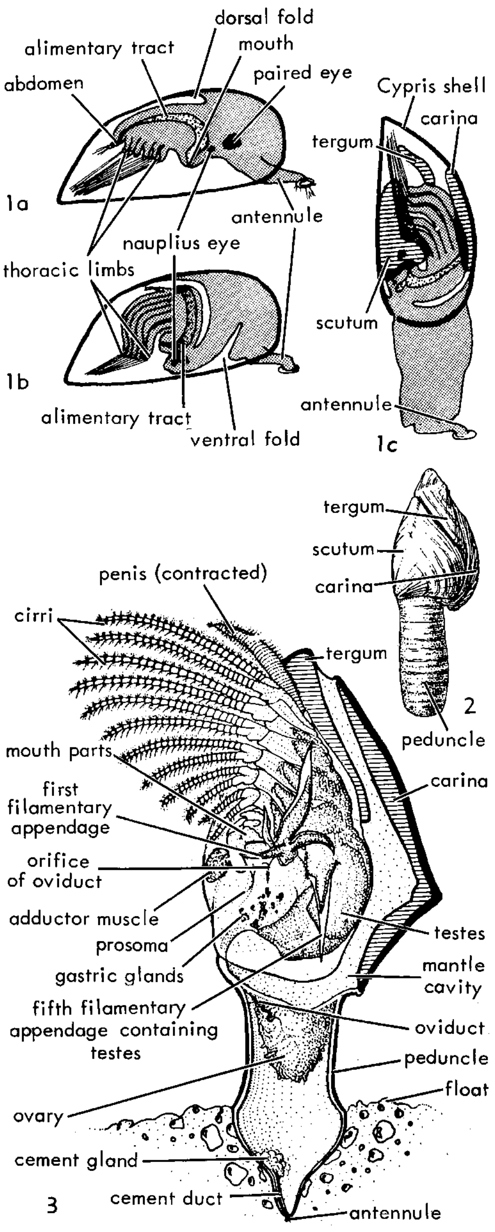

FIG. 21. Types of extant crustaceans—cirripeds.

1. *Lepas* sp., immature stages proving crustacean nature of cirripeds; *1a,b,* free-swimming cypris larvae, much enl.; *1c,* initial attached stage, much enl.
2. *Lepas anatifera,* goose-neck barnacle from North Sea showing stout, moderately flexible stalk, ×1.
3. *Lepas fascicularis,* lepadomorph thoracican barnacle from north Atlantic, with calcareous plates on right side of body removed to show enclosed body and thoracic appendages (cirri), ×1.8.

[*1-2,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *3,* from D. P. Henry in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960.]

Many copepods inhabit fresh waters, and it happens that the only known fossils occur in Miocene lake deposits. Despite what must have been vast numbers of marine Cenozoic forms, probable Mesozoic, and possible Paleozoic copepods, such representatives of the class are lacking in the paleontological record.

BRANCHIURANS

Branchiurans, unknown as fossils, are ectoparasites on marine and fresh-water fishes—hence are called fish lice. They have a disc-shaped cephalothorax 5 to 25 mm. in diameter with dorsal compound eyes and ventral suctorial cups for attachment to the host in some. The limbless abdomen lacks somite divisions.

CIRRIPEDS

The cirripeds are a varied group of highly modified crustaceans characterized by permanent fixation of adults, lacking compound eyes except in larval stages. In the order named Thoracica, which includes the barnacles and which alone is represented by fossils, the body, with head end downward, is enclosed by movable or somewhat firmly united calcareous plates (Fig. 21, 22). Six pairs of upwardly directed biramous thoracic limbs (called cirri) function in producing water currents by back-and-forth and inward-drawing movements which serve for gathering food particles carried to the mouth (Table 1). Abdominal somites are lacking.

Some barnacles attach themselves to the shells of sea turtles or to flippers, flukes, and jaws of whales (Fig. 22,*2*), as well as to

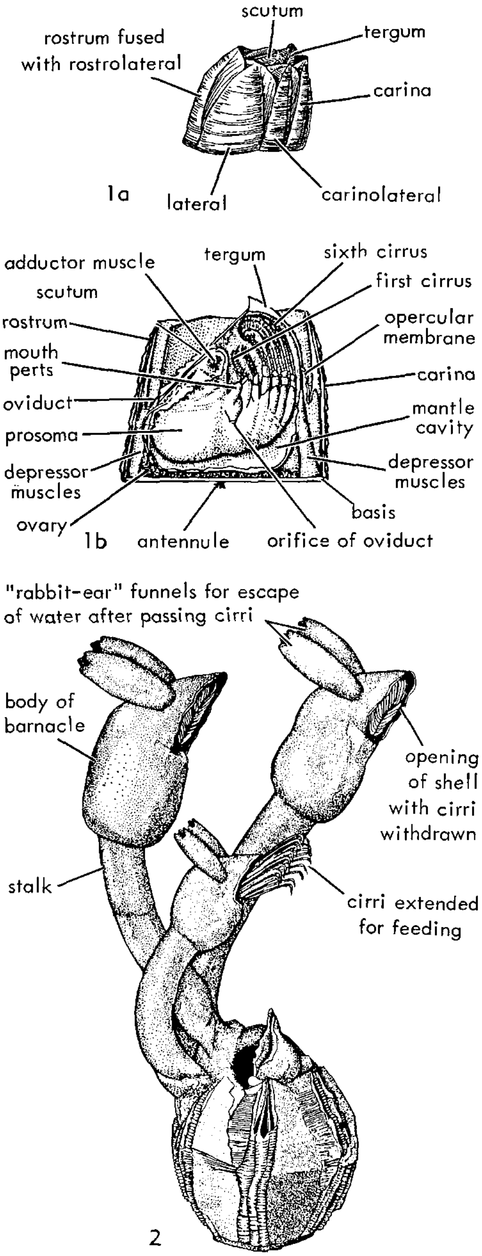

FIG. 22. Types of extant crustaceans—cirripeds.

1. *Balanus hameri,* balanomorph thoracican barnacle from north Atlantic; *1a,* side view of calcareous shell showing component valves, ×1; *1b,* same with part of shell removed to show body of cirriped within it, ×2.
2. Whale barnacles, which live attached to whales and are carried about by these hosts, illustrating a commensal rather than parasitic association; subglobular acorn barnacle *(Coronula diadema)* below and three rabbit-eared goose-neck barnacles *(Conchoderma auritum)* fastened to the acorn barnacle, ears oriented toward tail of swimming whale, ×0.7.

[*1a,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *1b,* from D. P. Henry in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960; *2,* from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill, publ., copyright 1949.]

some other marine animals, different kinds of barnacles showing high specificity not only in choosing particular hosts but in their location on the host. Because the uninvited crustacean travelers which are carried about in this manner do not derive nourishment from their host or seem to harm it in any way, these barnacles are not true external parasites but simply are benefitted by their life-long free ride in presumably food-rich waters.

Other groups of cirripeds are distinguished by lack of skeletal covers, some by less than six pairs of thoracopods, or none at all, and some by extreme adaptation for parasitic mode of life (e.g., *Sacculina,* which lacks an alimentary tract and has no appendages).

MALACOSTRACANS

Most highly developed, greatly varied, and generally considered most representative of the Crustacea are groups brought together in the class Malacostraca. Collectively, these are distinguished by the possession of compound eyes which in many are borne on stalks near front of the head, by a thorax composed of eight somites which typically is covered by a carapace (Fig. 17) (Table 1), and by an abdomen of six or seven somites, most of which generally bear pairs of appendages. Malacostracans vary widely in shape and size, ranging from diminutive forms only 2 or 3 mm. in length to the giant Japanese crab with 3.6 m. spread of its front limbs. They live in all sorts of environments, but chiefly in shallow seas not far from coasts. Relatively numerous as fossils, although much less so than ostracodes, their paleontologic record equals that of the ostracodes in extending probably from Lower Cambrian to Recent.

PHYLLOCARIDS

The phyllocarid malacostracans are characterized by the presence of a proportionally large bivalved carapace which may be hinged along the dorsal margin as in ostracodes or may lack such hingement. The carapace is not fused to any of the thoracic somites. Eyes are stalked. The thoracic limbs are all alike, consisting of biramous, usually foliaceous ventral appendages of the somites. The abdomen, which is relatively slender, has seven somites, with pleopods borne by all except the hindmost one. A telson with caudal furca is present (Table 1, Fig. 19,*8*). Leptostracans, which are the only extant phyllocarids, mostly do not exceed a length of 12 mm. in adults but some more than three times as large are known. Archaeostracans (L.Ord.-U. Trias.) may attain a length of 75 cm. Modern phyllocarids are chiefly inhabitants of shallow seas, but they range to a depth of at least 2,500 m.

EOCARIDS

Exclusive of the phyllocarids, all malacostracans are grouped together in the subclass Eumalacostraca, and of these the oldest and only division not represented by living forms comprises the Eocarida. Eocarids are caridoid (shrimplike) crustaceans with a moderately large carapace which is not fused to the thoracic somites (Fig. 17,*2,3*). It bears a single transverse groove. The thoracic limbs are biramous and closely similar to one another, with protopod consisting of a single segment. Diagnostic features are furcal lobes and a median articulated spine on the telson attached to the sixth abdominal somite (Table 1).

SYNCARIDS

The syncarids are mainly characterized by entire lack of a carapace, evidence from fossils, which include moderately common late Paleozoic and some Mesozoic forms, indicating that absence of this body cover is a primary feature, rather than secondary, as in certain isopods, amphipods, and cumaceans (Fig. 18,*3,4*). In different genera the eyes are stalked, sessile, or absent. The pereiopods are biramous and none are chelate or subchelate. A seminal receptacle may be present but no egg-carrying structures (oostegites) on appendages. Although modern syncarids are fresh-water crustaceans (excepting a single brackish-water species at mouth of the Amazon), Brooks (*Treatise,*

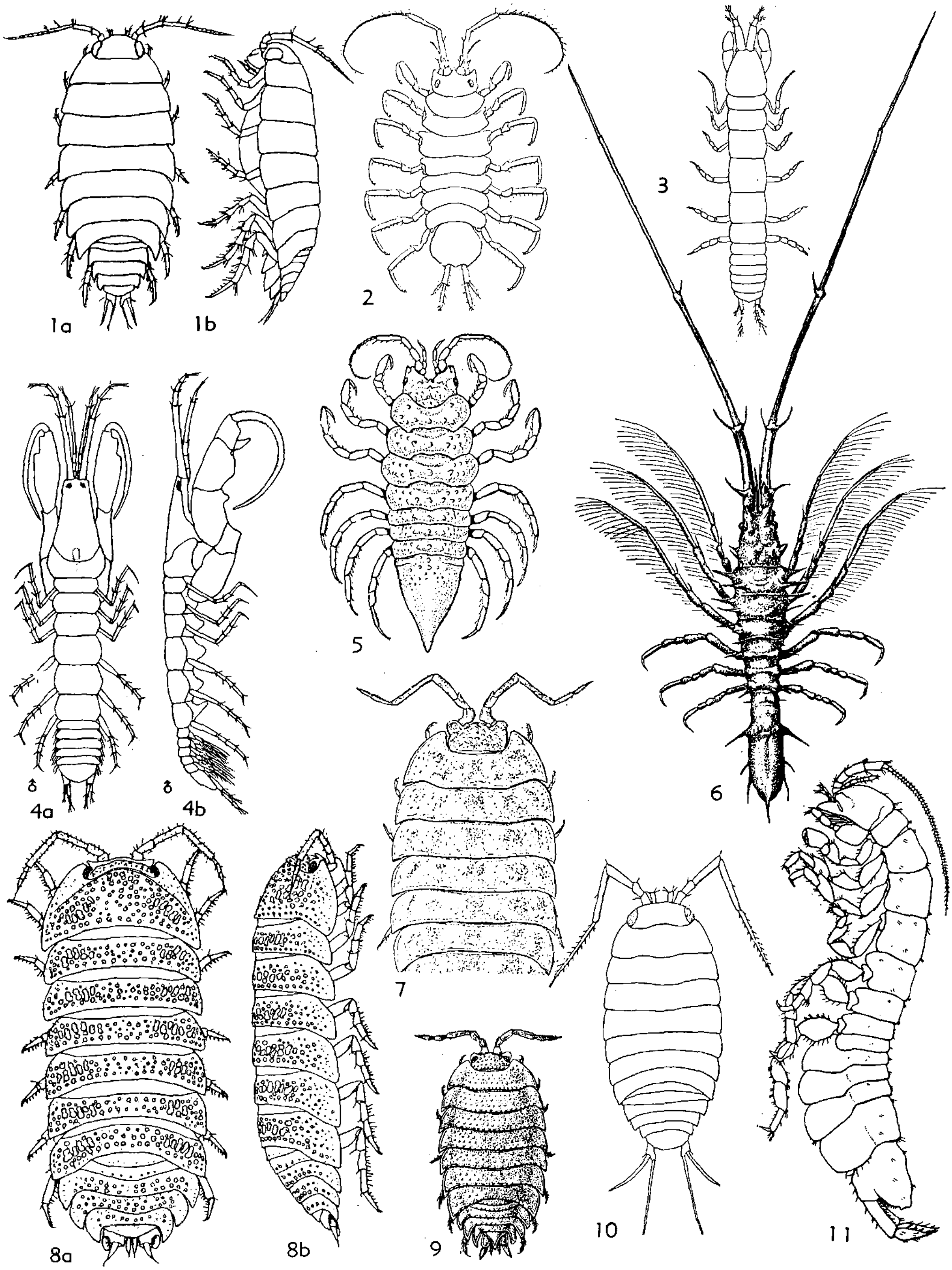

FIG. 23. Types of crustaceans illustrating diversity of groups, all extant—isopod and tanaidacean peracarids (Malacostraca).

1, 7-10. Oniscoid terrestrial isopods.——*1. Ligidium hypnorum,* inhabiting damp forests, northwestern Europe; *1a,b,* dorsal and side views of female, ×4.——*7. Porcellio spinicornis,* female from New York, ×3.——*8. Scleropactes zeteki,* female from Panama; *8a,b,* dorsal and side views, ×3.5.——*9. Porcellio scaber,* female from northern Europe, ×2.——*10. Ligidium*

p. *R*352) judges that nearly all Paleozoic forms undoubtedly were marine. The relatively indistinct differentiation of thorax and abdomen found in this group is a primitive character possessed by no other malacostracan.

PERACARIDS

A very large assemblage of malacostracans which includes most kinds not classed as decapods or stomatopods is placed in the superorder Peracarida. The most important peracarid groups are amphipods (nearly 4,000 extant species), isopods (approximately 3,000 Recent species) cumaceans (700 modern forms), mysidaceans (more than 500 extant species), and tanaidaceans (at least 350 living species). In addition, each of the mentioned divisions is represented by fossils, oldest of which are Permian isopods, cumaceans, and tanaidaceans (ignoring the order Anthracocaridacea, two Mississippian genera, tentatively classed as peracarids).

The chief common characteristics of the Peracarida are invariable fusion of the first thoracic somite to the cephalon, carapace (when present) never fused to more than four thoracic somites, peduncles of antennae typically three-segmented, mandibles with movable structure termed the lacinia mobilis in all but parasitic and highly specialized forms, first pair of thoracopods modified as maxillipeds, eggs and young nearly always carried in a marsupium formed by oostegites (Fig. 18,*1*,*2*). Comparative information on somites of peracarids and their appendages is given in Table 1. Peracarid eyes may be stalked or sessile, but at least two small subterranean species of minor groups (Spelaeogriphacea, Thermosbaenacea, Fig. *6-7*) are blind, as are several burrowing or cave-dwelling isopods and amphipods.

A majority of peracarid species are marine shallow-water crustaceans, but many descend to abyssal depths. Isopods, amphipods, and tanaidaceans are both marine and nonmarine, mysidaceans and cumaceans predominantly marine, and remaining minor peracarid groups restricted to continental waters.

MYSIDACEANS

Mysidaceans, because of their shrimplike form and possession of a well-developed carapace for protection of the head and thorax, are interpreted to be more generalized, and hence more primitive than other peracarid crustaceans. Commonly, adults range in length from 12 to 20 mm. (maximum 200 mm.). They have movable stalked eyes, biramous antennules, and antennae with scalelike exopods. The first one, two, or three (rarely four) thoracic somites are fused to the cephalon and appendages of the first one or two are modified to function as maxillipeds (Table 1, Fig. 18,*1*,*2*,*11*). Ramified gills occur at the base of thoracopods in some and abdominal limbs may function as swimming organs (pleopods). A well-defined tail fan is formed by a pair of uropods and median telson. The mysidaceans are widely distributed, essentially pelagic animals which commonly migrate vertically during day and night, but they also live on the sea bottom and even burrow into it temporarily. A very few are found in fresh waters. They

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FIG. 23. *(Continued from facing page.)*

longicaudatum, female from eastern USA, ×3.

2. Asellote marine isopod, *Janira alta,* from east coast of USA, dorsal view, ×3.3.

3. Marine tanaidacean, *Heterotanais limicola,* dorsal view of female from Massachusetts Bay, ×14.

4. Fresh-water tanaidacean, *Nototanais beebei,* taken from stomach of catfish in British Guiana; *4a,b,* dorsal and side views, ×25.

5-6. Valviferan marine isopods.——*5. Synidotea muricata,* from near-shore off Arctic coast of Alaska, ×11.7.——*6. Arcturus purpureous,* female from north Atlantic at depth of 900 m., ×2.5.

11. Phreatoicid fresh-water isopod, *Phreatoicus assimilis,* amphipod-like female from northern Europe, ×5.

[*1, 4, 8* from Van Name, 1936; *2-3, 5-7, 10* from Richardson, 1905; *9, 11* from W. T. Calman in Lankester, *Treatise on Zoology,* by permission, A. & C. Black, publ.]

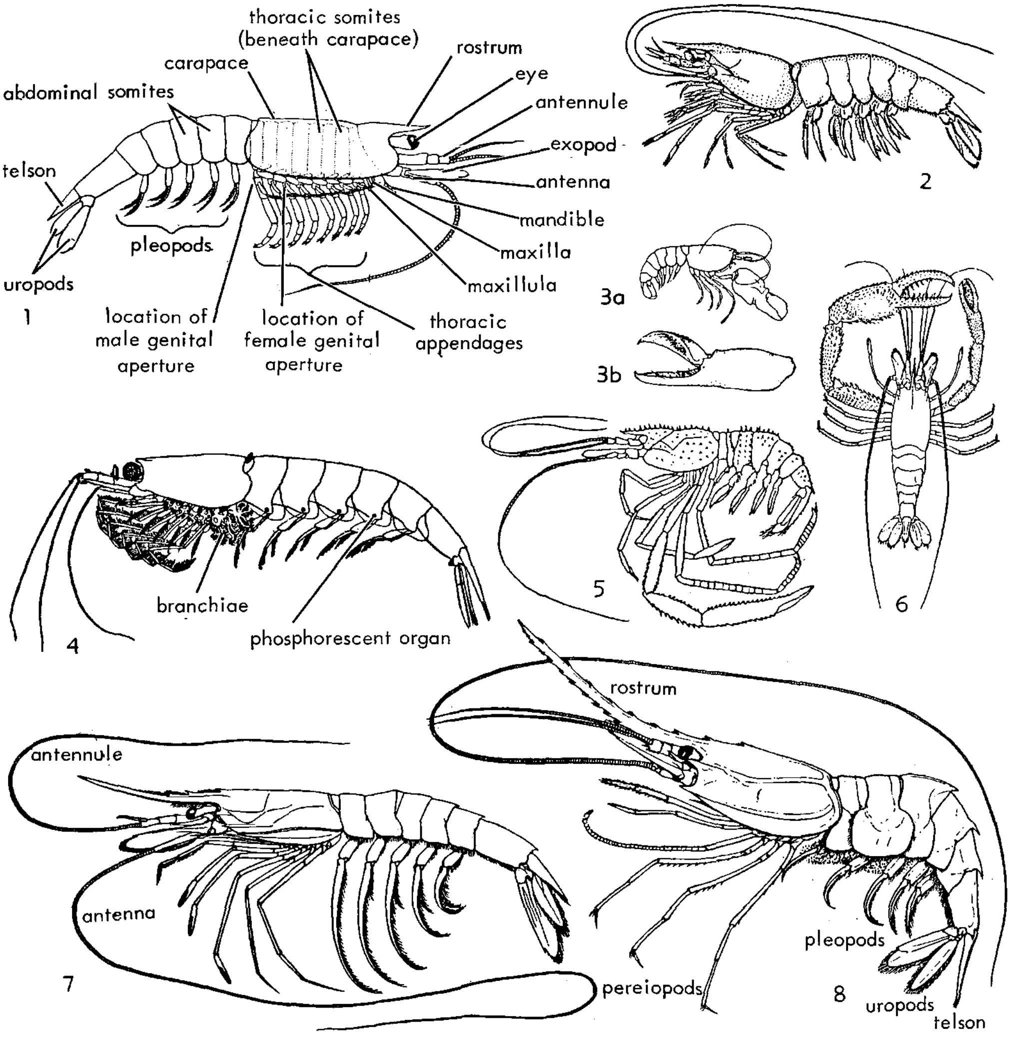

Fig. 24. Types of crustaceans illustrating diversity of groups, all extant eucarid Malacostraca.

1. Generalized macruran decapod showing morphological elements of exoskeleton, and "caridoid facies."

2. Penaeid prawn, *Penaeus setiferus,* jumbo shrimp abundant in warm-waters of Gulf of Mexico, ×0.25.

3. Snapping shrimp, *Alpheus heterochelis,* provided with over-developed first pair of pereiopods capable of making loud popping noises; *3a,* side view, ×0.5; *3b,* distal part of cheliped, ×1.3.

4. Euphausiid, *Meganyctiphanes norvegica,* wide-ranging pelagic crustacean characterized by phosphorescent organs on abdominal pleura and large light-sensitive eyes, ×0.8. Euphausiids are a main food source for whales.

5. Stenopodid shrimp, *Stenopus hispidus,* distinguished by prominence of third pair of chelate pereiopods, ×0.6.

6. Tropical fresh-water prawn, *Macrobrachium faustinum,* characterized by exceptionally long chelate second pereiopods and in some species large size (to length of 30 cm. or more), ×0.3.

7. Deep-sea penaeid prawn, *Aristeus coruscans,* with very elongate antennules and antennae, glands at base of latter emitting phosphorescence, ×0.3.

8. Caridean prawn, *Heterocarpus alphonsi,* marked by prominent spinose rostrum, first pereiopods developed as prominent maxillipeds, third pair with multiarticulate distal parts, and humped abdomen, ×0.7.

[*1, 7-8,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *2-3; 5-6,* from F. A. Chace in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960; *4,* from Watase in Borradaile & Potts, *The Invertebrata* (4th edit., 1963), by permission, Cambridge University, publ.]

are mostly carnivorous predators and scavengers, but also are filter-feeders and plant-eaters. Chiefly Recent, a few fossil forms are known from Triassic and Jurassic formations.

CUMACEANS

A well-developed carapace covers the anterior part of the thorax and projects in front of the head of cumaceans. It is fused to at least the first three thoracomeres, in some also to the fourth, and rarely to fifth and sixth somites. Laterally expanded parts of the carapace provide gill chambers. Eyes are sessile (when present) and usually joined together as a single median sight organ. The antennules may be biramous, the antennae without exopods, and the first three thoracopods are modified as maxillipeds (Table 1, Fig. 18,*5*). The slender abdomen is sharply set off from the thorax, its somites limbless in females but some of them bearing pleopods in males. A pair of slender spikelike uropods and telson, which may be absent, do not form a tail fan.

Cumaceans mostly range in length of adults from 1 to 12 mm., but a few of them reach a length of 35 mm. They are marine, near-coast to abyssal bottom-dwellers which burrow in mud or sand with the front of the carapace protruding. A few brackish- and fresh-water species are known. Their stratigraphic range is Upper Permian to Recent.

TANAIDACEANS

The body of tanaidaceans is cylindrical or somewhat depressed and nearly uniform in width throughout. It is diminutive, for very few adults are more than 10 mm. long, not counting forward and backward projecting appendages. As a group, these peracarids are distinguished by shortness of their carapace, which extends from the head over only two thoracic somites (Fig. 18,*9*). It is fused to these somites and lacks lateral expansions such as those of cumaceans but provides very small gill chambers. If eyes are present, they are located on short immovable stalks. The first pair of thoracopods are developed as maxillipeds; the second ones are chelate, generally with large chelipeds. Although the abdomen is abbreviated, its somites are distinct;[1] pleopods may be present or absent and the pair of terminal filiform uropods does not form a tail fan (Table 1).

Tanaidaceans are almost exclusively sea-bottom-dwellers inhabiting burrows. They are distributed from strand lines to depths of 6,000 m. A few forms are found in brackish waters. The group ranges from Permian to Recent.

ISOPODS

In isopods a carapace has disappeared, so that the head with its sessile eyes and all somites are exposed. Body shapes are many, but nearly all are depressed. Limbs of the first thoracic somite (or rarely first two) function as maxillipeds and those of the remaining seven are nonchelate uniramose pereiopods (Table 1, Fig. 19,*2*). Most isopods do not have the equal legs called for by their name. Commonly the pereiopods are divided into groups, the first three being directed forward, the fourth one sideward, and the fifth to seventh backward (Fig. 23,*1,9*) or they may display a different arrangement (Fig. 23,*2-6,8,11*). Also, these groups tend to be specialized in different ways. The coxopodites of the thoracic limbs may be fused with the pleura so that in females the plates (oostegites) which form a brood pouch appear to arise from the sterna. Appendages of the abdominal somites of isopods are pleopods with broad platelike endopodites and exopodites adapted both for swimming and respiration. Pleopods may develop air-breathing pseudotracheae in terrestrial forms. A feature of some isopods is ability to roll up their body into a ball with only the dorsal side of the somites exposed, the ventral side and appendages being tucked neatly inside.

Isopods are both predatory and scavengers with biting mouth parts. Some feed on wood and sea weeds. A few kinds infest fishes and other crustaceans as parasites.

Typical isopods range in length from 1 to 20 mm. Greatest size is attained by

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[1] Last somite (6th) is fused with telson, as in isopods.

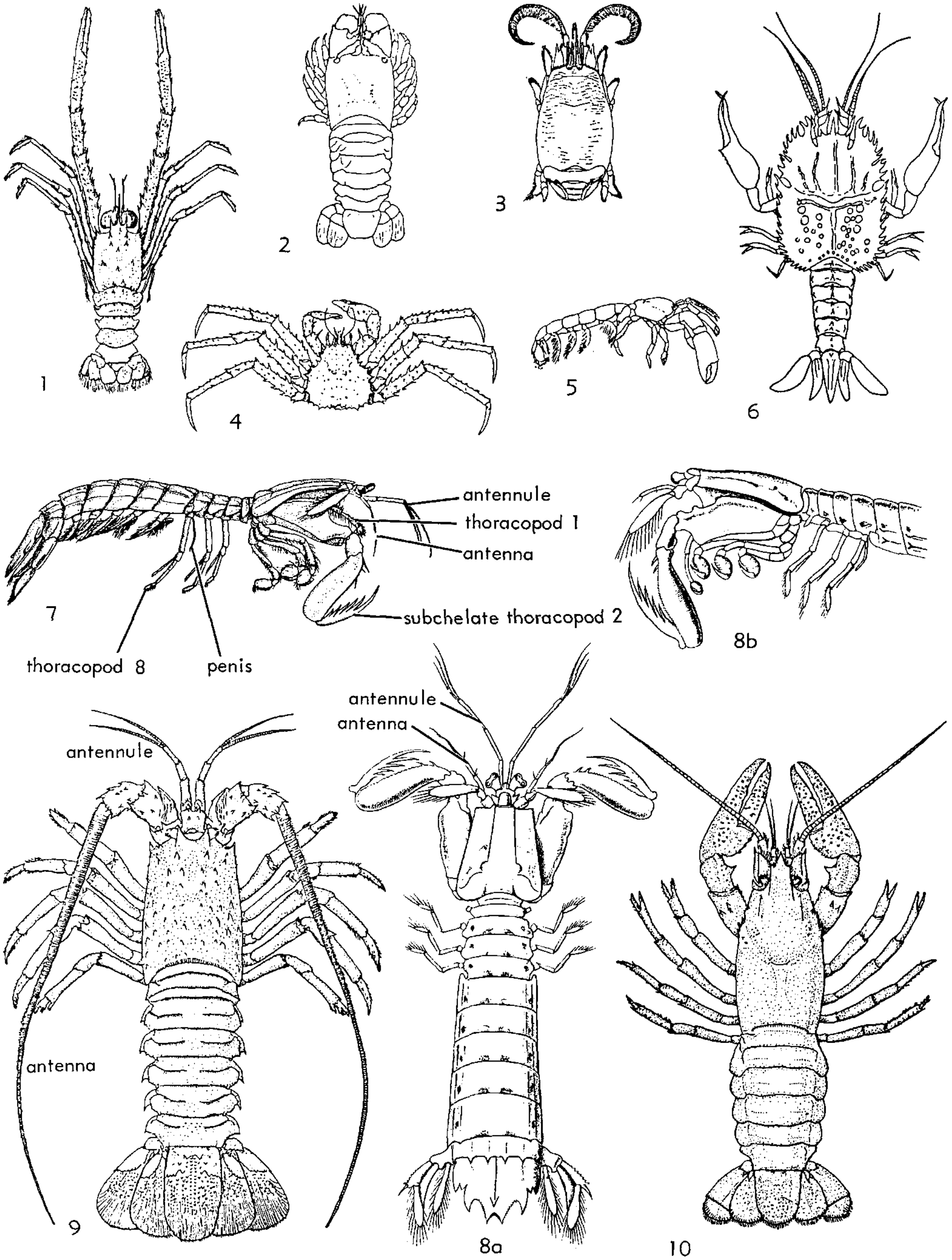

FIG. 25. Types of crustaceans illustrating diversity of groups, all extant Malacostraca.

1-2, 5-6, 9-10. Lobster-like decapods.——*1.* Galatheid anomuran, *Munida evermanni,* marine form with long slender chelipeds, symmetrical abdomen with broad tail fan used for swift backward swimming, ×0.7.——*2.* Shovel-nosed Spanish lobster, *Scyllaridia aequinoctialis,* marked by absence of rostrum and chelae, stoutly armored, ×0.15.——*5.* Mud shrimp, *Cal-*

an abyssal isopod *(Bathynomus)*, some individuals of which range from 200 to 300 mm. in length.

The recorded geologic range of isopod peracarids is Triassic to Recent.

AMPHIPODS

The amphipods, commonly called sandhoppers on beaches and scuds in aquatic environments, correspond to isopods in lacking a carapace and in having unstalked sessile eyes. They are medium-sized crustaceans (adult length 3 to 12 mm., maximum 140 mm.) which prevailingly differ from isopods in the laterally compressed form of their body, rather than dorsoventral flattening. The first and second thoracic somites are fused to the cephalon[1] (Fig. 18,*8*; 19,*7*). The thoracic limbs lack exopodites, the first pair being modified as maxillipeds, the second and third pairs usually chelate or subchelate and prehensile, and others having more than one form (Table 1). In general, amphipods are poor walkers. The abdominal appendages generally consist of three pairs of multiarticulate pleopods next behind the thorax and others resembling uropods not developed as a fan tail.[2] The last three pairs of abdominal limbs are used by sandhoppers to kick the ground in jumping.

Amphipods are most abundant in marine environments, ranging from the shore line to abyssal depths. Approximately 15 percent of described species inhabit fresh waters of continents and islands distributed from virtual sea level to an altitude of at least 4,000 m. Some 80 species are air-breathing forms. Excluding some Devonian tracks and trails doubtfully attributed to amphipods, the geologic distribution of amphipods is recorded from Eocene to Recent.

EUCARIDS

Malacostracans with the carapace fused dorsally to all somites of the thorax are classified as eucarids, chief kinds of which are the familiar shrimps, prawns, crayfishes, lobsters, and crabs belonging to the Decapoda (Fig. 17,*1*; 24,*1-8*; 25,*1-6,9-10*; 26,*1-12*; 27,*1*). Eucarids differ from the peracarids in lacking brood pouches formed by oostegites in females and absence of the movable structure called lacinia mobilis on the mandible, as well as in more obvious morphological distinctions. All eucarids have stalked eyes. Besides the decapods, crustaceans designated as euphausiaceans are included in this assemblage.

EUPHAUSIACEANS

Euphausiaceans are medium-sized (adult length 20 to 30 mm., maximum 90 mm.) shrimplike forms (Fig. 24,*4*), not very numerous as to species (about 85 in two families) but abundant enough in all oceans to furnish the major food of whales, one of which may gulp down two or three tons

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[1] In Caprellidea, but only first thoracic somite in Gammaridea.

[2] Except in Hyperiidea, for example.

FIG. 25. *(Continued from facing page.)*

lianidea laevicauda, thin-shelled burrower with large chelate first pereiopods, ×0.3.——*6*. Blind, deep-sea eryonid decapod, *Polycheles crucifer,* with relatively thin shell, carapace laterally widened and dorsally flattened, ×1.1.——*9*. Commercially important spiny lobster or langouste, *Panulirus interruptus,* heavily armored decapods lacking rostrum and chelae, ×0.12. ——*10*. Fresh-water crayfish, *Orconectes limosus,* with firm shell, large chelipeds, and short rostrum, ×0.8.

3-4. Anomura.——*3*. Mole crab, *Emerita talpoida,* shallow-sea mud-burrower marked by elongate oval carapace and short nonchelate limbs, ×0.9. ——*4*. Free-moving king crab, *Lithodes maja,* relative of hermit crabs with asymmetrically arranged abdominal plates in females, living on well off-shore sea bottoms, ×0.6.

7-8. Stomatopods, characterized by powerful raptorial subchelae of second pereiopods, posterior thoracic somites resembling those of elongate abdomen.——*7*. *Squilla mantis,* side view of male, ×0.7.——*8*. *Squilla desmaresti; 8a,b,* dorsal and side views of male, ×0.8.

[*1-6, 9-10,* from F. A. Chace in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960; *7,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *8,* from A. Gerstaecker in H. G. Bronn, *Klassen und Ordnungen des Tierreichs,* by permission, Akademische Verlagsgesellschaft, publ.]

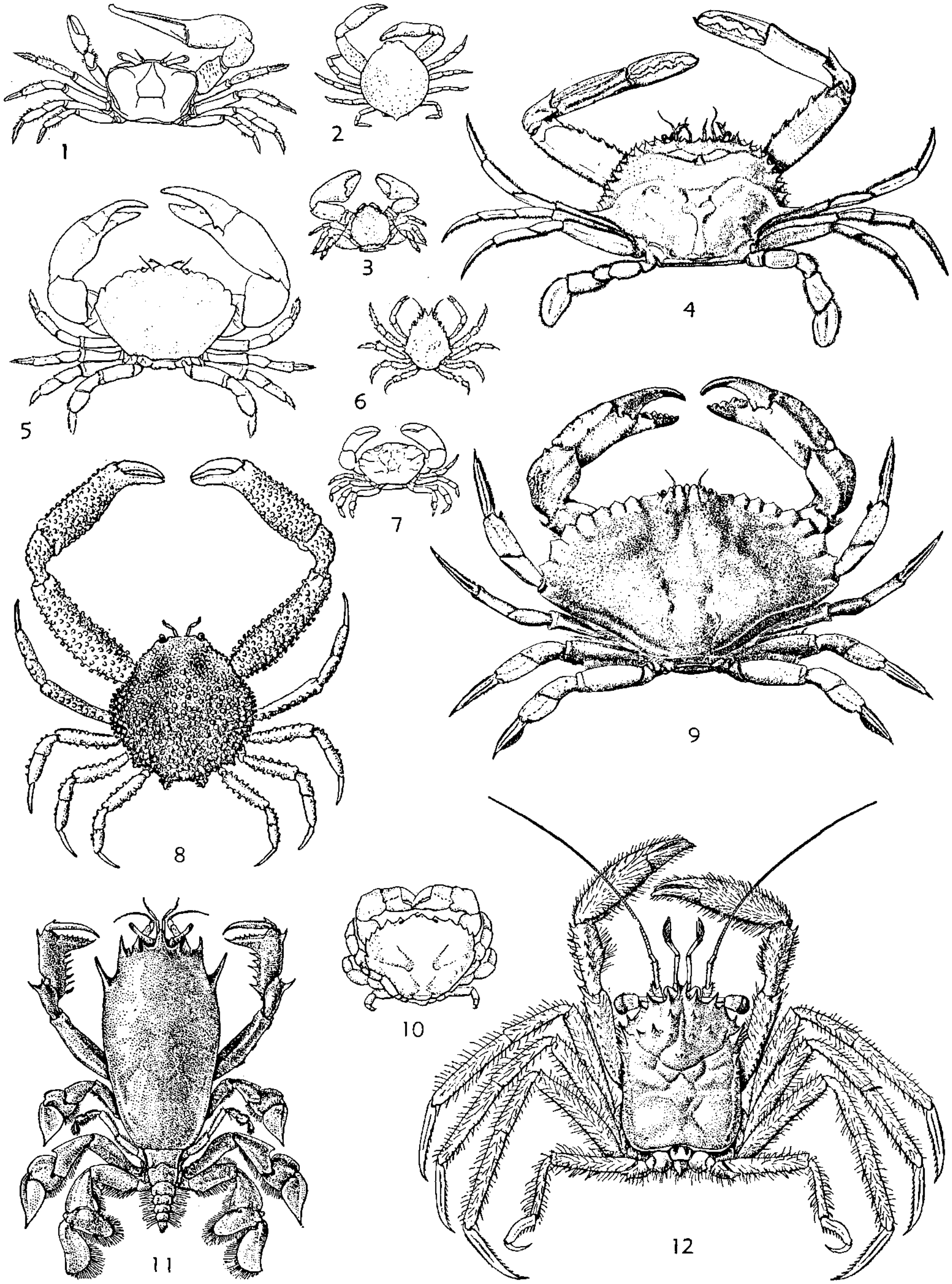


FIG. 26. Types of crustaceans illustrating diversity of groups, all extant eucarid Malacostraca (decapods—crabs).

1. Fiddler crab, *Uca pugilator,* inhabitant of sandy sea shores distinguished by strongly disparate chelipeds, ×0.6.

2. Purse crab, *Persephona punctata,* oxystomate form characterized by ovoid carapace, ×0.2.

3. Porcellanid crab, *Petrolisthes tridentatus,* so-of them for a meal. They also furnish food for seals, penguins, petrels and other creatures of the sea far from land. Euphausiaceans are found in neritic belts but most of them are pelagic, living at depths to more than 2,000 m. in daytime and near the ocean surface at night. This pronounced diurnal migration and the possession of phosphorescent organs are distinctive attributes of this and some other groups.

The carapace of euphausiaceans usually bears a transverse cervical furrow and extends forward in a short rostrum. Laterally it does not form branchial chambers, and thus the feather-like gills of the biramous swimming thoracopods are plainly visible from the side. Anatomical features that differentiate euphausiaceans from decapods are small size of the maxillary exopodite (scaphognathite) and lack of maxilliped adaptation of any anterior thoracopods, Pleopods of the moderately elongate abdomen are biramous; the terminal somite bears a small tail fan.

The euphausiaceans are filter-feeders, living on planktonic diatoms and other microorganisms or they are raptorial carnivores. Before reaching adult size, they pass through numerous larval stages, one or two years being required for this development.

No undoubted fossil euphausiacean has been discovered.

DECAPODS

The decapod eucarids are so named because limbs of the thorax behind anterior ones modified to form maxillipeds consist of five pairs. The maxillipeds comprise three limb-pairs (Table 1) and in front of them the large exopod (scaphognathite) borne by the maxilla is a distinguishing decapod character. The ten legs behind the maxillipeds are uniramous appendages adapted for locomotion, either crawling or swimming, except that in many decapods (e.g., lobsters, crayfishes, crabs) the first pair of limbs bear chelae which are incapable of aiding locomotion (Fig. 17,*1;* 24,*2-8;* 25,*1-6, 9-10;* 26,*1-12*). Uncommonly, other limbs may be similarly modified (e.g., rearmost two pairs in hermit crabs) (see Fig. 37,*1*). In relatively elongate (macrurous) decapods (Fig. 17,*1*), any of the five rear pairs of thoracopods may be chelate (Fig. 24,*2-3, 5-8;* 25,*5-6,10;* 28,*13*); the anterior five somites of their extended abdomen bear pairs of biramous pleopods and the sixth (terminal) one supports laterally widened uropods and a telson which together make a tail fan (Fig. 17,*1;* 28,*13*). So-called brachyurous (short-tailed) types, represented by a host of crabs and some other forms, commonly have a cephalothorax which is dorsoventrally flattened, longitudinally shortened, and laterally widened. Their abdomen is much reduced, typically lacking a fan tail (Fig. 26).

Decapods include marine forms, many of them pelagic (not only shrimplike macrurous types but swimming crabs), species most commonly found in brackish waters, abundant inhabitants of fresh-waters, and not a few terrestrial air-breathers. Some are

FIG. 26. *(Continued from facing page.)*

called rock-slider distinguished from true crabs by much-reduced and chelate fifth pereiopods and well-developed tail fan, ×0.7.

4. Marine swimming crab, *Portunus xantusii,* with hind pair of pereiopods paddle-like, ×0.5.

5. Stone crab, *Menippe mercenaria,* edible form with stout chelae, found along sea shores, ×0.13.

6, Spider crab, *Mithrax acuticornis,* slow-moving shallow-water marine form, known also as decorator crab because of habit of attaching seaweeds and sessile invertebrates to dorsal side of its carapace for concealment, ×0.3.

7. Mud crab, *Eurypanopeus abbreviatus,* small shore crab resembling stone crabs, ×0.5.

8. Oxystomatous crab, *Randallia agaricias,* with triangular mouth frame extended forward over epistome, ×1.3.

9. Cancroid crab, *Cancer productus,* relatively large commercially important marine form, ×0.3.

10. Dromiid crab, *Dromia erythropus,* with hindmost pereiopods modified for holding sponges, tunicates, or bivalves over carapace for concealment, ×0.13.

11. Raninoid crab, *Raninoides louisianensis,* primitive burrower with narrow extended abdomen and most limbs modified for digging, ×0.7.

12. Homolid crab, *Homola barbata,* with subrectangular carapace, ×0.7.

[*1-3, 5-7, 10,* from F. A. Chace in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960; *4,* from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill, publ., copyright 1949; *8-9, 11-12,* from Rathbun, 1925, 1930, 1937.]

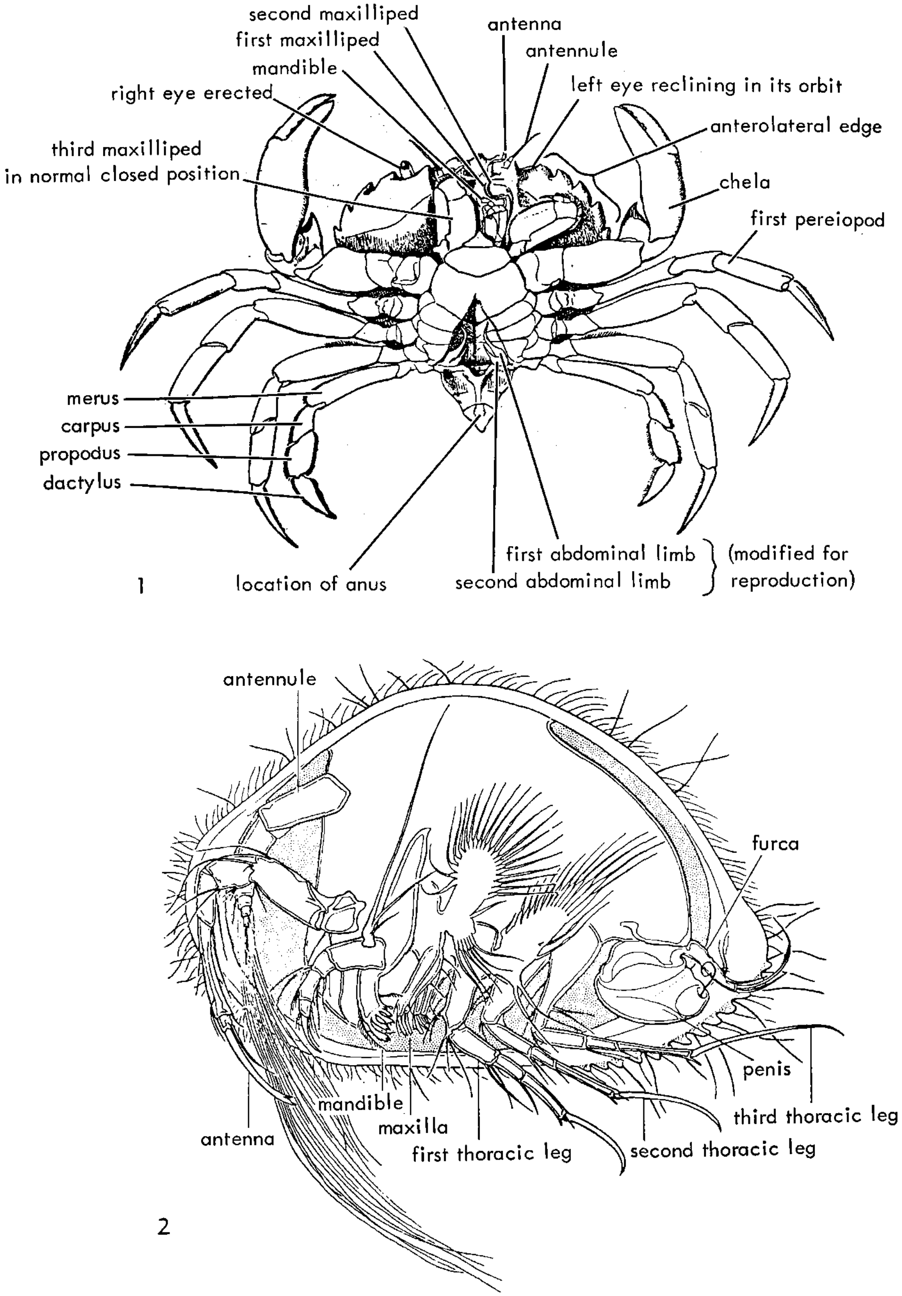


FIG. 27. Morphology of Crustacea—appendages.

1. Ventral view of shore crab, *Carcinus maenas*, showing diversely formed limbs, including abdominal ones modified for reproduction, visible only by turning abdomen backward from normal tucked in position, ×1.
2. Side view of marine podocopid ostracode, *Bairdia frequens*, with left valve removed to show appendages of male, mostly concealed within carapace, ×65.

[*1*, from Shipley & MacBride in Borradaile & Potts, *The Invertebrata* (4th edit., 1961), by permission, Cambridge University Press, publ.; *2*, from Kesling, 1961, *Treatise on invertebrate paleontology,* Part Q.]

burrowers and some can climb trees. True crabs (about 4,500 Recent species) slightly outnumber all other decapods combined. The known geologic distribution of decapods ranges from Permotriassic to Recent.

Morphological features of this very important group of crustaceans are described and illustrated in detail in the chapter on decapods by GLAESSNER (p. *R*401). For comparison with other assemblages which are surveyed briefly here as introduction to systematic treatment of the various divisions of Crustacea, it is sufficient to provide selected illustrations, including some with labeled parts of the exoskeleton (Fig. 27,*1*).

HOPLOCARIDS

The Hoplocarida are comparable to the Eucarida in containing crustaceans of larger than average size and in being highly developed in morphological features. Extant hoplocarids, all of which are known as stomatopods, range in length of adults from approximately 20 mm. to more than 300 mm. (1 foot); two kinds of late Paleozoic hoplocarids, called palaeostomatopods, have lengths of 3 and 13 mm. Stomatopods include fewer than 200 described species, as against more than 8,600 species of modern eucarids.

Stomatopods have an elongate, narrow body like that of a flattened caterpillar. Their shallow carapace is formed by fusion of the cephalic cover with that of the anterior three thoracic somites. Head somites bearing the large stalked and movable eyes and the antennulae are free, being visible in front of the carapace. Four thoracic somites behind the carapace also are exposed, as are the six abdominal ones, last of which bears a tail fan composed of uropods and a telson (Fig. 25,*7-8*).

Mouth parts consist of strongly calcified mandibles, small flattened maxillules, and much larger maxillae which are also flattened plates. Anterior thoracopods are not modified as maxillipeds. Instead, the first pair are slender hairy appendages, probably used for cleaning. The second thoracic legs are very strong and heavy raptorial weapons with distal claws turned back like blades of a penknife (subchelae) (Fig. 25,*7-8*; 29,*1*). This claw and limb closely resemble the distinctive corresponding structures of a praying mantis, and accordingly, the stomatopods commonly are called mantis shrimps. In several species the claws and apposed penultimate limb segment are provided with fixed and movable sharp spines, on which prey caught by the claws is impaled and easily held. The next three pairs of thoracopods are shorter and more slender than the second pair; they also are tipped with raptorial claws used for cutting up food and carrying it to the mouth. The last three thoracic limbs are walking legs which lack subchelae. The first five abdominal somites bear pairs of pleopods (Fig. 25,*7*).

All known kinds of stomatopods, except for representatives of four genera found in Jurassic and Cretaceous rocks, live in present-day seas.

GENERAL MORPHOLOGY

The body of crustaceans is composed of a linear succession of divisions termed **somites** (or metameres), each of which generally is somewhat depressed or compressed, rather than circular in transverse section (Fig. 17). Their number varies widely (Table 1), as does also fusion together of different groups. The dorsal part of the exoskeleton surrounding a somite is called **tergum** (or tergite), the ventral part **sternum** (or sternite), and the part on either side **pleuron** (or epimere). The pleura may be extended downward to protect appendages borne by the somites. More or less distinctive groups of somites having characters that differ from one another commonly are defined as separate **tagmata** (or regions). These comprise the **head** (or

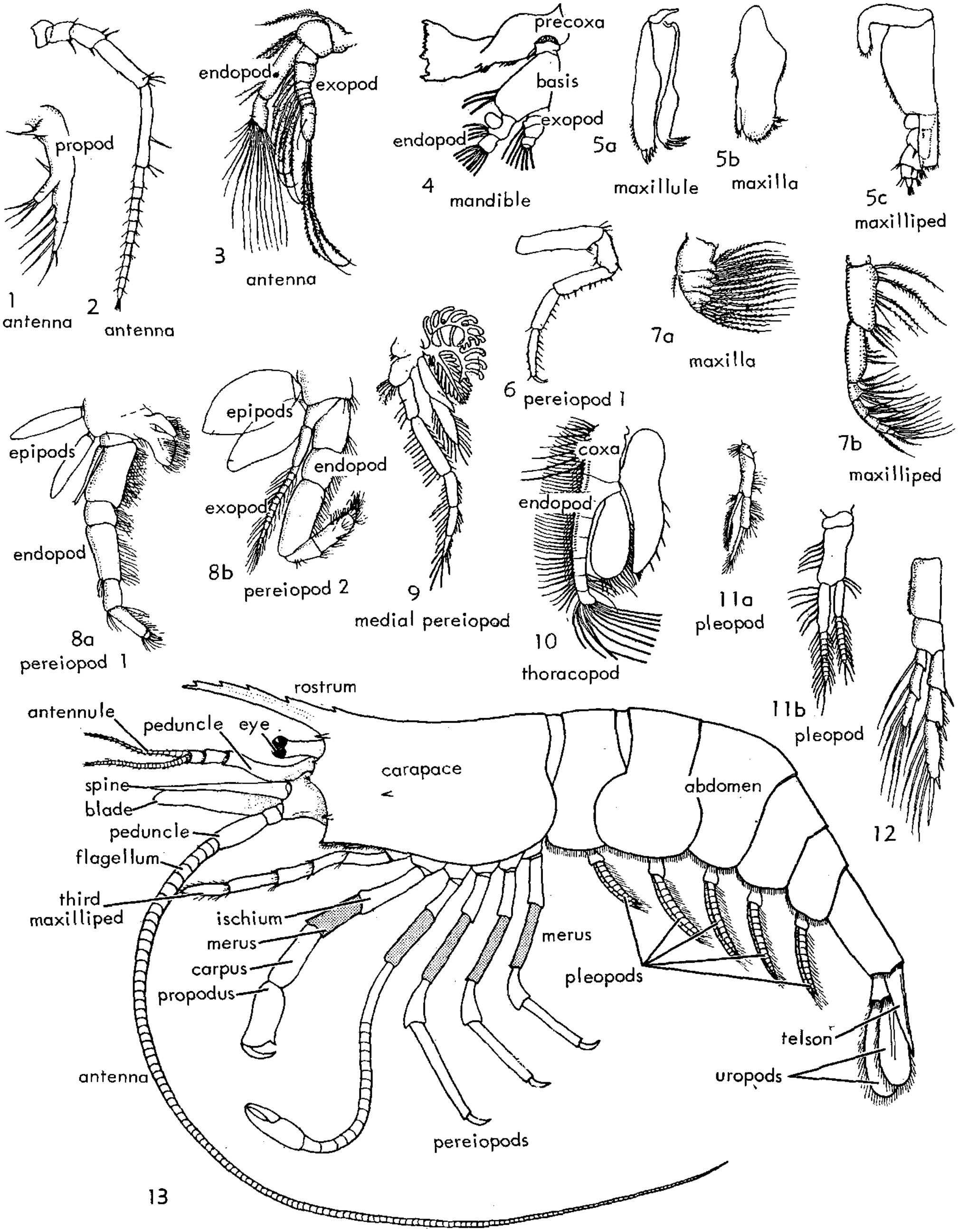


FIG. 28. Morphology of Crustacea—appendages.

1. Limb (antenna) of second pair of naupliar appendages of branchiopod *Triops* (notostracan), enl.

2,5-6. Appendages of terrestrial isopod, *Ligidium hypnorum,* enl.——*2,5.* Tactile (antenna) and food-working (maxillule, maxilla, maxilliped) appendages of head region.——*6.* Walking limb (pereiopod).

3-4,7,12. Head and thoracic appendages of copepod, *Calanus* sp., enl.——*3.* Sensory biramous head appendage (antenna).——*4,7.* Food-working head appendages (mandible, cephalon), **thorax** (or pereion), and **abdomen** (or pleon), or the first two may be united as a **cephalothorax.** Tergites fused together may form a **carapace** of variable size and shape, in some crustaceans (e.g., ostracodes, phyllocarids) having the form of a hinged or hingeless bivalve shell.

HEAD REGION

The simplest sort of head region in crustaceans is seen in the characteristic larva of the group, known as the **nauplius** (see Fig. 35,*1a*). It consists of fused somites which bear three pairs of appendages, two (antennules, antennae) in front of the mouth and one (mandibles) behind it. A single compound median eye is located anteriorly. In more advanced stages two additional somites with appendages termed maxillules and maxillae become coalesced with the one carrying the pair of mandibles. Thus, counting the embryonic frontmost somite **(acron)** with eye or eye lobes but no appendages, the crustacean head region comprises basically three preoral and three postoral somites, the one with maxillae being rearmost. In several crustacean groups (e.g., copepods, isopods, amphipods, decapods), however, anterior trunk somites become joined to the head and their appendages, differentiated as maxillipeds, aid in feeding (Fig. 28,*5c,7b*) (Table 1). The separation of head from thorax is then indistinct, or at least quite arbitrary. Because the maxilliped-bearing somites usually show features of transition to those behind them and because the skin fold forming the carapace first arises from the maxillary somite, the true head of crustaceans is held to exclude somites behind the maxillae-bearing one.

A furrow (mandibular groove) immediately behind the mandibles persists in some crustaceans (e.g., *Chirocephalus, Triops*—branchiopods, *Mysis*—malacostracan), setting off the three somites with appendages of the nauplius head from those bearing maxillules and maxillae. Another furrow delimits the head and thorax in some forms. A median forward-projecting part of the carapace in many crustaceans is termed the **rostrum** (Fig. 17,*1*).

THORAX AND ABDOMEN

Unlike somites of the head region which generally are similar in nature, containing the principal sense organs and structures used in feeding, somites of the thorax and abdomen are dissimilar in various ways and degrees (Fig. 17-20, 23-27). Commonly those of the thorax bear limbs, whereas abdominal somites carry a different sort of limbs or are limbless. The boundary between thoracic and abdominal regions may be sharply marked by changes in shape of the somites and their appendages, or it may be difficult to define consistently and clearly. Generally, the thorax is considered to extend backward to include the somite bearing the male genital aperture (Table 1). The number of combined postcephalic somites ranges from one or two in the limbless stump of some ostracodes to more than 60 in some branchiopods. The terminal somite of the abdomen very commonly bears a spikelike telson and associated with this may be a pair of caudal rami forming the so-called **caudal furca.** Also, in eumalacostracans appendages (uropods) expanded in leaf-shaped manner constitute part of a tail fan, useful as rudder and as propelling organ for backward swimming.

FIG. 28. *(Continued from facing page.)*

maxilla, maxilliped).——*12.* Swimming appendage of thorax (thoracopod).

8. Thoracic appendages (pereiopods) of fresh-water syncarid malacostracan, *Anaspides tasmaniae,* enl.

9. Pereiopod of marine euphausiacean (Malacostraca), enl.

10. Thoracic limb of marine leptostracan, *Nebalia bipes* (Malacostraca), enl.

11. Swimming appendages of crayfish, *Astacus,* enl.

13. Side view of caridean prawn, *Pandalus* (marine malacostracan) showing skeletal morphology, especially varied nature of appendages borne by head region, thorax, and abdomen, approx. ×1.

[*1, 3, 7-8, 12,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *4, 9-11,* from Borradaile & Potts, *The Invertebrata* (4th edit., 1963), by permission, Cambridge University Press, publ.; *2, 5-6,* from Van Name, 1936; *13,* from Schmitt, 1921.]

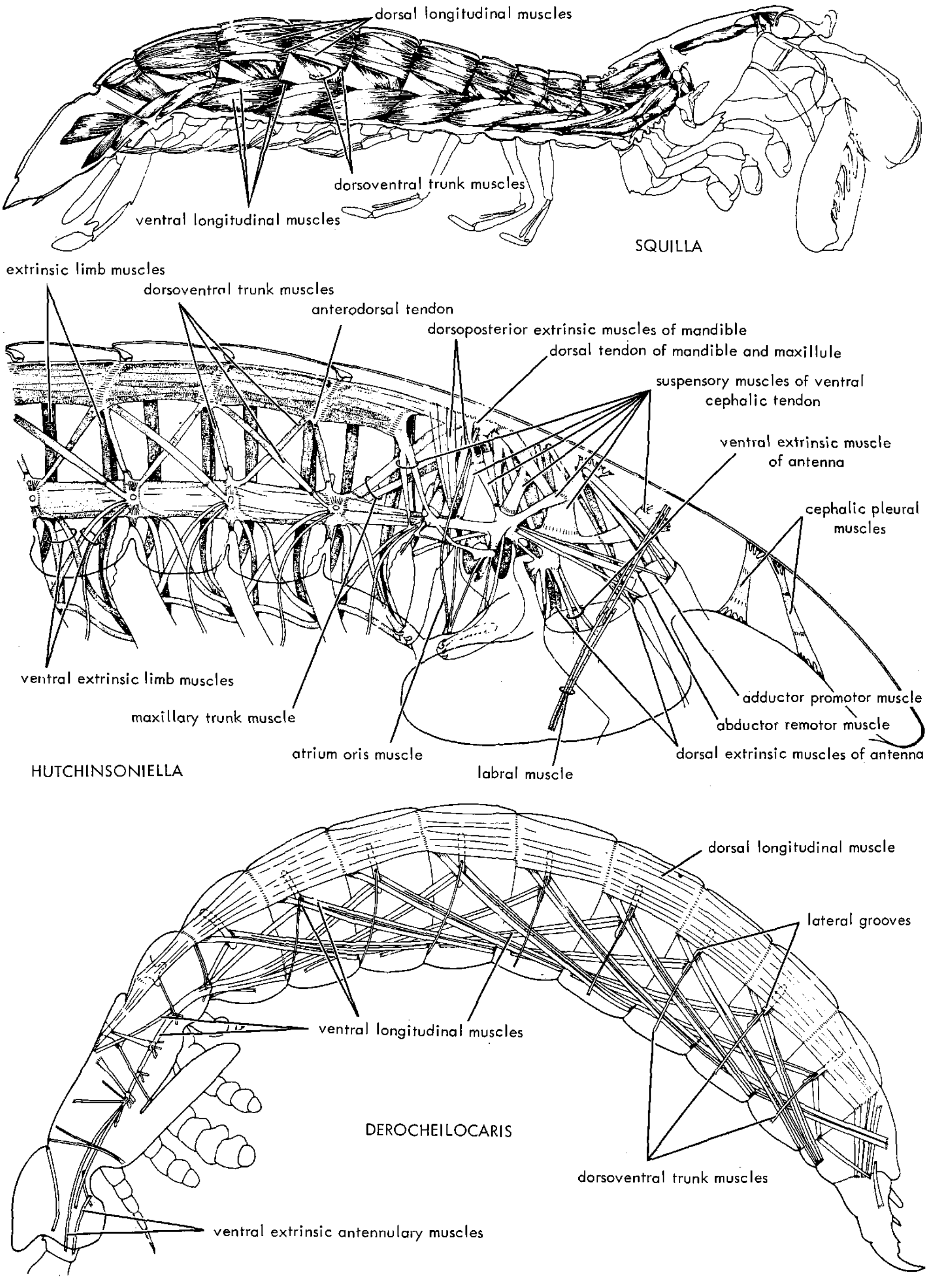


FIG. 29. Morphology of Crustacea—muscle systems in advanced and relatively simple, primitive examples (from Hessler, 1964).

1. Stomatopod malacostracan, *Squilla empusa,* medial view of left side showing trunk musculature, approx. ×1.

2. Cephalocarid, *Hutchinsoniella macracantha,* left half of cephalon and anterior part of thorax viewed from mid-line showing trunk muscula-

APPENDAGES

The paired appendages of crustaceans typically are biramous, with outer **(exopod)** and inner **(endopod)** branches joined to a common stem **(protopod),** but some (e.g., antennules of many but not all forms) may be uniramous (Fig. 17, 28). Prevailingly, the appendages are relatively slender and these represent the type named **stenopodium,** which commonly is well jointed, with few or numerous segments. Broader and flatter limbs, such as characterize the thorax and abdomen of many branchiopods, have a thin cuticle which allows movement without need for joints; this type is called **phyllopodium.** Outward from the body the segments of well-jointed appendages are differentiated as **coxa, basis, ischium, merus, carpus, propodus,** and **dactylus,** or where very numerous and similar to one another (e.g., antennules, antennae, exopods of swimming appendages) they are not separately indicated (Fig. 27,*1;* 28,*13*). The endopods of crustacean limbs may be generalized in form, but mostly they are modified to serve a wide variety of functions. Among these are sensory perception, locomotion, respiration, prehension and comminution of food, sex recognition and attraction, reproduction, incubation of eggs and larvae, self-protection, and nearly all others that pertain to successful existence. Thus, the possession and use of appendages are prime requisites of crustaceans.

Names given to crustacean appendages depend to some extent on their form and function, but mostly take account also of their location. In the head region, from the front backward, the paired appendages are the sensory antennules and antennae (Fig. 17; 28,*1-3,13*), followed behind the mouth by the food-working mandibles, maxillules, and maxillae (Fig. 17; 28,*4-5,7a*). The food-handling work of the three last-mentioned pairs is done by their proximal segments **(gnathobases).** Appendages of the thoracic region are collectively designated as **pereiopods** and **thoracopods** (Fig. 17; 27,*1;* 28, *6,8-10,13*). The anterior thoracopods in some crustaceans (termed **maxillipeds**) aid in feeding (Fig. 28,*5c,7b,13*). Abdominal appendages are called **pleopods** or rearmost ones **uropods.** The abdominal limbs chiefly serve functions of locomotion, especially in swimming. In many crustaceans pleopods are lacking. Also a **telson** may form a spike-like rear extremity.

Pereiopods are adapted for walking, crawling, or swimming and may be variously modified for digging, grasping or shearing prey, and for brood-carrying. Those bearing pincer-like claws **(chelae)** are **chelipeds** or **gnathopods;** their chelae range from small to very large and powerful (e.g., numerous lobsters, crabs, other decapods) (Fig. 26; 27,*1*). In stomatopods, the most distal segment of front thoracopods is reflexed so as to bear against the one preceding it and this type of limb is called subchelate; the **subchelae** of the second thoracopods are enlarged spinose structures which resemble the stout raptorial limbs of a praying mantis and serve the same function (Fig. 25,*7-8*). Among peracarid malacostracans, leaflike pereiopod elements **(oostegites)** of females are used for protection of eggs and larvae. Exceptionally modified thoracopods are the biramous **cirri** of thoracican cirripeds (Fig. 21,*3;* 22,*1b*).

Typical pleopods of most malacostracans are biramous swimming appendages formed by subequal exopod and endopod extending from the protopod extremity. The two branches of each pleopod may be coupled together by tiny hooks (retinacula) to form a more efficient oarlike structure. In some groups of crustaceans (e.g., isopods, stomatopods) the pleopods are altered to function as gills. Terminal ones (uropods) of many crustaceans are shaped and arranged

FIG. 29. *(Continued from facing page.)*

ture and proximal part of extrinsic limb musculature, much enl.

3. Mystacocarid, *Derocheilocaris typicus,* medial view of right half of body showing trunk musculature and origins of few cephalic extrinsic limb muscles, much enl.

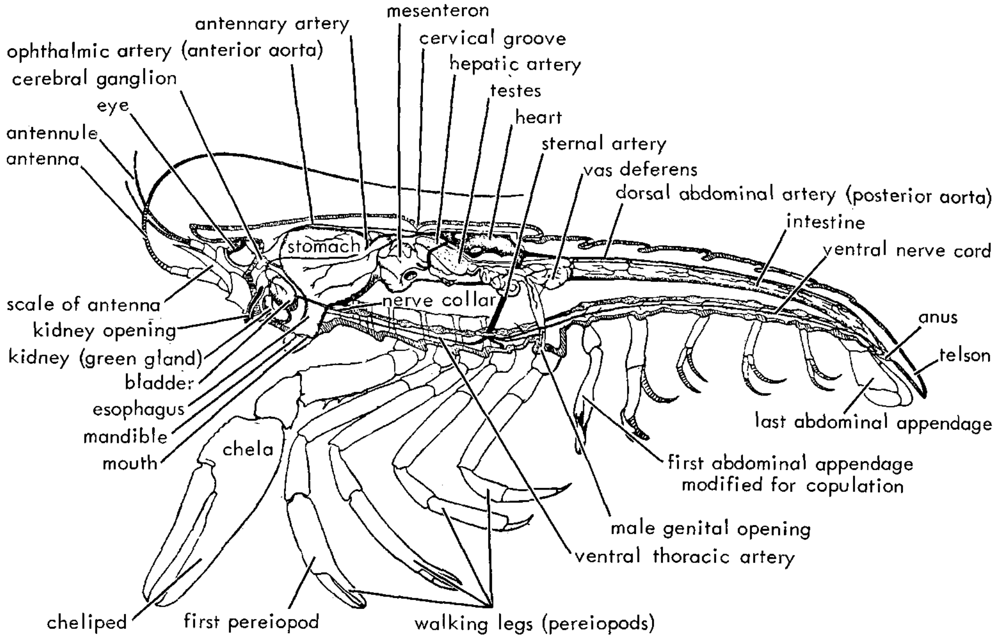


FIG. 30. Morphology of Crustacea. Median longitudinal section of crayfish, *Astacus astacus,* with appendages attached to right side of head and body. Internally, placement and some divisions of digestive and nervous systems are shown. [From Shipley & MacBride in Borradaile & Potts, *The Invertebrata* (4th edit., 1963), by permission, Cambridge University Press, publ.]

as parts of a powerful tail fan for steering and backward swimming. Also a very common structure at end of the abdomen is a caudal furca.

INTERNAL FEATURES

Internal features of crustaceans which call for notice include some aspects of the inner side of their exoskeleton, but chiefly concern soft parts such as their musculature and digestive, circulatory, respiratory, nervous, glandular, and reproductive systems. These vary widely in nature and complexity, functioning in ways dictated by organization of the body, diversity of habit, and adaptations to environment developed in each group.

MUSCULATURE

Movements of the body for walking, crawling, burrowing, and swimming, for feeding, for breathing, and for copulating are controlled by many sorts of muscles, some oriented longitudinally and others transversely or obliquely in relation to somites and to segments of appendages. Individual muscles may be relatively long or short and weak or powerful. Commonly they are attached to ingrowths of cuticle termed **apodemes** or directly to the inner surface of the hardened integument of the body. Even in primitive forms such as cephalocarids, mystacocarids (Fig. 29) and branchiopods their number and complexity are great. In ostracodes, the pattern of muscle scars on the valve interiors (Fig. 19,*10b*) is found to be helpful in classification. Commonly, crustacean muscles are supplied with only a few nerve fibers, some of which serve to stimulate and others to inhibit contraction.

DIGESTIVE SYSTEM

The digestive system of crustaceans varies considerably in different groups, ranging from a simple, straight alimentary canal extending from mouth to anus without perceptible differentiation into regions, to complex types in which parts of the tract are distended into a foregut, a midgut, and a hindgut (Fig. 30; 31,*1*).

The front part of the **foregut,** or **stomodeum,** is esophageal in nature, whereas the strongly muscled and generally enlarged rear part comprises a **stomach** or gizzard. This may be lined with small teeth to form a gastric mill that serves for mastication of food. Bristles may be present to strain particles of food.

The **midgut** or mesenteron is a digestive and absorptive region, lined with tubules of cells which secrete digestive enzymes or serve for absorption of digestive products. At its anterior end are paired digestive glands, which may branch to form a "liver."

At its posterior extremity the midgut opens into an intestine or **hindgut** (also called **proctodeum**). The hindgut, which may be absent, passes waste material along for ejection at the anus. With few exceptions, the anal opening is located on the rearmost somite of the abdomen, on the underside of the telson.

The alimentary canal is absent throughout the life of the cirriped group known as Rhizocephala and it may be undeveloped in other parasitic forms. The food of these parasites is absorbed through the skin.

CIRCULATORY SYSTEM

The circulatory system of crustaceans generally consists of one or more branching arteries that conduct blood from the heart, which lies in a pericardial blood sinus, to the various organs (Fig. 30; 31,*1,3;* 32). The blood, a pale fluid bearing leucocytes in most forms but containing hemoglobin in some branchiopods, percolates from arteries through the tissues and collects in hemocoelic sinuses. Primitive branchiopods (Anostraca) and also peracarid malacostracans have an elongate heart and blood flows through a single, short artery. The heart is absent in Cirripedia and many copepods and ostracodes and the blood circulates by movements of the body and the alimentary canal. In higher Crustacea (decapods) the blood flows from the general hemocoel of the body ventrally into sternal and lateral sinuses and vents to the gills for oxygenation (Fig. 30; 31,*3;* 32). Carbon dioxide is exchanged for oxygen in the gills and nitrogenous wastes are removed in excretory organs. The blood returns through venous channels to reenter the polygonal heart through openings termed ostia.

RESPIRATORY SYSTEM

Respiration in smaller crustaceans is effected through the general surface of the body. The process may be supplemented in forms with stronger cuticle by differentiation of appendages or lining of the carapace to form **gills** or **branchiae** (Fig. 32). Limbs of branchiopods serve in respiration as well as for other functions. Epipods are branched and folded in Malacostraca to form gills. The euphausiaceans have branchiae on all thoracopods, which are progressively larger and more complex from front to rear. The inflated carapace of some peracarids (Cumacea) is due to large lateral **branchial chambers,** each containing a large epipod composed of a complex gill and an exhalant siphon. Branchial chambers are also seen in decapods, in the thoracic region and protected by extension of the carapace (Fig. 31,*3;* 32). The gills may be differentiated by their points of origin as podobranchs, arthrobranchs, and pleurobranchs.

Isopods respire through rami of the abdominal limbs, but when they become terrestrial the integument takes the form of branching tubules resembling tracheae. Some land crabs also have special adaptations for air breathing in the form of vascular papillae on the lining of the gill chamber.

NERVOUS SYSTEM

The nervous system in primitive crustaceans consists of a mass of antennal ganglia behind the mouth united by nerve cords passing around the esophagus. These connect with a widely separated ladder-like chain of nerve cords extending longitudinally, passing through all of the somites, and connected crosswise by short commissures (Fig. 31,*5*). In other groups varying degrees of complexity are seen. The two halves of the ladder coalesce into a ventral chain, with a ganglionic mass above the esophagus comprising a "brain" from which nerves extend to the eyes and antennae (Fig. 31, *1,4*). In the decapods additional centers are developed in the brain and a subesophageal ganglion at the front end of the ventral

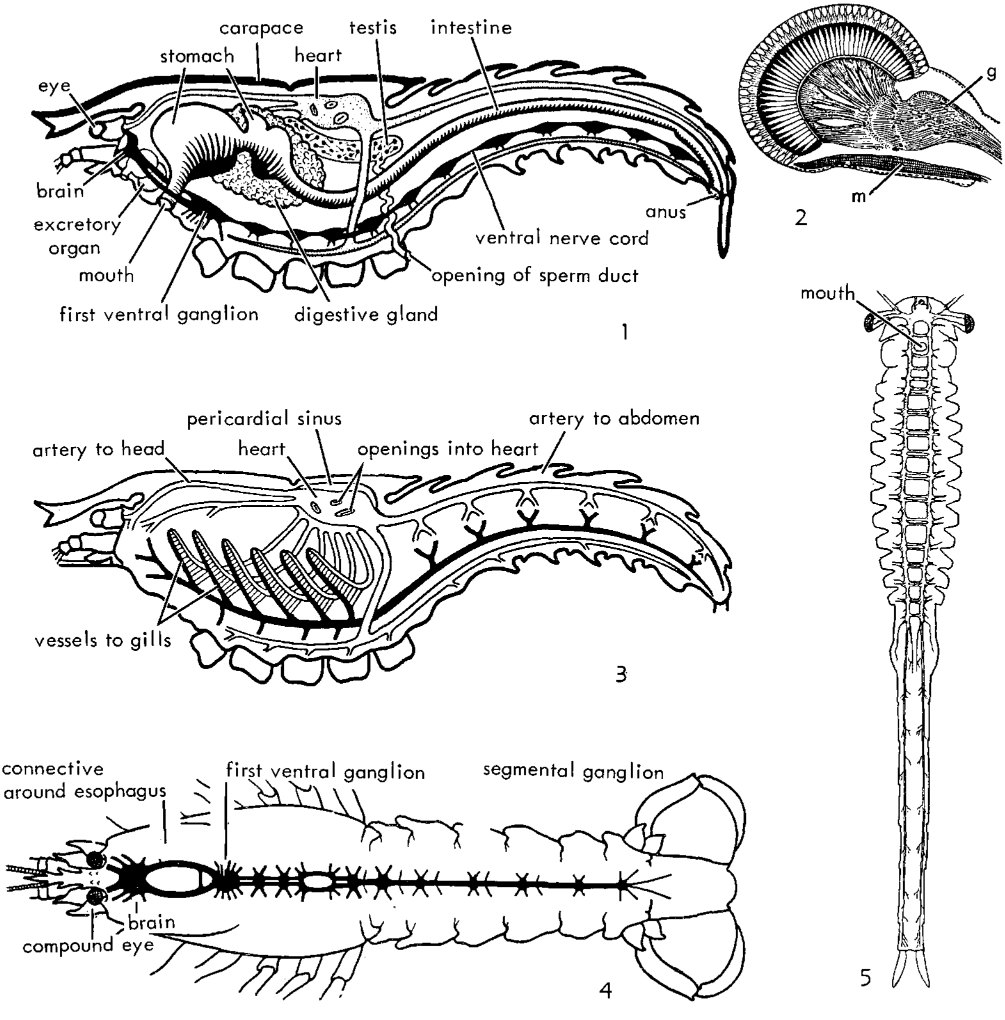


FIG. 31. Morphology of Crustacea—digestive, nervous, and circulatory systems.

1. Internal anatomy of lobster, *Homarus,* shown in diagrammatic median longitudinal section. Digestive system not segmented but divided into anterior esophageal region, stomach surrounded by digestive glands, and intestine. Nervous system clearly segmental, located on ventral side of alimentary canal.

2. Horizontal medial section of eye and ocular stalk of anostracan branchiopod, *Branchipus,* showing visual cells (ommatidia) joined to optic ganglia *(g)* of eyestalk, muscle *(m)* controlling movement of stalk, below, much enl.

3. Diagram of circulatory system of lobster showing main blood channels. Blood returning from tissues passes through gills before returning to heart.

4. Nervous system of lobster diagrammatically represented from dorsal side, with nerve ring around esophagus and gangliated double nerve cord running near ventral mid-line of body.

5. Ladder-like nervous system of anostracan branchiopod, *Branchinecta paludosa,* transverse commissures in thoracic region but lacking in abdominal part of body.

[*1,3-4,* from Ralph Buchsbaum, *Animals without backbones,* by permission, The University of Chicago Press, publ., copyright 1948; *2,5,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.]

nerve cord innervates the oral appendages, green glands, esophagus, and muscles of the front part of the thorax.

Sense organs are of several kinds and may be well developed. Many crustaceans possess an unpaired median eye comparable to that of the nauplius larva, or they have a pair of compound eyes. The median eye functions as the only organ of vision in copepods (Fig. 20), but is vestigial in various primitive crustaceans or may persist in advanced types accompanying the compound eyes. The median eye is divided into three pigmented masses filled with retinal cells meeting nerve fibers at their outer ends. Compound eyes are sessile or set on movable peduncles and consist of a number of visual units (ommatidia) each surrounded by pigment and all covered by a cornea, which is a transparent region of the cuticle usually divided into lenslike facets (Fig. 31,*2*). Eyes are reduced or not developed in some deep-sea decapods, some syncarids, and other blind crustaceans.

In addition to the sense of sight, the sense of touch and perhaps of taste and other sensations are transmitted by hairlike setae on the antennae and antennules and other parts of the body. The setae are hollow chitinous shafts containing nerves which transmit sensations to the nervous system. Olfactory setae sensitive to chemical stimuli perform a function similar to smelling and are responsible for leading lobsters into the bait traps. For the sense of balance there is an organ, the **statocyst,** located at the base of each antennule of many crustaceans to enable them to orient themselves with respect to the force of gravity. It consists of a pit with hair-lined walls which usually contains sand grains and other minute foreign bodies that enable the statocyst to function for equilibration. Also, statocysts occur in the uropods of various mysids.

GLANDULAR SYSTEMS

Excretory organs of Crustacea include two pairs of glands at the bases of the antennae and maxillae, opening forward (Fig. 31,*1*). The two usually are not functional at the same time, the **antennal glands** commonly functioning in the larval stage, whereas the **maxillary glands** operate in the adult. Each type has an end sac and ectodermal ducts leading to the exterior. In adult ostracodes, however, they lack openings. The antennal gland is known as the green gland in the Malacostraca and is well developed, being commonly dilated into a bladder or extended into diverticula. In other crustacean groups various additional glands may be excretory, for example, the caeca of the midgut in barnacles and ectodermal glands at bases of thoracic limbs in leptostracans (e.g., *Nebalia,* Fig. 19,*8*).

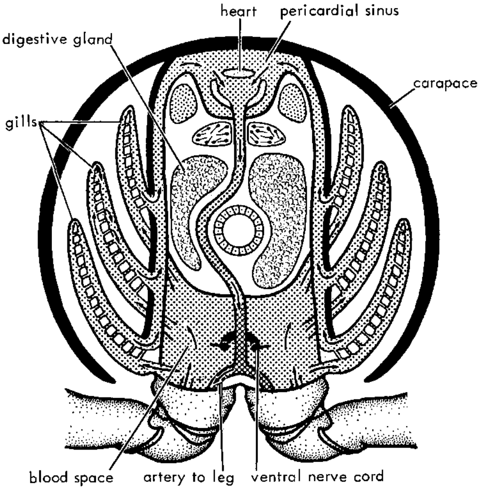


FIG. 32. Morphology of Crustacea. Transverse section through thorax of lobster, *Homarus,* showing relations of gill chambers to other organs and path of blood circulating through some main channels. [From Ralph Buchsbaum, *Animals without backbones,* by permission, The University of Chicago Press, publ., copyright 1948.]

In addition to these and the digestive glands already mentioned, are various types of **dermal glands.** Some of these in the vicinity of the mouth secrete a mucous substance which binds together small food particles to aid in swallowing them. Others on the surface of the body and limbs of amphipods secrete a protective covering. A gelatinous secretion produced by some freshwater copepods is resistant to desiccation.

Cement glands secrete substances serving in Cirripedia for attachment of the animals to supporting surfaces or, in some other crustaceans, for agglutination of sediment in building tubular burrows. The cypris larvae of cirripeds have cement glands

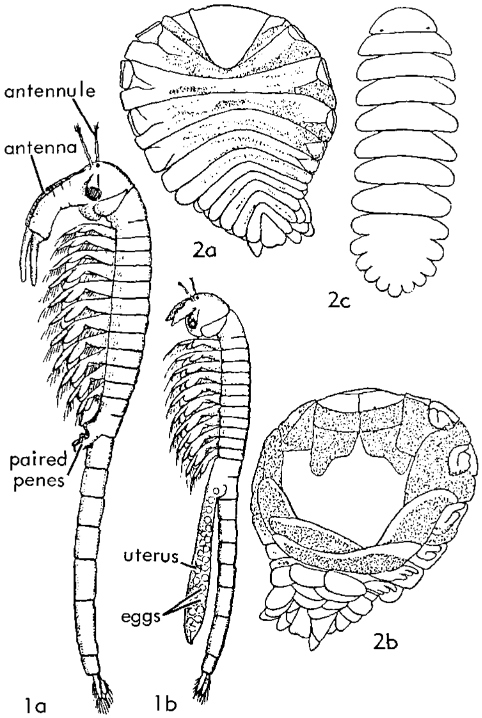


Fig. 33. Morphology of Crustacea—sexual dimorphism.

1. Anostracan branchiopod, *Branchinecta paludosa;* side views of male *(1a)* and female *(1b)* showing differences both in form and size. Ordinarily dimorphic males are smaller than females, but here the reverse is true, ×2.7.
2. Epicaridean fresh-water isopod, *Probopyrus floridensis,* which lives parasitically on gills of other crustaceans; *2a,b,* dorsal and ventral sides of female, showing asymmetry and width subequal to length, ×8; *2c,* dorsal side of male, which is much smaller than female, long-bodied, and symmetrical, ×27.

[*1,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *2,* from Richardson, 1905.]

located at ends of antennules opening through discs, by which they become attached to fixed objects. In the Lepadomorpha secretions of cement glands form vesicular balls which serve to keep the barnacles afloat.

Many pelagic crustaceans, such as the euphausiaceans (Malacostraca) have dermal glands **(photophores)** that secrete a phosphorescent or luminous substance (Fig. 24, *4*). In Decapoda and Mysidacea the secretion may come from the excretory organs or from other locations on the body and limbs. The light emitted in this way, which is brilliant blue-green in euphausiaceans, may be used to attract prey, for illumination of surroundings, or for protection of a group.

Another gland is the **sinus gland** located in the eyestalks, which has been found to store hormones controlling the molting cycle, formation and development of eggs within the ovary, and color changes.

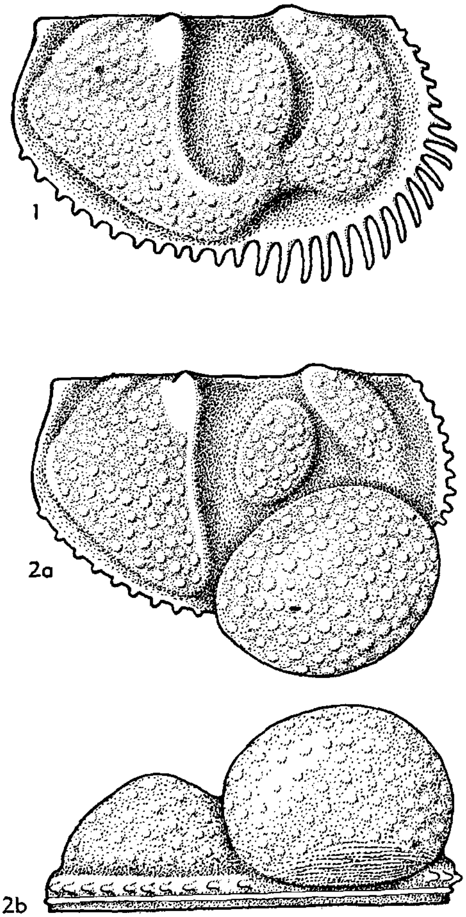


Fig. 34. Sexual dimorphism in Crustacea exhibited by carapaces of male ostracode *(1)* and female *(2a,b)* specimens of *Beyrichia ḳiaeri* Henningsmoen, from Upper Silurian of Norway; *1,2a,* side views of right valves; *2b,* ventral view of right valve; ×22 (Kesling, 1957). The female valves are chiefly distinguished by the expanded brood pouch developed in the anteroventral region.

REPRODUCTIVE SYSTEM

The sexes of most crustaceans are separate, although some cirripeds, parasitic isopods, and certain other forms are hermaphroditic. Parthenogenesis occurs in various lower crustaceans. The reproductive system generally consists of internal tubular gonads, ovaries or testes, placed in the thorax dorsally and laterally from the digestive canal. Paired reproductive ducts of both sexes commonly pass laterally and ventrally to separate openings on specific thoracic appendages (Table 1). In most groups the male tends to be smaller than the female, even extremely minute in some parasitic forms. During copulation of various decapods and other crustaceans **spermatophores** (packets of sperm bound together by mucous secretion) are emitted from the male genitalia and transferred to a pouch-like cavity of the female termed the **seminal receptacle** or **vesicle** (Fig. 17,*3*). This is connected internally to the oviducts with a median aperture opening to the exterior of the thorax, although in some forms it may be external and temporary. Its function is merely to hold the immobile sperm until time of fertilization, when eggs are emitted by the female. After extrusion, the eggs are carried in some manner for a time by many crustaceans in a brood pouch, adhering to the body, or attached to appendages under the abdomen.

DIMORPHISM

Sexual dimorphism is a common attribute of crustaceans but by no means universal. It is prevalent in such branchiopod groups as conchostracans, cladocerans, and anostracans (Fig. 33,*1*), marked by differences in size and shape of males and females, as well as in the nature of some appendages. Commonly males are smaller than females, but the reverse may be true (e.g., anostracan *Branchinecta,* which also has antennae much larger than those of females, Fig. 33,*1*). In epicaridean isopods, as illustrative of strong dimorphism in another group, the females are greatly modified in shape and symmetry from the smaller males (Fig. 33,*2a-c*); in some of these crustaceans the females are so specialized as to be little more than formless sacs containing eggs.

Well-developed sexual dimorphism characterizes the bivalved carapace of numerous genera of ostracodes, especially in such marine fossil groups as Ordovician-to-Permian palaeocopids (Fig. 34). In a host of copepods dimorphism is marked by differences in body shape and nature of the appendages, very evident in some but less so in others. As a rule, advanced types of crustaceans, as represented by the highly diverse malacostracans, display modest distinctions between males and females, rather than accentuated ones, and these relate more to the nature of appendages than to body size and shape.

Extreme dimorphism is found in some parasitic crustaceans, for example, rhizocephalan cirripeds with relatively huge sac-like females which carry hyperparasitic larval males (e.g., *Peltogaster,* see Fig. 39,*1*). A curious effect of parasitism is seen in crabs infested by rhizocephalans, for the male crabs "degenerate" into female-like forms and females revert to juvenile types with loss of their gonads.

GLOSSARY OF MORPHOLOGICAL TERMS

The exceptional variety and complexity of morphological features displayed by crustaceans have led to an unusually large number of morphological terms. The following list does not undertake to be exhaustive, but it brings together for convenient reference essentially all terms used in the *Treatise* for exoskeletal features and provides also numerous synonyms. In general, the usage preferred by *Treatise* authors is indicated by terms which are accompanied by definitions, alternative designations lacking such definitions but providing a cross reference (e.g, abdominal limb. *See* pleopod, uropod.).

Acknowledgment is made to *Treatise* authors who have given special help in preparation of the glossary: M. F. GLAESSNER, R. R. HESSLER, L. B. HOLTHUIS, W. A. NEWMAN, W. D. I. ROLFE, and PAUL TASCH.

abdomen. Trunk tagma following thorax and including telson; somites either without limbs or (in Malacostraca) bearing pleopods or uropods or both; in crabs bent sharply forward under thorax and much wider in females than in males; *syn.,* pleon. *See* also metasome, urosome.

abdominal limb. *See* pleopod, uropod.

abdominal process. Finger-like projection (one to several) on dorsal surface of cladoceran abdomen; may help to retain eggs in brood chamber.

abdominal somite. Any single division of body behind thorax; *syn.,* pleomere, pleonite.

abreptor. Postabdomen of cladocerans, bent forward from junction with body and terminating in 2 claws with spines and teeth on their concave sides.

acanthopod. In Cirripedia (Thoracica), appendage where rami of cirrus have setae along lesser curvature much reduced; setae of greater curvature arranged in transverse row, as strong sharp spines at each articulation (cf., ctenopod, lasiopod).

acron. Anteriormost part of body carrying eyes, not considered to be true cephalic somite; *syn.,* ophthalmic somite, presegmental region. [Some authors recognize as protocephalon anterior part of head bearing eyes and antennules, thus interpreting cephalon as composed of only 4 somites.]

adductor muscle (of carapace). Muscle attached to carapace for pulling it to body (thorax) or connecting halves of bivalve shell (e.g., Conchostraca, Ostracoda, Leptostraca) or valves of cirriped capitulum for closure of them. In Cirripedia, any transverse muscles, particularly that of maxillary segment, for closure of aperture; in Thoracica, adductor (adductor scutorum) acts upon scutal plates or valves.

adductor pit. In cirripeds, depression on interior of scutum for attachment of adductor muscle, located between adductor ridge and occludent margin.

adductor ridge. In cirripeds (Balanomorpha), linear elevation on interior of scutum between adductor pit and tergal margin.

aesthetasc. *See* esthetasc.

aesthete. See esthetasc.

afferent channels. Openings through which water passes to gills, in brachyuran crabs generally located in front of bases of chelipeds.

ala (pl., **alae**). One of pair of posteriorly directed cephalic-shield extensions; in cirripeds (Balanomorpha), triangular lateral part of compartment plate delimited from paries, which is overlapped by adjacent compartment plate with or without radius.

aliform apophyses. Incurved anterior and posterior extremities of growth lines (e.g., Conchostraca, characteristic of *Ipsilonia*).

ambulatory leg. *See* pereiopod.

anal spines. Single row of spines on either side of cladoceran postabdomen (e.g., Sididae, Holopedidae, Daphniidae). [In addition, some cladocerans possess lateral spines (e.g., Macrothricidae, Chydoridae).]

antenna (pl., **antennae**). One of pair of anterior appendages of head region placed morphologically next behind antennule, uniramous in some crustaceans but biramous in all nauplii and in adults of most classes; may be extremely long and composed of multitudinous small segments or reduced to mere rudiment or lacking; *syn.,* second antenna.

antennal carina. *See* carapace carina, a.

antennal gland. *See* green gland.

antennal groove. *See* carapace groove, a.

antennal region. *See* carapace region, a.

antennal scale. *See* scaphocerite.

antennal spine. *See* carapace spine, a.

antennula. *See* antennule.

antennular scale. *See* stylocerite.

antennule. One pair of morphologically frontmost appendages of head region, usually filiform and multiarticulate, uniramous except in Malacostraca where it is generally biramous or even triramous; may be larger or smaller than morphologically next following appendages named antennae; *syn.,* antennula, first antenna.

anterior tubercle. Swelling or small protuberance in anterior region of carapace of Archaeostraca; polygenetic, includes the "optic tubercle" of some authors.

anterolateral region. *See* carapace region, b.

aperture. Posteroventral opening into cirriped mantle cavity.

apex. Upper angle of scutum or tergum of cirripeds.

apicobasal ridge or furrow. In cirripeds longitudinal feature which divides tergal slip (tergum) from rest of valve.

apodeme. Infold of exoskeleton serving for attachment of muscles.

appendix interna. Medial projection stemming from pleopodal endopods, serving to unite members of each pair of pleopods; *syn.,* stylamblys.

appendix masculina. Complex median process of endopod of second pleopods of male Caridea and some isopods; serves in copulation.

arm. Merus of cheliped (obsolete term).

arthrobranch. Gill of decapods attached to articular membrane between limb and body; *syn.,* arthrobranchia.

arthrobranchia (pl., **arthrobranchiae**). *See* arthrobranch.

arthrophragm. *See* endophragm.

article. Individual element of crustacean appendage; *syn.,* joint, segment.

articular furrow. In cirripeds, groove on tergal margin of scutum or scutal margin of tergum forming part of articulation between these plates.

articular ridge. In cirripeds (Balanomorpha), linear elevation on tergal margin of scutum or scutal margin of tergum close to articular furrow and with it forming articulation between these plates.

atrium oris. Preoral cavity, bounded ventrally by posteriorly directed labrum, dorsally by ventral surface of cephalon just behind mouth, and laterally by paragnaths and mandibles.

attractor epimeralis muscle. Important muscle in many decapods, inserted along line of branchiocardiac groove in carapace.

basal margin. In cirripeds, lower edge of scutum or tergum or other plate.

basicarinal angle. Intersection of basal and carinal margins of cirriped tergum.

basicerite. Second segment of antennal peduncle (in Caridea bearing scaphocerite).

basilateral angle. In cirripeds, intersection of lateral and tergal margins of scutum; *syn.,* basitergal angle.

basioccludent angle. Intersection of basal and occludent margins of cirriped scutum.

basiophthalmite. Proximal segment of eyestalk, articulating with distal segment (podophthalmite) which bears corneal surface of eye.

basipod(ite). *See* basis.

basis (pl., **bases**). Limb segment adjoining coxa on its distal side and commonly bearing endopod and exopod; *syn.,* basipod(ite); in nonpedunculate cirripeds comprises basal calcareous or membranous plate which furnishes anchorage to foreign body or substrate.

basiscutal angle. Intersection of basal and scutal margins of cirriped tergum.

basitergal angle. Intersection of basal and tergal margins of cirriped scutum.

beaked apex. In cirripeds (Balanomorpha), upper angle of tergum produced into long narrow point.

biformes. Carapaces reflecting sexual dimorphism (e.g., Conchostraca), marked by differing valve proportions for each sex of same species (DADAY); a given species may have carapaces that are "biformes."

biramous. Two-branched; crustacean limb in which basis bears both exopod and endopod.

blood rooms. Network of anastomosing cavities in body of conchostracans which provide for circulation of blood (SARS).

body chamber. In cirripeds, interior of shell containing soft parts of animal.

body of mandible. *See* mandible body.

body ring. Combined tergite and sternite of single somite, bearing legs or legless (as used by some specialists on Notostraca, not equivalent to somite).

body somite. Generally refers to unit division of thorax + abdomen in contrast to cephalic somite.

branchia (pl., **branchiae**). Thin-walled finger-like or leaflike structure extending outward from limb or secondarily from side of body, functioning for respiration; *syn.,* gill. [Special types are termed arthrobranchs, pleurobranchs, and podobranchs, depending on their place of attachment, and dendrobranchs, phyllobranchs, mastigobranchs, and trichobranchs, depending on their shape. In Cirripedia (Balanomorpha) pair of leaflike fleshy extensions of mantle lining, within mantle cavity, presumed to be respiratory in function.]

branchial carina. *See* carapace carina, b.

branchial cavity. *See* branchial chamber.

branchial chamber. Space between body and wall of carapace enclosing branchiae; *syn.,* gill chamber.

branchial glands. Masses of connective-tissue cells surrounding venous channels in branchiae and devoid of ducts.

branchial region. *See* carapace region, c.

branchiocardiac carina. *See* carapace carina, c.

branchiocardiac groove. *See* carapace groove, b.

branchiostegal area. Part of carapace extending laterally and downward over branchiae.

branchiostegal spine. *See* carapace spine, b.

branchiostegite. Part of carapace extending over top and side of branchial chamber.

buccal cavity. Hollow space on ventral side of body containing mouth parts, in Malacostraca bounded by epistome in front and free edges of carapace on sides.

buccal frame. Structure of brachyuran decapods enclosing mouth parts, its sides formed by free anterolateral edges of carapace, its front delimited by epistome, and commonly closed by operculiform third maxillipeds.

calceolus (pl., **calceoli**). Complex sensory filaments on antennules of some amphipods.

calyptopis stage. Third larval stage in euphausiaceans, characterized by differentiation of abdomen and appearance of compound eyes.

capitulum. In pedunculate cirripeds portion of carapace enclosing trophic structures, commonly armored by calcareous plates.

carapace. Cuticular, varyingly calcified structure comprising cephalic shield and fold of integument arising from posterior border of maxillary somite extending over trunk, usually covering it laterally as well as dorsally; commonly fused to one or more thoracic somites and in many forms having mid-dorsal hinge.

carapace adductor muscle. *See* adductor muscle.

carapace angles. In Leaiidae (Conchostraca), angle made by straight dorsal margin with anterior rib (α) and with posterior rib (β); these angles may have utility in tracing evolutionary development and in stratigraphic zonation.

carapace carina. Narrow ridge variously located on surface of decapod carapace——named types:

a) **antennal.** Narrow ridge extending backward from antennal spine.

b) **branchial.** Narrow ridge extending backward from orbit over branchial region.

c) **branchiocardiac.** Narrow ridge marking off branchial from cardiac regions of carapace.

d) **gastroorbital.** Narrow ridge extending backward from supraorbital spine.

e) **lateral.** Narrow ridge on side margin of carapace.

f) **orbital.** Narrow ridge on margin of orbit.

g) **posterior.** Transverse narrow ridge in front of carapace marginal groove.

h) **postorbital.** Narrow ridge slightly behind orbital margin and parallel to it.

i) **postrostral.** Narrow ridge behind rostrum extending along dorsal mid-line of carapace.

j) **rostral.** Longitudinal narrow ridge continuous with lateral margin of rostrum.

k) **subhepatic.** Narrow ridge extending backward from branchiostegal spine.

l) **submedian.** Narrow ridge on either side of postrostral carina and parallel to it; may join rostral carina.

m) **supraorbital.** *See* gastroorbital carina.

carapace costae. Closely spaced radial ridges, grading from fine to coarse, that become obsolete near umbo and do not cross it (=radial lirae, radial riblets, accessory ribs) (e.g., Conchostraca, especially Estheriellidae, in which valves generally have more than 5 costae).

carapace costellae. Fine radial ridges that run from ventral margin to and across umbo, and are usually numerous on any given valve (e.g., Conchostraca).

carapace groove. Furrow on surface of decapod, generally dorsal——named types:

a) **antennal.** Furrow on carapace extending backward from vicinity of antennal spine.

b) **branchiocardiac.** Oblique furrow approximately in middle of posterior half of each side of carapace, separating branchial and cardiac regions and reaching dorsomedian part of carapace well behind cervical or postcervical grooves; may be longitudinal, connecting cervical and postcervical grooves, or extending backward from submedian point on postcervical groove.

c) **cervical.** Transverse furrow in median part of carapace between gastric and cardiac regions, curving forward toward antennal spine.

d) **gastroorbital.** Short longitudinal furrow branching from cervical groove at level of orbit and running toward it.

e) **hepatic.** Short longitudinal furrow connecting cervical with postcervical and branchiocardiac grooves, more or less continuing antennal groove.

f) **inferior.** Transverse furrow extending from junction or hepatic and cervical grooves toward side margin of carapace, more or less continuous with cervical groove.

g) **marginal.** Furrow close to posterior edge of carapace and parallel to it.

h) **postcephalic.** One of three transverse furrows on carapace of many fossil decapods.

i) **postcervical.** Furrow located behind cervical groove and parallel to it, dividing cardiac region into two parts.

j) **submedian.** Longitudinal furrow in submedian dorsal part of carapace closely adjacent to postrostral carina.

carapace growth line. Peripheral margin of successive membranes added to shell during each molt (e.g., Conchostraca).

carapace horn. Anterodorsal termination of carapace valves in some Archaeostraca; may be indurated (e.g., *Ceratiocaris*) or produced into long processes (e.g., *Caryocaris*).

carapace lirae. Raised, linear, fine concentric ridges parallel to growth lines and occupying an interspace e.g., Conchostraca).

carapace region or area. Differentiated portion of decapod carapace surface distinguished in descriptions and used in classification——named types:

a) **antennal.** Anterior marginal part of carapace bordering orbital region laterally and also touching hepatic, pterygostomial, and, in some forms, frontal region.

b) **anterolateral.** Lateral part of carapace bordering subhepatic or hepatic regions.

c) **branchial.** Lateral part of carapace behind pterygostomial region and overlying branchiae, divided by some authors into epibranchial, mesobranchial, and metabranchial subregions.

d) **cardiac.** Median part of carapace behind cervical groove or suture, between urogastric and intestinal areas.

e) **frontal.** Anteromedian part of carapace including rostrum and area behind it.

f) **gastric.** Median part of carapace in front of cervical groove and behind frontal region; divided by some authors into epigastric, mesogastric, metagastric, protogastric, and urogastric subregions.

g) **hepatic.** Part of carapace which may touch antennal, cardiac, and pterygostomial regions.

h) **intestinal.** Short transverse part of carapace behind cardiac region, designated by some as posterior cardiac lobe.

i) **jugal.** *See* pterygostomial region.

j) **orbital.** Part of carapace behind eyes, bordered by frontal and antennal regions.

k) **pterygostomial.** Anterolateral part of carapace on ventral surface located on opposite sides of buccal cavity.

l) **subhepatic.** Part of carapace below hepatic region and extending below lateral edge of latter.

carapace spine. Sharp projection of carapace important for classification——chief types:

a) **antennal.** Spine on front margin of carapace slightly below orbit.

b) **branchiostegal.** Spine on front margin of carapace or slightly behind it about halfway between antennal and pterygostomial spines.

c) **hepatic.** Spine in hepatic region of carapace below lower branch of cervical groove and behind it.

d) **infraorbital.** Spine on lower angle of orbit.

e) **postorbital.** Spine at moderate distance behind middle of orbit.

f) **postrostral.** Dorsomedian spine immediately behind rostrum.

g) **pterygostomial.** Spine on anterolateral angle of carapace.

h) **suborbital.** Spine at moderate distance below middle of orbit and slightly beneath it.

i) **supraorbital.** Spine at moderate distance obliquely behind and above orbit (may be placed on postorbital carina).

carapace tooth. Small sharp spinous projection in varied locations——named types:

a) **cardiac.** Tooth on mid-line of carapace just behind cervical groove.

b) **gastric.** Tooth on mid-line of carapace just in front of cervical groove.

c) **lateral.** Tooth placed on lateral margin of carapace (includes anterolateral, mediolateral, posterolateral teeth).

d) **orbital.** Tooth on orbital margin.

e) **posterior.** Tooth on mid-line of carapace just in front of posterior margin between it and marginal groove.

f) **pregastric.** Tooth on mid-line of carapace between gastric tooth and rostrum.

g) **rostral.** Tooth on rostrum; may be single (e.g., scyllarid palinurans) or multiple and classified as upper, lower, or lateral (e.g., nephropid astacideans and natantian crabs).

cardiac notch or incision. Indentation on posterior margin of carapace (e.g., some Alpheidae).

cardiac region. *See* carapace region, d.

cardiac tooth. *See* carapace tooth, a.

cardo. Basal segment of maxillula articulating with head.

caridean lobe. External rounded projection on basal part of exopod of first maxilliped (e.g., Caridea).

caridoid facies. Aspect of primitive Eumalacostraca distinguished by enclosure of thorax by carapace, movably stalked eyes, biramous antennules, scaphocerite-bearing antennae, thoracopods with natatory exopods, elongate abdomen ventrally flexed and powerfully muscled, and caudal fan.

carina. Any keel-like structure, as on dorsum of pleon of some amphipods; in cirripeds, single compartment plate at end of shell where cirri are protruded, or adjacent to tergum, possessing alae only. *See* carapace carina.

carinal. In cirripeds (Thoracica), toward or adjacent to compartment plate termed carina.

carinal latus. *See* latus (carinal), a.

carinal margin. In cirripeds (Thoracica), edge of tergum adjacent to carina, occluding with carinal margin of opposed tergum.

carinate. Conchostracan valve bearing rib(s), chiefly applicable to Leaiidae.

carinolateral. Compartment plate of cirripeds located on either side of carina, with radii on cardinal side and alae on rostral side; *syn.,* latus (cardinal).

carpocerite. Distal (5th) segment of antennal peduncle.

carpopod(ite). *See* carpus.

carpus. Segment of limb located next distally from merus and joined to propodus proximally; *syn.,* carpopod(ite), wrist.

caudal appendage. In cirripeds, one of terminal, multiarticulate or uniarticulate, uniramous paired appendages, homologous with caudal furca of other crustaceans.

caudal fan. Combination of laterally expanded uropods and telson turned backward to form powerful swimming structure or means of steering and balancing; *syn.,* tail fan, rhipidura.

caudal filament. *See* caudal ramus.

caudal furca. Pair of caudal rami.

caudal ramus. Single appendage of terminal abdominal somite paired with another to form caudal furca, both articulated with telson; usually rodlike or bladelike but may be filamentous and multiarticular (caudal filament); *syn.,* cercus, cercopod, caudal style, stylet.

caudal style. *See* caudal ramus.

cement gland. Special concentrations of cells in dermal cover of cirripeds which function for secreting calcareous substance of valves; possibly equivalent to dermal glands of other crustaceans.

cephalic flexure. Forward or even upward deflection of anterior sterna of some decapods.

cephalic shield. Chitinous, more or less calcified covering structure of head region formed of fused tergites of cephalic somites commonly having pleura.

cephalic somite. Unit division of head region, generally recognized as one of five such parts which bear distinctive paired appendages (antennules, antennae, mandibles, maxillules, maxillae) in addition to "precephalic" acron bearing eyes.

cephalomere. Cephalic somite.

cephalon. Most anterior tagma, bearing eyes, mouth, 2 pairs of antennae, and 3 pairs of mouth-part appendages (e.g., Branchiopoda, Ostracoda, Leptostraca, *Bathynella*); *syn.,* head.

cephalosome. Head region when this includes only somites bearing maxillipeds or gnathopods, or both.

cephalothorax. Anterior part of body composed of united cephalic and thoracic somites, latter comprising not only those with appendages modified as mouth parts or for food capture but others with relatively unmodified appendages, all forming a fused complex.

[Note. The most common definition of cephalothorax seems to be "unit resulting from fusion of one or more thoracic segments to cephalon." This seems too all-inclusive, for it can be applied to the very common situation in which only the first thoracic segment (because its limb is a maxilliped) is fused to the cephalon. A unit of this sort is not well fitted to the concept of cephalothorax. Fusion of thoracic segments to the cephalon seems to follow 2 patterns: (1) not all thoracic segments become fused, and the limbs of those that do become modified as mouth parts or for food capture (copepods, peracarids, stomatopods); (2) all thoracic segments become fused, including those which bear relatively unmodified locomotory appendages (eucarids). Gnathothorax is proposed as a term applicable to case 1 and cephalothorax is appropriate for designation of case 2. HESSLER & ROLFE]

cercopod. *See* caudal ramus.

cercus (pl., **cerci**). *See* caudal ramus.

cervical furrow. *See* cervical groove.

cervical groove. *See* carapace groove, c.

cervical notch or incision. Strong indentation of carapace at level of cervical groove (e.g., scyllarid palinurans).

cervical sinus. Rounded to angular indentation at front of cladoceran carapace along dorsal edge, exposing rear part of head.

cervical suture. *See* cervical groove.

chela. Pincer-like distal part of limb consisting of opposed movable, and immovable fingers.

chelate. Bearing chela (chelae).

cheliped. Any thoracopod bearing chelae.

cincinnulus (pl., **cincinnuli**). *See* retinaculum.

cirrus (pl., **cirri**). Multiarticulate food-gathering appendage of "thoracic" region of cirriped, normally one of six pairs, each with 2 long hairy rami curled toward mouth.

clasper. Appendage, including antenna, that serves for attachment in copulation or as organ for fixation in parasites.

clypeus. Part of head carrying labrum; plate on anterior medial part of head formed by fusion of basal segments of antennae (e.g., *Branchipus,* also Hexapoda).

colleteric gland. In Cirripedia (Rhizocephala), a single or paired saclike gland in female or hermaphrodite, producing viscid material binding eggs together.

comb collar. In Cirripedia (Acrothoracica), retractable membranous collar supporting row of numerous uniform setae at superior angle of aperture.

compartment. *See* compartment plate.

compartment plate. In sessile cirripeds (Verrucomorpha, Balanomorpha), rigid articulated skeletal element (valve) forming part of shell wall; *syn.,* mural plate.

compound eye. Array of contiguous ommatidia having common optic nerve trunk; paired.

compound rostrum. In cirripeds (Balanomorpha), projection formed by fusion of rostrolateral plates, forming compound compartment overlapping latera, and on which radii may develop (cf. rostrum).

conchostracan carapace interspace. Area between any 2 growth lines of conchostracan carapace; synonyms used interchangeably include intervales, growth zone, growth band.

conchostracan carapace interval. Space between any 2 ribs, costae, or costellae on conchostracan carapace.

conchostracan carapace ribs. Strong radial ridges radiating from and across umbo of conchostracan carapace, with intervals of variable width between any pair and commonly nodose at intersections of growth lines; may be partial or embryonic in expression; synonyms include longitudinal striae, carinae, radials, diagonal ridges, radial costae, and keels. [Characterize Leaiidae, never exceeding 5 in number on any given leaian valve; ribs also occur in *Protomonocarina* and *Limnadiopsileaia.*]

copepodid. Postnaupliar developmental stages of copepods.

cormopod(ite). *See* thoracopod(ite).

cormus. *See* thorax.

cornea. Transparent cuticle covering ommatidia of compound eye.

corpus mandibulae. *See* mandible body.

coxa. Segment of limb directly attached to sternite of body (except rarely in forms having distinguishable precoxal segment); *syn.,* coxopod(ite).

coxal plate. Lateral expansion of pereiopod coxa joined broadly to lateral margins of tergites.

coxepipod(ite). Coxal exite.

coxite. *See* protopod(ite).

coxopod(ite). *See* coxa.

ctenopod. In cirripeds, appendage where rami of cirrus have setae arranged in linear series along lesser curvature, like a comb (cf. acanthopod; lasiopod).

cycladiformes. Conchostracan carapaces having dorsal margin of valves forming obtuse angle with posterior margin (DADAY).

cyclops stage. Post-metanaupliar stage in ontogeny of some copepods.

cypris stage. Ostracode-like larval stage (e.g., Cirripedia).

cyrtopia stage. Fifth larval stage in euphausiaceans in which antennae no longer serve for locomotion.

dactyl. *See* dactylus.

dactylopod(ite). *See* dactylus.

dactylus. Distalmost segment of limb; *syn.,* dactylopod(ite).

deflexed front. Broadly downturned front marginal part of carapace in some decapods.

dendrobranch. Type of gill having tubes divided into arborescent bundles.

denticle. In cirripeds (Balanomorpha), primary or secondary toothlet on sutural edge of radius of compartment plate or opposed buttress of adjoining plate, serving to strengthen articulation of plates.

depressor muscle. In Cirripedia (Balanomorpha), muscle inserted at basicarinal angle of tergum, for which depressor muscle crests are usually developed.

depressor muscle crests. In cirripeds (Balanomorpha), elevated denticles on interior of tergum near basicarinal angle for attachment of depressor muscles (crests may extend apically).

depressor muscle, lateral. In Cirripedia (Balanomorpha), muscle inserted on basitergal angle of scutum, for which lateral depressor muscle pit, depression or crests may develop.

dermal gland. Single cell or concentration of cells in epidermis of body and limbs, traversed by canals and communicating with surface by fine ducts, their functions various and possibly corresponding to cement glands of cirripeds.

deuterocerebrum. *See* mesocerebrum.

diaeresis. Transverse groove on posterior part of exopod (rarely also endopod) of uropod appendage, in some forms dividing exopod into 2 movably connected parts.

distal. Direction away from central part of body; opposite of proximal.

dorsal organ. Thickened glandular area of hypoderm of dorsal surface just behind head in various branchiopods, isopods, amphipods, mysidaceans, tanaidaceans, and syncarids, its function obscure.

dorsal plate. Spindle-shaped division of carapace in some astacidean decapods (Erymidae) intercalated in median suture; may be related to dorsal organ.

dorsoventralis posterior. Important muscle in crayfish and other decapods connecting head apodemes with internal surface of carapace just behind cervical groove.

doublure. Reflexed ventral continuation of carapace integument.

efferent channels. Passageways through which water moves away from gills and out of branchial region.

endite. Inwardly (medially) directed lobe of precoxa, coxa, basis, or ischium.

endognath. Endopod (inner and principal branch) of maxilliped.

endophragm. Wall formed by union of apposed apodemes forming part of endoskeleton of some decapods; *syn.*, arthrophragm.

endophragmal skeleton. Complex internal skeletal structure formed by fusion of apodemes in decapods providing framework for muscle attachment, generally not strongly calcified.

endopleurite. Lateral apodeme of endoskeleton in decapods.

endopod(ite). Innermost ramus of limb arising from protopod basis; in the Eumalacostraca typically composed of 5 segments (ischium, merus, carpus, propodus, dactylus).

endoskeleton. Internal hard parts of some decapods consisting mainly of endophragms.

endosternite. Mesodermal tendonous plate below anterior part of alimentary canal (e.g., Notostraca); also firm calcareous plate between nerve cord and alimentary canal in anterior part of thorax in some crabs.

endostome. Palate-like part of buccal frame in some brachyuran decapods; *syn.*, palate.

ephippium (pl., **ephippia**). Semielliptical part of dorsal region in each valve of cladoceran branchiopods altered to form encasement for eggs, shed as unit and constructed in manner that facilitates ultimate hatching after desiccation (especially characteristic of Daphniidae).

epibranchial lobe or area. Anterior part of branchial region of decapod (brachyuran) carapace.

epibranchial space. Part of gill chamber above (external to) gills.

epigastric lobe or area. Anterior extension of gastric region of decapod (brachyuran) carapace.

epimeral fold. Steep fold of endopleurites in some decapods connected with branchiostegite to form branchial chamber.

epimere. Lateral downfold of tergite; *syn.*, epimeron, pleurepimere, pleurite, pleuron (pl., pleura), pleura (pl., pleurae), tergal fold.

epimeron (pl., **epimera**). *See* epimere.

epipod(ite). Laterally directed ramus (exite) of coxa; may be present or absent.

episternum. Posterolateral projection of various sterna of decapods.

epistome. Plate of varying shape between labrum and bases of antennae in brachyuran decapods, also defined as sternum of antennal somite.

esophagus. Anterior part of alimentary canal between pharynx or mouth and stomach or stomodeum; *syn.*, oesophagus.

esthetasc. Sensory seta covered by delicate cuticle projecting from most antennules and antennae; *syn.*, olfactory hair, esthete.

esthete. See esthetasc.

exhalant passage. Canal in front of gill chamber containing scaphognathite which functions for driving water outward, leads to large anterior opening.

exite. Laterally directed ramus of protopodal segment of limb (e.g., Notostraca).

exognath. Exopod (outer and secondary branch) of maxilliped.

exopod(ite). Outer ramus of limb arising from protopod basis; may contain variable number of segments or be much reduced or lacking.

exoskeleton. Entire horny (in part chitinous) more or less calcified outer covering of crustacean body and its appendages.

eye. Visual organ, in Crustacea either compound or naupliar (simple).

eyestalk. Peduncle movably articulated with head, carrying eye at its distal extremity, may be divided into 2 or 3 segments and may be retractable; *syn.*, ocular peduncle.

filamentary appendage. Membranous process developed on body in many cirripeds (Ascothoracica, Lepadomorpha) commonly on bases of cirri; may contain branches of testes; presumed to be respiratory in function.

filter chamber. Space beneath thorax (e.g., phyllocarids) enclosed by ventral body wall and rhythmically moved thoracopods which functions for food-gathering from currents sucked into it.

fingers. Scissor-like blades of claw end of cheliped, one finger movable and other immovable (fixed); very exceptionally *(Psalidopus)* both fingers are movable.

first antenna. *See* antennule.

first maxilla. *See* maxillule.

fixed finger. Immovable distal part of propodus of chela; *syn.*, pollex, thumb.

flabellum. Thin distal exite of branchiopod gnathobase with setose margin.

flagellum (pl., **flagella**). Slender, multiarticulate distal part of antennule, antenna or exopod.

foregut. *See* stomodaeum.
frena. Tegumentary folds holding eggs (Cirripedia).
front. Part of crab carapace between orbits.
frontal appendage. One pair of filaments arising in many Anostraca from bases of antennae but independent of them; may be ramified.
frontal band. Glandular organ of adhesion in frontal region of various parasitic copepods serving for attachment to host fishes.
frontal organs. Sensory cells or setae on front surface of heads of some branchiopods, copepods, and decapods.
frontal plate. Modified rostrum of brachyuran decapods which bears downward projecting process between antennules that unites with epistome.
frontal region. *See* carapace region, e.
frontolateral horn. One of pair of tubular frontolateral extensions of cuticle of cirriped nauplii (except Ascothoracica), apparently perforate at tips and provided with mass of gland cells at bases.
furca. *See* caudal furca.
furcal ramus. Branch of caudal furca.
furcilia stage. Fourth larval stage in euphausiaceans, marked by movable compound eyes that project beyond edge of carapace.
galea. Outer distal hoodlike lobe of 2nd segment of maxillule; adjacent to inner spiny lobe (lacinia).
gastric groove. Longitudinal furrow on either side of median carina on stomatopod carapace.
gastric mill. Apparatus of varying complexity in stomodeum which serves to break up food; consists of framework of movably articulated ossicles developed as thickened and calcified part of stomodeal lining, most highly specialized in decapods.
gastric region. *See* carapace region, f.
gastric tooth. *See* carapace tooth, b.
gastrolith. Discoid calcareous nodule common in stomodeum of some decapods
gastroorbital carina. *See* carapace carina, d.
gastroorbital groove. *See* carapace groove, d.
genital region. *See* urogastric lobe or area.
gill. *See* branchia.
gill chamber. *See* branchial chamber.
glaucothoe stage. Ontogenetic stage in larval development of pagurid decapods.
gnathal lobe. Masticatory endite of mandible; *syn.,* masticatory process.
gnathobase. Endite which through medial contact with opposite member of its pair serves for comminution of food; may also serve in food transport.
gnathopod. Chelate or subchelate, prehensile maxilliped (e.g., Amphipoda); also used for first two prehensile pereiopods of amphipods whether chelate or subchelate.
gnathothorax. Tagma resulting from fusion of gnathal somites (mandibular, two maxillary) with one or more thoracic somites, limbs of which are modified to act as mouth parts. *See* cephalothorax.
gonad. Hollow reproductive organ in either sex, cavity communicating with pair of efferent ducts (pair in some parasitic isopods).
gonapophysis. Median process arising from base of first or second pleopods of male syncarids.
gonopod. Modified male pleopod serving for transmittal of spermatophores to female.
gonopore. Outlet for genital products, generally placed constantly in different crustaceans; *syn.,* sexual pore.
green gland. One of pair of complex excretory glands located in antenna on front of head of decapod (e.g., crayfish); *syn.,* antennal gland.
groove. *See* carapace groove.
haft organ. Pear- to wedge-shaped appendage of some branchiopods (e.g., *Limnadopsis*) attached to mid-dorsal surface of head at narrower end; *syn.,* frontal organ, affixing organ.
head. *See* cephalon.
head apodeme. Fused endopleurite and endosternite forming place for muscle attachment at anterior end of skeleton in Astacidea.
hemocoel. Lacunar system extending throughout much of body, filled by blood.
hemocyanin. Copper-containing respiratory pigment in blood of malacostracans.
hemoglobin. Oxygen-carrying protein coloring substance of red plasma in blood, found in some crustaceans (e.g., Ostracoda), may be colored or colorless in conchostracans, present also in blood of anostracans, cladocerans, notostracans, some harpacticid and parasitic copepods, branchiurans, and some parasite cirripeds.
hepatic caeca. Pouchlike diverticula generally connected with mesenteron, serving functions of liver; *see* hepatopancreas.
hepatic groove. *See* carapace groove, e.
hepatic region. *See* carapace region, g.
hepatic spine. *See* carapace spine, c.
hepatopancreas. Digestive gland consisting of ramified tubules spread through cephalothorax performing functions of both liver and pancreas.
heterochelate. Chelae of left and right chelipeds differing in shape and size.
hindgut. *See* proctodeum.
hinge line. Mid-dorsal line of junction of two valves composing carapace, permitting movement between them (e.g., Conchostraca, Ostracoda, Phyllocarida).
hinge nodes. Localized thickened parts of right-valve hinge of phyllocarids, somewhat elongate in line of hinge and serving to strengthen it.
hypobranchial space. Part of gill chamber below gills.
hypopharynx. *See* metastoma.
hypostoma. *See* metastoma.
hypostome. *See* metastoma.
imbricate plates. *See* lower latera.
incisor process. Biting portion of gnathal lobe of mandible; *syn.,* pars incisiva.
inferior groove. *See* carapace groove, f.
inframedian lateral. *See* latus (inframedian), b.
inframedian latus. Valve of some cirriped shells located below upper latus.

infraorbital spine. *See* carapace spine, d.

inner lamina. In cirripeds, innershell layer of compartmental plate separated from outer lamina by parietal tubes.

interantennular septum. Plate in some malacostracans that separates one antennular cavity from other; *syn.,* proepistome.

interlaminate figure. In Cirripedia (Balanomorpha), simple or arborescent lines seen running between epicuticle of outer lamina through longitudinal septa into inner lamina, when paries is sectioned parallel to base.

intestinal region. *See* carapace region, h.

intestine. Elongate slender posterior part of alimentary canal, in some crustaceans partly corresponding to mesenteron and invariably to part of proctodeum.

intraparies (pl., **intraparietes**). Secondary lateral margin of carina in some cirripeds (Lepadomorpha).

ischiocerite. Third segment of antennal peduncle.

ischiopod(ite). *See* ischium.

ischium. Third limb segment distal from body articulating with basis and comprising first segment of endopod; *syn.,* ischiopod(ite).

joint. Articulation (most commonly applicable to movable connection of individual segment of appendage with neighbors or body but relates also to movable connection of body parts); loosely and undesirably employed as synonym of segment.

jugal region. *See* carapace region, i.

kentrogon. In Cirripedia (Rhizocephala), dedifferentiated cells of female or hermaphrodite cyprid larva, at time they are being extruded through cyprid first antenna into host crustacean; or of male cyprid, being extruded into mantle cavity of female.

knee. Point of most pronounced flexure of endopod.

labium. *See* metastoma.

labrum. Unpaired outgrowth arising just in front of mouth and more or less covering it; *syn.,* upper lip.

lacinia. Inner distal spiny lobe of 2nd segment of maxillule, adjacent to outer hoodlike lobe (galea).

lacinia mobilis. Small, generally toothed process articulated with incisor process of mandible.

lappet. Downhanging lateral part of carapace.

lasiopod. In Cirripedia (Lepadomorpha), appendage where rami of cirrus have setae arranged in groups along lesser curvature; like brushes (cf. ctenopod; acanthopod).

latera. *See* latus.

lateral. Plate of cirriped shell between carinolateral and rostrum; *syn.,* latus.

lateral bar. In Cirripedia (Acrothoracica), pair of chitinous thickenings (best developed in Cryptophialidae) running from chitinous apertural thickenings medially down each side of mantle sac.

lateral carina. *See* carapace carina, e.

lateral depressor pit. In cirripeds, small hollow near basitergal angle of scutum for attachment of lateral depressor muscle.

lateral gastrocardiac markings. Insertions of attractor epimeralis muscle in most Brachyura, in which the branchiocardiac groove has disappeared.

lateral margin. Differentiated edge of carapace in some advanced macrurans and many brachyurans.

lateral tooth. *See* carapace tooth, c.

latus (pl., **latera**). In cirripeds (Lepadomorpha), any of paired plates forming part of shell, not including carina and rostrum or opercular plates (scutum, tergum); *syn.,* lateral. Includes following different types:

a) **carinal.** Plate located on either side of carina, with radii on carinal side and alae on rostral side; corresponds to carinolateral in Balanomorpha.

b) **inframedian.** Plate beneath median latera in some cirripeds (e.g., *Arcoscalpellum*).

c) **lower.** Plate in some cirripeds (e.g., *Zeugmatolepas*) near basis; *syn.,* imbricate plate(s).

d) **median.** One of series of plates between carina and rostrum which may be disposed in whorls (e.g., *Scillaelepas*).

e) **rostral.** Plate located on either side of rostrum, with radii on both rostral and carinal sides; corresponds to rostrolateral in Balanomorpha.

f) **upper.** Plate between carinal and rostral latera just below opercular valves (e.g., scalpellids).

limnadiiformes. Conchostracan carapaces exhibiting recurvature of posterior margin near dorsal line, characteristic of several of the Limnadioidea; pseudorecurvature observed in some leaiids.

linea (pl., **lineae**). Linear marking on carapace.

linea anomurica. Longitudinal groove or uncalcified line on carapace of many anomuran decapods.

linea branchiostegalis. Longitudinal groove or uncalcified line extending backward from front margin of carapace slightly above branchiostegal spine and reaching to or beyond hepatic spine (e.g., palaemonid carideans).

linea dromica. Feature on carapace of dromiid crabs comparable to linea thalassinica; *syn.,* linea dromiidica.

linea dromiidica. *See* linea dromica.

linea homolica. Feature similar to linea thalassinica and possibly equivalent to it.

linea lateralis. Longitudinal groove or uncalcified line extending backward from front margin of carapace below orbit, in some forms to rear extremity of carapace (e.g., some penaeids).

linea thalassinica. Longitudinal groove or uncalcified line on dorsal part of carapace extending from anterior margin below antennal spine across entire length of carapace to its posterior edge (most thalassinoid decapods).

longitudinal septum. In cirripeds (Balanomorpha), wall of tubes disposed normal to inner and outer laminae of compartment plate and separating them; *syn.,* parietal septum.

lower lateral. Valve in shell of some cirripeds; *see* latus (lower), c.

lower lip. *See* metastoma.

male-cell receptacle. In Cirripedia (Rhizocephala), pocket or pair of pockets within mantle cavity of female into which dedifferentiated cells of male cyprid migrate and differentiate into "testes."

manca. Young of some Peracarida (e.g., Isopoda, Tanaidacea, Cumacea) in which last thoracopod is lacking.

mancoid stage. Postlarval leptostracan that differs from adult in having rudimentary 4th pleopod.

mandible. One of third pair of cephalic appendages used to masticate food.

mandible body. Inflated base (coxa) of mandible providing for attachment of mandibular muscles; *syn.*, body of mandible, corpus mandibulae.

mandibular foramen. Relatively large opening in body of mandible for passage of transverse adductor muscle.

mandibular palp. Distal articulated part of mandible that functions as aid in feeding or cleaning.

mantle. Fleshy structure of cirripeds strengthened by five calcified plates (carina, terga, scuta).

mantle cavity. Space in cirripeds occupied by body, opening by posteroventral aperture.

manus. Broad proximal part of cheliped propodus (i.e., this propodus minus fixed finger); *syn.*, palm.

marginal groove. *See* carapace groove, g.

marsupium. Brood pouch.

masticatory process. *See* gnathal lobe.

mastigobranch. Slender respiratory process at base of epipod(ite); *syn.*, mastigobranchia (pl., mastigobranchiae).

mastigopus stage. Larval stage in ontogeny of some decapods equivalent to permanent adult form of *Leucifer* (penaeid).

maxilla (pl., **maxillae**). Appendage next behind maxillule serving functions in feeding and respiration; *syn.*, second maxilla.

maxillary gland. Excretory organ located in maxillary segment, having its duct opening on maxilla; *syn.*, shell gland.

maxilliped. Anterior thoracic limb (one, two, or three) modified to act as mouth part, its body segment usually fused to cephalon.

maxillipede. *See* maxilliped.

maxillipes (pl., *maxillipedes*). *See* maxilliped.

maxillule. Cephalic appendages next behind mandible, serving as mouth part; *syn.*, first maxilla, maxillula. In cirripeds, also termed inner maxilla.

median articulated spine. Projection of telson in eocarids, seemingly not homologous with skeletal structure of any extant crustacean.

median dorsal plate. Elongate plate separating carapace valves posterodorsally (Phyllocarida Rhinocarina).

median eye. Sessile unpaired eye of nauplius larva which persists in some adults; *syn.*, naupliar eye.

median lateral. *See* latus (median), d.

megalopa stage. First postlarval stage in ontogeny of crabs, not developed in macruran decapods or other crustaceans; *syn.*, megalops stage.

megalops stage. *See* megalopa stage.

meropod(ite). *See* merus.

merus. Fourth limb segment distally from body, its proximal extremity articulating with ischium; usually forms first long segment of cheliped and pereiopod; *syn.*, meropod(ite).

mesenteron. Mid-portion of alimentary tract of endodermal origin with surface commonly increased by pouchlike extensions which serve as digestive glands and aid absorption of partly digested food; *syn.*, midgut.

mesobranchial lobe or area. Intermediate part of branchial region of decapod (brachyuran) carapace.

mesocerebrum. Ganglion of antennular somite; *syn.*, deuterocerebrum.

mesogastric lobe or area. Medial division of gastric region of decapod (brachyuran) carapace, generally pentagonal in outline with long narrow forward prolongation.

mesosome. Collective term for all free thoracic somites behind head.

mesosternum. Median plate arising from sternum in many brachyurans.

metabranchial lobe or area. Posterior part of branchial region of decapod (brachyuran) carapace.

metacerebrum. Ganglion of antennal somite; *syn.*, tritocerebrum.

metagastric lobe or area. Posterior division of gastric region of decapod (brachyuran) carapace; may be ill-defined or undifferentiated.

metanauplius. Postnaupliar larva with same general body and limb morphology as nauplius, but having additional limbs.

metasoma. *See* metasome.

metasome. In copepods, part of prosome consisting of free thoracic somites in front of major articulation; in amphipods first three abdominal somites bearing unmodified pleopods.

metastoma. Lower lip behind mandibles, usually cleft into pair of lobes termed paragnatha; *syn.*, hypostoma, hypostome, hypopharynx, labium, lower lip, paragnath.

metazoea. Last stage of zoea larva in Brachyura.

metopon. Entire preoral area in decapods, including parts of mandibular somite.

midgut. *See* mesenteron.

molar process. Grinding portion of gnathal lobe of mandible; *syn.*, pars molaris.

movable finger. Dactylus of chela.

mucro (pl., **mucrones**). Spine on inferoposteal angle of carapace in some Cladocera.

mysis stage. Post-cypris larval stage in ontogeny of most crustaceans, characterized by presence of biramous limbs on all thoracic somites; *syn.*, schizopod larva.

naupliar eye. Unpaired median eye found in naupliar larval stages and commonly in more mature stages as well; *syn.*, median eye.

nauplius (pl., **nauplii**). Early larval stage having only antennules, antennae, and mandibles.

neck organ. *See* nuchal organ.

nephropore. Elevated outlet of antennal gland, located on coxa of antenna.

notum. Posterior part of dorsal region of macruran decapod carapace.

nuchal organ. Sense organ on upper side of head in many branchiopods; *syn.,* neck organ.

occipital notch. Angulated indentation at rear of head in some conchostracans.

occludent margin. In cirripeds, margin of scutum and tergum forming aperture and occluding with comparable margins of opposed scutum.

occludent teeth. In cirripeds, small projections on occludent scutal margin formed by extensions of external growth ridges that interdigitate with similar teeth on margin of opposed scutum.

ocellus (pl., **ocelli**). Unpaired median eye, common in some branchiopods (e.g., Notostraca) and copepods (e.g., Cyclopoida) but otherwise uncommon.

ocular bulla. Knob on inner surface of carapace connecting lower and upper orbital margins with basal segment of antenna, serving for protection of eye.

ocular papilla. Anterior projection on eyestalk of some mysidaceans.

ocular penduncle. *See* eyestalk.

oesophagus. *See* esophagus.

olfactory hair. Sensory seta covered by delicate cuticle projecting from most antennules and antennae; *syn.,* aesthetasc, esthetasc, aesthete, esthete.

ommatidium (pl., **ommatidia**). Cylindrical or prismoidal visual constituent of compound eye covered by transparent cuticle (cornea).

oostegite. Inner medially directed lamella arising from coxa of pereiopod in females participating in formation of mid-ventral marsupium.

oostegopod. Appendage of genital somite in some branchiopods modified as brood pouch.

opercular valve. Movable plate in orifice of cirriped shell, one of pairs of scuta and terga joined to sheath by opercular membrane.

operculum. In cirripeds, terga, scuta and associated membranes (Balanomorpha), or tergum and scutum of one side (Verrucomorpha), forming apparatus guarding aperture.

ophthalmic somite. *See* acron.

optic lobe. Ganglion of brain for nervation of eye.

orbit. Circular opening in front part of some decapod carapaces enclosing eyestalk.

orbital carina. *See* carapace carina, f.

orbital hiatus. Gap in orbital margin of carapace at its lower (inner) angle.

orbital region. *See* carapace region, j.

orbital tooth. *See* carapace tooth, d.

orifice. Opening in upper part of cirriped shell containing opercular valves.

ostium (pl., **ostia**). Valve of heart.

oviduct. In females passageway from ovary to uterus and leading to genital aperture.

ovigerous frena (pl., **frenae**). In Cirripedia (certain Lepadomorpha), fleshy ridge or flap on interior mantle surface, adhering to and holding egg masses (ovigerous lamellae) in place.

ovigerous lamella. In Cirripedia, eggs adhering in one or more lamellae, within mantle cavity and in certain Lepadomorpha, held in position by ovigerous frenae.

palate. *See* endostome.

palm. *See* manus.

palp. Reduced distal portion of limb, usually only one of its rami, but may comprise both rami plus basis; usually consists of distal 2 or 3 segments following merus.

palp foramen. Small circular opening in body of mandible communicating with mandibular palp.

palpus (pl., **palpi**). Oval setose mandibular endopod of cirripeds, attached directly to mandible (Acrothoracica) or to lateral margin of labrum (Thoracica).

paracopulatory organ. Specialized endopod of pleopod in some Isopoda serving accessory function in copulation.

paragnath. *See* metastoma.

paries (pl., **parietes**). Median triangular part of cirriped compartment plate, with lower edge attached to basis and adjoined laterally by margins of carinal tectum.

parietal plate. One of different kinds of shell elements forming calcareous wall surrounding body of cirripeds.

parietal septum. In cirripeds, same as longitudinal septum.

parietal tube. One of myriad porelike canals in longitudinal septum of balanomorph cirripeds, disposed normal to inner and outer laminae of compartment plate and separating them; *syn.,* parietal pore, longitudinal pore, longitudinal tube.

pars ampullaris. Bottle-shaped diverticulum on entrance of caeca into pyloric chamber of stomach in syncarids.

pars incisiva. *See* incisor process.

pars molaris. *See* molar process.

parva stage. First postlarval stage in ontogeny of Caridea.

peduncle. Basal portion of certain appendages; also fleshy part of body in some cirripeds (Lepadomorpha), between capitulum and attachment to substrate with or without armor of chitinous or calcareous beads, scales, or filaments.

penicillus (pl., **penicilli**). Tuft of fine hairs resembling small brush.

penis (pl., **penes**). Male copulatory organ. [May be exceptionally long in some cirripeds.]

peraeopod. *See* pereiopod.

pereion. Anterior portion of trunk, usually provided with locomotory appendages; differs from thorax in excluding somite of maxillipeds; *syn.,* pereon.

pereionite. Thoracic somite; *syn.,* pereonite.

pereiopod. Locomotory thoracopod; *syn.,* peraeopod, pereopod, ambulatory leg, walking leg.

pereon. See pereion.

pereopod. *See* pereiopod.

pericardium. Blood sinus surrounding heart and communicating with it by pair of ostia in each somite except terminal one, may run entire length of trunk above gut.

peritrophic membrane. Chitinous sheath secreted around feces (e.g., some Ostracoda).

petasma. Abdominal appendage modified as gonapophysis in males of some eucarids, syncarids, and stomatopods.

pharynx. Part of alimentary tract next to mouth and adjoining esophagus.

photophore. Luminous organ generally located on eyestalk, limbs or abdomen of various crustaceans.

phyllobranch. Gill with leaflike filaments; *syn.,* phyllobranchia.

phyllobranchia (pl., **phyllobranchiae**). See phyllobranch.

phyllopodium (pl., **phyllopodia**). Leaflike thoracic appendage of some crustaceans (e.g., Branchiopoda) including maxillulae and maxillae of Decapoda.

phyllosoma stage. Early schizopod larval stage in ontogeny of palinurid and scyllarid lobsters.

pleomere. *See* abdominal somite.

pleon. Abdomen of crustacean.

pleonite. *See* abdominal somite.

pleopod. Limb of any of first five abdominal somites in Eumalacostrica (six in Phyllocarida), in many crustaceans adapted for swimming; *syn.,* swimmeret.

pleotelson. Structure formed by fusion of one or more abdominal somites with telson, as in most isopods.

pleura (pl., **pleurae**). *See* epimere.

pleural lobe. *See* epimere.

pleural suture. Line of splitting apart of carapace in molting, corresponding to linea dromica, and present in all brachyurans.

pleurepimere. *See* epimere.

pleurite. *See* epimere.

pleurobranch. Gill of decapods attached directly to body wall; *syn.,* pleurobranchia.

pleurobranchia (pl., **pleurobranchiae**). *See* pleurobranch.

pleuron (pl., **pleura**). *See* epimere.

pleuropod. *See* precoxa.

podobranch. Gill placed on epipods of thoracopods; *syn.,* podobranchia.

podobranchia (pl., **podobranchiae**). *See* podobranch.

podomere. Individual segment of limb; *not* syn. joint.

podophthalmite. One of 2 segments of eyestalk, articulating with basophthalmite proximally and bearing corneal surface of eye distally.

pollex. *See* fixed finger.

postabdomen. *See* telson.

postcephalic groove. *See* carapace groove, h.

postcervical groove. *See* carapace groove, i.

postcervical notch or incision. Strong indentation of carapace at level of postcervical groove (e.g., scyllarid palinurans).

posterior cardiac lobe. *See* intestinal carapace region.

posterior carina. *See* carapace carina, g.

posterior gastric pit. One of 2 small depressions near mid-line of dorsal exterior of decapod carapace marking insertion point of stomach muscle.

posterior tooth. *See* carapace tooth, e.

postlarval stage. Ontogenetic stage reached after completion of all nauplius-to-zoea or megalopa metamorphoses, marked by initial appearance of adult characters.

postorbital carina. *See* carapace carina, h.

postorbital spine. *See* carapace spine, e.

postrostral carina. *See* carapace carina, i.

postrostral spine. *See* carapace spine, f.

postsegmental region. Telson.

precoxa. Limb segment proximal to coxa, present only in certain subclasses; *syn.,* pleuropod.

pregastric tooth. *See* carapace tooth, f.

pre-epipod(ite). Secondary ramus of coxa directed outward (e.g., *Chirocephalus*).

presegmental region. *See* acron.

prezoea stage. Just-hatched larva still covered by embryonic cuticle.

primary denticle. *See* denticle; primary denticle disposed normal to suture edges of compartment plate.

primordial valve. Chitinous plate in Cirripedia (Lepadomorpha and Verrucomorpha) having a distinctive honeycomb appearance, developing at incipient umbones of terga, scuta and carina, during metamorphosis.

proctodaeum. *See* proctodeum.

proctodeum. Posterior part of alimentary canal lined with cuticle of ectodermal origin that is continuous with anus; *syn.,* hindgut, proctodaeum.

proepistome. *See* interantennular septum.

prosarthema. Scale implanted on inner margin of basal segment of antennular peduncle in Penaeidae.

prosoma. *See* prosome.

prosome. Anterior region of body, commonly limited behind by major articulation. In cirripeds, large saclike body in position of "head" in front of (and rostral from) thoracic limbs, supporting trophi and commonly first cirri.

protocephalon. *See* acron.

protocerebrum. Ganglion of first (preantennulary) somite.

protogastric lobe or area. Anterolateral division of gastric region of decapod (brachyuran) carapace.

protopod(ite). Proximal portion of limb, consisting of precoxa, coxa, and basis, fused together in some forms; its distal edge generally bearing endopod(ite) and exopod(ite); *syn.,* coxite, sympod(ite).

protozoea stage. Larval stage in ontogeny of some decapods preceding zoea stage.

proventriculus. Elaborated anterior part of alimentary canal in some crustaceans (e.g., Isopoda) adapted for pressing juices from food and straining out solid particles.

proximal. Direction toward center of body; opposite of distal.

pseudepipod(ite). Lateral ramus arising from proximal portion of exopod or from basis just proximal to exopod.

pseudorostrum. Anterior portion of gnathothorax in Cumacea, formed by pair of anterolateral parts of cephalic shield grown forward so as to meet medially in front of true rostrum.

pseudotrachea. Respiratory structure developed in pleopods of some Isopoda for air-breathing; they consist of small ramified tubules inside limb opening outward in slitlike apertures and filled with air.

pterygostome. *See* pterygostomial region.

pterygostomial region. *See* carapace region, k.

pterygostomial spine. *See* carapace spine, g.

radius (pl., **radii**). In cirripeds (Balanomorpha), lateral part of compartment plate adjoining paries, marked off from it by change in direction of growth lines and by depressed exterior surface; overlaps ala of adjoining compartment plate.

ramus. Branch of limb or other appendage (e.g., caudal furca).

raptorial claw. Generally strong, curved and toothed dactylus suited for catching prey (e.g., *Squilla*).

receptaculum seminalis. *See* seminal receptacle.

retinaculum (pl., **retinacula**). Small hook at tip of appendices internae (e.g., Caridea), one of many serving to join left and right pleopods together; *syn.,* cincinnulus.

rostral angle. In cirripeds angle of plate directed toward rostrum.

rostral carina. *See* carapace carina, j.

rostral plate. Anteriorly projecting, unpaired, movably articulated, median extension of carapace (e.g., Phyllocarida); *see* rostrum, compound rostrum.

rostral tooth. *See* carapace tooth, g.

rostrolateral. In cirripeds, one of pair of compartment plates lying between and overlapping rostrum and laterals, having radii on both rostral and cardinal sides and tending to fuse with rostrum; *see* latus (rostral), e.

rostrum. Anteriorly projecting, unpaired, usually rigid median extension of carapace between eyes or eyestalks; in cirripeds (Thoracica) unpaired valve between laterals and opposite carinal at basiscutal end of capitulum, simple and provided with alae in lower balanomorphs but compound and overlapping laterals in higher balanomorphs; *see* compound rostrum.

saw bristles. Row of heavy setae on gnathal lobe of mandible between molar and incisor processes in many Eumalacostraca, especially Peracarida.

scale. In cirripeds (Lepadomorpha), platelet on side of peduncle. *See* scaphocerite.

scaphocerite. Exopod(ite) of antenna in Eumalacostraca; *syn.,* scale. [Similar structure occurs on antennules of Leptostraca.]

scaphognath(ite). Exopod comprising boat-shaped extension of maxilla opposite endopod.

schizopod larva. Ontogenetic stage characterized by presence of biramous limbs on all thoracic somites; *syn.,* mysis stage.

scutal margin. In cirripeds, articular edge of tergum adjoining scutum, or edge of any other plate abutting scutum.

scutum (pl., **scuta**). Valve of cirriped shell opposite carina and adjacent to peduncle in some forms (Lepadomorpha) or opercular in others (Balanomorpha).

second antenna. *See* antenna.

second maxilla. *See* maxilla.

secondary denticle. *See* denticle; secondary denticle located on primary one and disposed normal to it.

segment. Individual component of crustacean limb connected by movable articulation with adjoining segments; *syn.,* podomere (not equivalent to somite, though used by some authors in this sense). (*not* joint.)

seminal receptacle. Diverticulum of oviduct or external pouch (some pygocephalomorph eocarids, isopod peracarids, and decapods) for storing spermatozoa delivered by male; *syn.,* receptaculum seminalis.

seminal vesicle. Sac in male independent of testes for storage of spermatozoa (e.g., some anostracans, Chirocephalidae); *syn.,* vesicula seminalis.

serration. Irregular saw-toothed outline on dorsal edges of some conchostracan valves where growth bands do not end on same hinge line; may have various expression from strongly serrate (e.g., Paleolimnadiopsidae) to subdued serrate (e.g., extant Caenestheriellia) and pseudoserrate (e.g., some extant *Cyzicus*).

seta (pl., **setae**). Hairlike process of cuticle with which it is articulated; in cirripeds, bristle or spine on trophi and cirri.

sexual pore. *See* gonopore.

sheath. In cirripeds (Balanomorpha), thickened upper part of internal shell wall and alae forming cylindrical collar to which opercular membrane is attached.

shell. In cirripeds, general term for hard parts of balanomorphs including compartment plates, basis (if calcareous), and opercular valves.

shell fold. Portion of carapace behind cephalic shield.

shell gland. *See* maxillary gland.

skeletal duplicature. Outer chitinous body cover of conchostracans shed during ecdysis, individual duplicatures being very thin whitish translucent layer resembling entire animal when floating in water; may occur also in notostracans and cladocerans.

somite. Division of body (head, thorax, abdomen) with exoskeleton comprising body-ring that is generally divisible into dorsal (tergite) and ventral (sternite) portions.

spermatheca. Pouch in oviduct of females for reception and retention of spermatozoa.

spermatophore. Packet of spermatozoa for transfer from male to female.

spur. In cirripeds (Balanomorpha), dependent projection on basal margin of tergum.

spur fasciole. See spur furrow.

spur furrow. In cirripeds (Balanomorpha), groove on outer surface of tergum extending to apex in line with spur; *syn.,* spur fasciole.

squama. *See* scaphocerite.

statocyst. Diminutive organ providing sense of balance, present in most crustaceans.

stenopodium. Slender, elongate limb composed of rodlike segments.

sternal canal. Internal skeletal structure of some crabs formed by meeting of sternal apodemes of opposite sides above nerve cord; may be developed as firm plate (endosternite) in anterior part of thorax.

sternal plastron. *See* sternum.

sternal process. Projection from mid-section of sternite of mysidaceans and pygocephalomorph eocarids, unknown as to function.

sternite. Sclerotized ventral surface of single body somite.

sternum (pl., **sterna**). Sternites of all body somites taken together, and abdomen; ventral segmented floor of thorax; *syn.,* sternal plastron.

stipe. Stemlike part of limb bearing squamate or other-shaped exopod (e.g., various eocarids).

stomodaeum. *See* stomodeum.

stomodeum. Anterior part of alimentary tract, ectodermal in origin and lined with cuticle continuous with mouth; includes esophagus and dilated part corresponding to stomach, and may contain so-called gastric mill of varying complexity for trituration of food; *syn.,* foregut; stomodaeum.

stridulating organ. Structure in which two parts of exoskeleton are rubbed together in order to produce sound, one part consisting of ridge or tuberculate or cross-ridged surface which is apposed to another part usually having single transverse ridge or tubercle.

stylamblys. *See* appendix interna.

style. *See* telson.

stylet. *See* caudal ramus.

stylocerite. Rounded or spiniform process on outer part of proximal segment of antennular peduncle in some decapods (e.g., natantian decapods); *syn.,* antennular scale.

subbranchial region. Ventrally placed part of brachyuran carapace corresponding in position to branchial region of dorsal part of carapace.

subcarina. In cirripeds (e.g., scalpellids), small unpaired plate below carina.

subchela. Distal extremity of limb developed as prehensile structure by folding back of dactylus against propodus or broadened part of it (e.g., Stomatopoda); may comprise propodus folded back against carpus; *syn.,* gnathopod.

subchelate. Provided with subchelae.

subesophageal ganglion. Nerve plexus below esophagus in head of malacostracans.

subhepatic carina. *See* carapace carina, k.

subhepatic region. *See* carapace region, l.

submedian carina. *See* carapace carina, l.

submedian groove. *See* carapace groove, j.

suborbital region. Narrow area bordering lower margin or orbit; may be ill-defined or indistinguishable.

suborbital spine. *See* carapace spine, h.

subrostrum. In cirripeds (e.g., scalpellids), small unpaired plate below rostrum.

suctorial structures. Mouth parts of ectoparasites modified for piercing body wall of host and for sucking out body fluids.

supra-anal plate. Portion of notostracan telson, usually tongue-shaped but may be spatulate to round; produced backward on dorsal side as a plate.

supra-esophageal ganglion. Nerve plexus above esophagus in head of malacostracans.

supraorbital carina. *See* carapace carina, m.

supraorbital spine. *See* carapace spine, i.

sutural edge. In cirripeds, margin of compartment plate along suture.

suture. In cirripeds (Balanomorpha, Verrucomorpha), line or seam at juncture of two compartment plates; also articulation line between joints.

swimmeret. *See* pleopod.

sympod(ite). *See* protopod(ite).

syncerebrum. *See* supra-esophageal ganglion.

tagma (pl., **tagmata**). Major division of body (e.g., head, thorax, abdomen), each composed of varying number of somites.

tail fan. *See* caudal fan.

tectum. Central part of carina in cirripeds (Lepadomorpha).

telopod. Part of limb distal to coxa.

telson. Last somite of body, bearing anus and commonly caudal furca or pair of cerci, growth zone for postcephalic somites located at its anterior edge; *syn.,* postabdomen, style (Archaeostraca).

telson head. Enlarged part of telson in Archaeostraca, with which furcal rami articulate.

tergal fold. *See* epimere.

tergal margin. In cirripeds (Thoracica), edge of scutum adjacent to tergum or edge of any plate abutting tergum.

tergite. Sclerotized dorsal surface of single body somite.

tergolateral margin. Angular inner edge of scutum in cirriped shells having upper laterals.

tergum (pl., **terga**). Dorsal part of exoskeleton comprising tergites of all body somites taken together; also valve of cirriped shell adjacent to carina and generally opercular.

terminal claw spines. Toothlike projections of varying size at concave end of postabdomen in cladocerans, having taxonomic value; few large *basal* spines near base of claw, minute *denticles* along greater part of claw, and spines of intermediate size grouped as *comb,* all serving for riddance of foreign particles and parasites.

thelycum. External pocket on ventral side of thorax in penaeid females which functions as seminal receptacle (receptaculum seminalis).

thoracic limb. Any limb attached to somite of thorax; *syn.,* thoracopod.

thoracomere. Somite of thorax.

thoracopod(ite). Limb attached to any thoracic somite; *syn.,* thoracic limb. [Maxillipeds and pereiopods are thoracopods.]

thorax. Tagma between cephalon and abdomen comprising anterior portion of trunk, last somite bearing most posterior genital pore or just anterior to this pore-bearing somite and nearly always limb-bearing; *syn.,* cormus (not precise equivalent of pereion).

thumb. *See* fixed finger.

transverse septum. Thin wall of cirripeds normal to longitudinal septum and parallel to basis, dividing parietal tubes into series of cells.

trichobranch. Gill of filamentous structure with hairlike projections from axis (e.g., crayfish); *syn.,* trichobranchia.

trichobranchia (pl., **trichobranchiae**). *See* trichobranch.

tritocerebrum. *See* metacerebrum.

trophi. Mouth parts of cirripeds, including labrum, mandibles, maxillules, maxillae, palpi, and in some, first pair of cirri.

trunk. Postcephalic portion of body; *syn.,* thorax.

umbo. Apical portion of either valve of bivalved crustaceans (e.g., Conchostraca, Phyllocarida); in cirripeds, central point on plate from which successive growth increments extend.

umbonal spine. Hollow, minute to large spinose projection of conchostracan carapace that may involve entire umbo; may be curved, looped, or represented as node or nipple. [Larval condition characteristic in Vertexiidae.]

upcurved growth lines. Upwardly bent growth lines covering tear in conchostracan shell-margin at site of injury.

upper lateral. Plate of some cirriped shells; *see* latus (upper), f.

upper lip. *See* labrum.

urogastric lobe or area. Posterior division of gastric region of decapod (brachyuran) carapace; sometimes called genital region.

uropod(ite). Limb of sixth abdominal segment of Eumalacostraca, generally fanlike but may be reduced or modified.

urosoma. See urosome.

urosome. In copepods, part of body behind major articulation marking posterior boundary of prosome; in amphipods, last three abdominal somites bearing modified appendages.

valve. Lateral part of divided carapace commonly joined to opposite part by hingement along dorsal mid-line (e.g., Ostracoda, Conchostraca, Leptostraca).

vas deferens. Duct in males for passage of spermatozoa from testis to penis.

ventral nerve chain. Ganglia or connectives on somites joined by single or double nerve cord running longitudinally beneath alimentary canal.

ventral platform. Part of archaeostracan telson head embracing proximal extremities of furcal rami.

vertex. Top part of head (cephalon).

vesicula seminalis. *See* seminal vesicle.

walking leg. *See* pereiopod.

wrist. *See* carpus.

zoea stage. Larval stage in ontogeny of various malacostracans but unknown in some.

ONTOGENY

EGGS AND LARVAL STAGES

Crustaceans hatch from eggs which in some groups (e.g., commonly in various branchiopods, ostracodes, cirripeds, isopods) are produced parthogenetically but generally by sexual fertilization. These may be released in extraordinary numbers directly into water surrounding females or carried in brood pouches until ready for hatching, but (except in very few) without releasing viviparous young. In some branchiopods (e.g., Cladocera) the brood pouch is located dorsally between the carapace valves. Among malacostracans, the Peracarida carry eggs in a brood pouch formed by overlapping plates (oostegites) borne by the bases of some of the thoracic limbs, and in Decapoda the eggs are attached to abdominal appendages of females.

A common denominator in the ontogeny of crustaceans is the larval stage of development known as the **nauplius** (Fig.

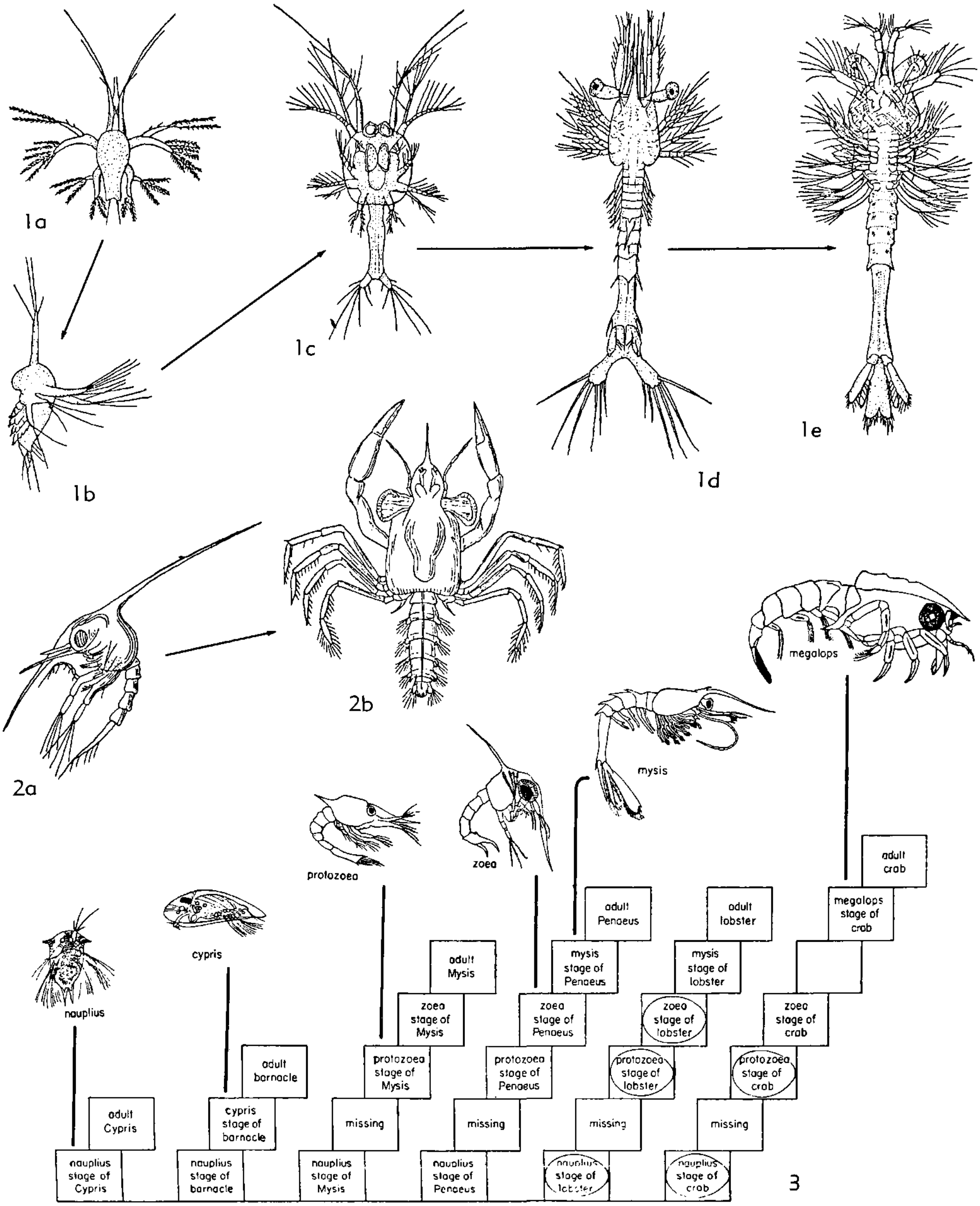


FIG. 35. Ontogeny of Crustacea (stages in ovals confined to eggs, others free-living). [For megalops, read megalopa.]

1. Larval stages of penaeid prawns (eucarid Malacostraca); *1a,* nauplius, ×53; *1b,* metanauplius, ×47; *1c,* zoea, ×25; *1d,* metazoea, ×23; *1e,* mysis, ×14.

2. Larval stages of crabs (decapod Malacostraca); *2a,* zoea, characterized by elongate cephalic spines, ×23; *2b,* megalopa stage of swimming crab, *Ovalipes,* ×11.7.

3. Recapitulation of larval stages in several crustacean groups (not to scale).

[*1-2,* from F. A. Chace in *Encyclopedia of science and technology,* by permission, McGraw-Hill Book Company, copyright, 1960; *3,* mod. from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill Book Company, copyright 1949.]

35,*1a*), which prevails widely as the first larval stage after hatching, or if not so, is suppressed within the egg (Schmitt, 1965, p. 35). The nauplius is a very minute, unsegmented, egg-shaped fore-runner of one or more successive larval stages or of next-following adult forms (e.g., cypris stage, Fig. 35). It is broadest in front, where a median eye provides vision. Behind this are three pairs of appendages—uniramous antennules, biramous antennae, and biramous mandibles. The mouth, covered by a large labrum, leads directly to a slender alimentary canal in which foregut, midgut, and hindgut are recognizable. In branchiopods and ostracodes transformation of the nauplius into juveniles and adults is gradual, with addition of somite after somite in successive molts by intercalation in front of the terminal somite (telson) of the abdomen. Immature instars may be numerous. Early stages in this process which differ perceptibly from the initial nauplius but which have not yet attained adult form are called metanauplii (Fig. 35,*1b*).

Recognition of the cirripeds as crustaceans is affirmed by their ontogeny, in which a free-swimming cyprid larval stage is particularly significant (Fig. 21,*1a-c;* 35,*3;* see Fig. 39,*2a,b*).

In the various crustacean classes post-nauplial larval stages named cypris, protozoea, zoea, mysis, and megalopa are recognized (Fig. 35), as well as several additional special ones. These differ vastly from one another in appearance and correspondingly in their morphological features, but tend generally to approach adults of their group. Most of the larval forms swim freely at or near the water surface. The commonly setose nature of their appendages and development of spinous processes, which in some are remarkably extended, undoubtedly serve as aids in flotation. Literally dozens of molts may occur during larval life, and still others after maturity is attained. Larval metamorphoses are entirely suppressed in crayfishes and river crabs, but this is not true of most other fresh-water crustaceans. A few marine crabs are known to be hatched with near-adult form, being thus decided exceptions to the rule.

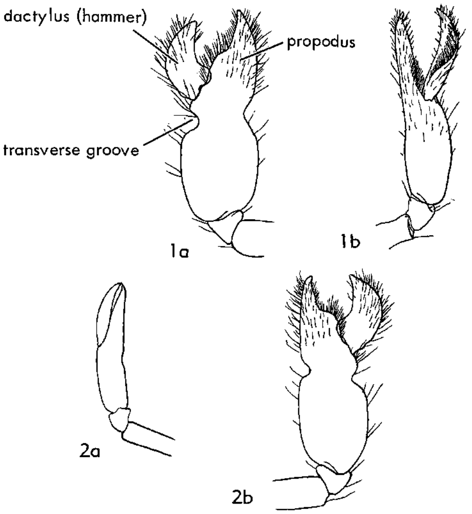


Fig. 36. Regeneration of appendages in Crustacea, illustrated by snapping shrimp, *Alpheus heterochelis,* in this instance accompanied by reversal in placement of larger and smaller front chelipeds, ×2.3 (mod. from Wilson, 1903).——*1a,b.* Chelipeds of left-handed male from North Carolina coast.——*2a,b.* Left and right chelipeds immediately after molting, small left one regenerated on stump of original larger cheliped with hammer-like dactylus and grooved propodus.

MOLTING AND GROWTH

A characteristic feature of crustaceans is molting of the exoskeleton effected by periodic resorption of some of the materials of the old skeleton and secretion of a thin new integument beneath it. The old skeleton, with lining of the front and rear ends of the alimentary canal is then (usually but not invariably) shed or molted. At the same time, by addition of water, the soft parts swell to a distinctly larger size beneath the thin elastic flexible new skeleton which later quickly hardens to form a relatively rigid cover. The molting process is termed **ecdysis.**

ADULTS AND LIFE DURATION

Adulthood is distinguished by qualitative stability of morphological features, for changes at times of molting become re-

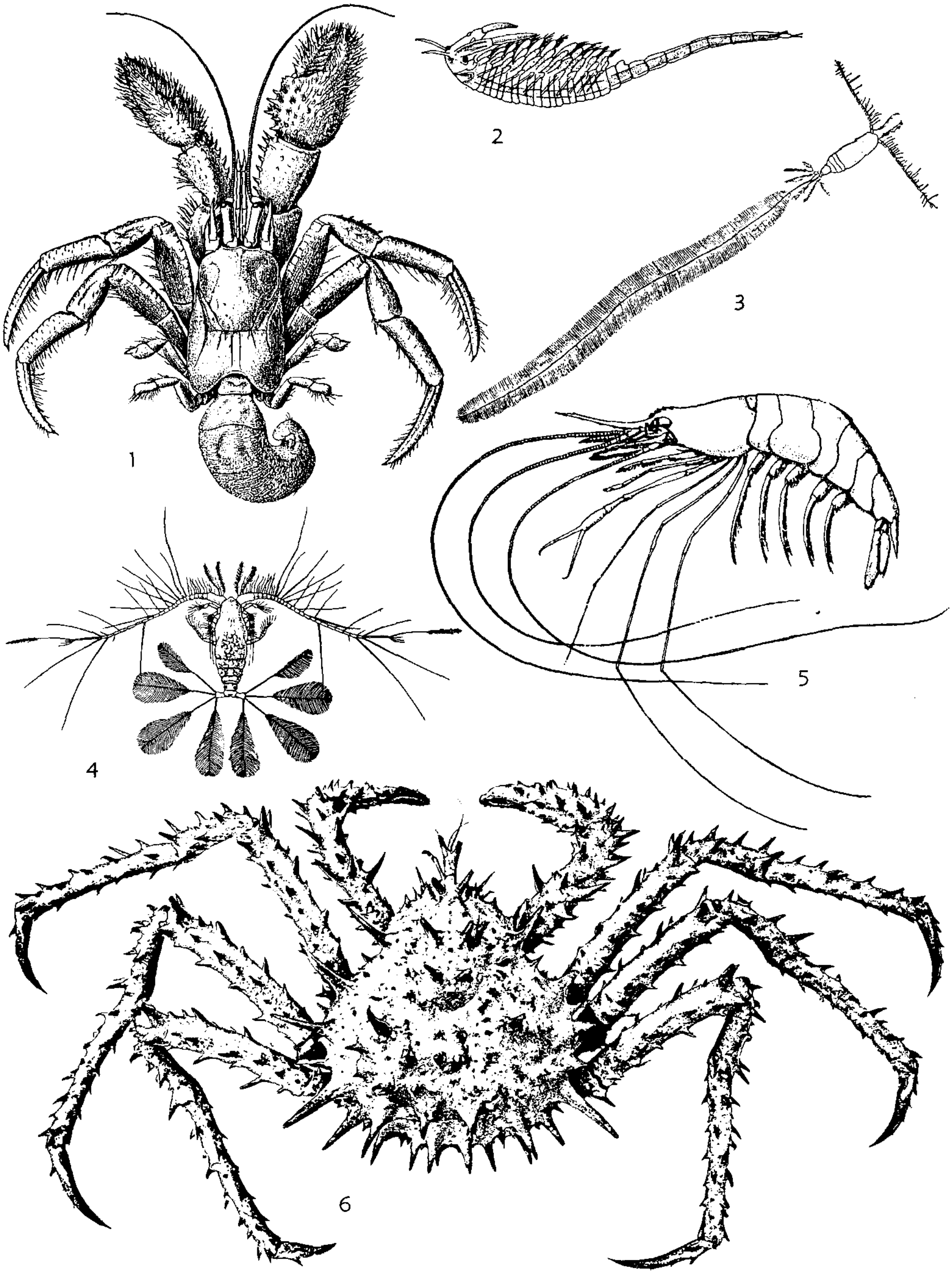


FIG. 37. Adaptation of Crustacea to diverse habitats and modes of life.

1. Dorsal view of hermit crab, *Pagurus setosus,* removed from snail shell which protects soft, asymmetrically twisted abdomen and into which most of crab's body can be withdrawn, ×0.7. This species lives along the Pacific coast of North America from Alaska to California at depths of 100 to 500 m. Other hermit crabs inhabit beaches above tidewater and range considerably in size.

2. Brine shrimp, *Artemia,* an anostracan branchiostricted to mere growth in size. No longer are external and internal structures modified significantly and no additions of somites or their appendages appear. Many species seem not to grow beyond an approximate limit in size, whereas others continue to increase in dimensions and bulk throughout life.

The duration of adult existence of most crustaceans is quite unknown. It may be measured in days or weeks in the case of some branchiopods but certainly in years for many balanomorph cirripeds and malacostracans. SCHMITT (1965, p. 110-111) has reported that the average life span of some crabs is three years and of others approximately 12 years. He estimated that probably the longest-lived among modern crustaceans are giant American lobsters *(Homarus americanus)* off the New England coast, for which a 35-pound individual was judged to be about 50 years old. The largest yet-caught specimen, with body length of two feet and weight of 44.5 pounds, on similar basis would be approximately 65 years old, an ancient patriarch.

AUTOTOMY AND REGENERATION

Appendages which are lost are regenerated during subsequent molting stages. Anostracan branchiopods such as *Artemia* have this ability to a marked degree, and it has been shown that regeneration is more rapid in salt water than in fresh water. Injured valves of conchostracans may show deformation in growth lines at points of repair.

Autotomy, or breaking-off of injured limbs, is demonstrated by decapods and various other crustaceans. The injured appendage is dropped at a preformed breaking plane by means of a reflex muscle action. A blood clot forms at the breaking plane, then a bud, which grows into a new limb, appears beneath the scar. The resulting regenerated limb may differ from the original; asymmetry of chelae may be reversed when the larger chela is lost, the regenerated one becoming a small cutting chela and the uninjured one assuming the crushing abilities (Fig. 36). When the eye stalk of a living lobster or prawn is removed, it may be replaced by an antenna. This is heteromorphic regeneration.

ADAPTATION

MODES OF LIFE

Crustaceans are generally aquatic animals, both marine and fresh-water, although they inhabit many diverse environments. Some live on land, in rock crevices, earth burrows or in trees, and some are parasites living on or within nearly every kind of animal, including other crustaceans. Body structures and appendages are adapted according to requirements of their habits and habitats.

FIG. 37. *(Continued from facing page.)*

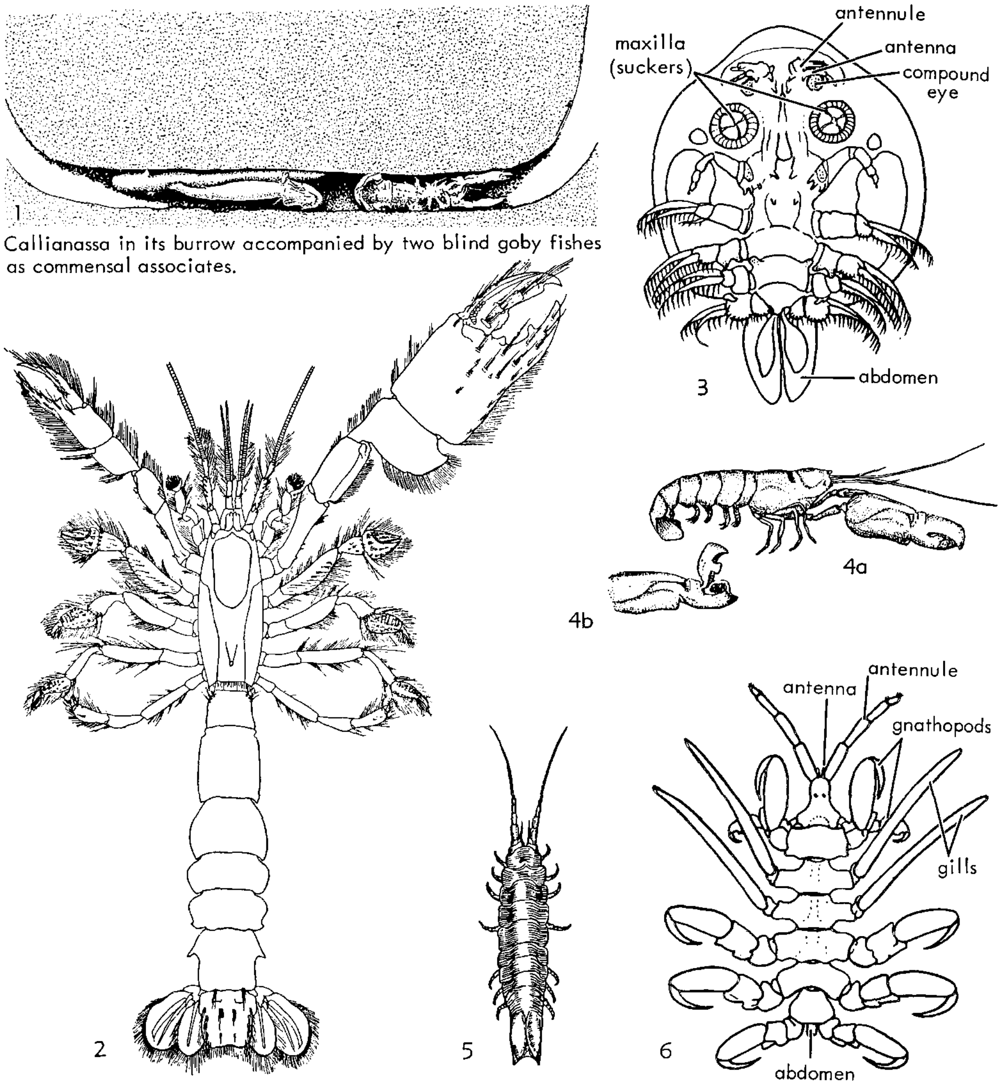
pod adapted to existence in hypersaline lakes and lagoons, where populations may be extremely large, ×3.3.

3-4. Open-ocean planktonic copepods with setose appendages which aid in flotation.——*3. Calocalanus* sp., ×10.——*4. C. pavo,* ×11.

5. Caridean prawn, *Palaemon tenuipes,* a decapod malacostracan adapted for living in brackish-water lagoons and estuaries, with very elongate and slender pereiopods supplementing antennules and antennae as feelers, ×0.7.

6. Female pagurid crab, *Paralithodes rathbuni,* from sea bottom off California coast at depth of 400 m. These crabs, relatives of hermit crabs, have abandoned use of mollusk shells for housing and with stout carapace of their own move about freely, females retaining asymmetry of ventral abdominal plates, ×0.5.

[*1,6,* from Schmitt, 1921; *2-3,* from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill Book Company, copyright 1949; *4,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *5,* from W. Buddenbrock in H. G. Bronn, *Klassen und Ordnungen des Tierreichs,* by permission, Akademische Verlagsgesellschaft, publ.]



Callianassa in its burrow accompanied by two blind goby fishes as commensal associates.

Fig. 38. Adaptation of Crustacea, including commensalism and parasitism.

1-2. Burrow-building shrimplike decapod, *Callianassa,* which is adapted to existence in shallow-sea mud bottoms and in gravelly beaches.——*1.* Longitudinal section of *Callianassa*-made permanent burrow in southern California beach sand, occupied by male *(C. affinis)* in feeding position and accompanied by pair of small commensal fishes. In this association a pair of shrimps invariably are hosts to a pair of fishes, each pair proportional to the other in size (small shrimps with small fishes and larger shrimps with larger fishes).——*2.* Dorsal view of female *C. goniophthalmus* from sea bottom off California coast at depth of 500 m., ×0.7.

3. Branchiuran fish louse, *Argulus japonicus*, common ectoparasite on goldfishes; ventral view of female, enl.

4. Pistol shrimp, *Alpheus californiensis,* a beach dweller; *4a,* side view of entire shrimp, ×0.7; *4b,* cocked claw of cheliped, ×0.7.

5. Marine isopod, *Pentidotea resecata,* which lives on stems of seaweeds, orienting its slender body along the stem and closely resembling the weed in color, thus gaining protection by inconspicuousness, ×0.7.

6. Caprellidean amphipod, *Paracyamus boopis,* so-called whale louse, because ectoparasitic on whales; dorsal view of male, ×4.

[*1,4-5,* from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill Book Company, publ., copyright 1949; *2,* from Schmitt, 1921; *3,6,* from S. F. Light *et al., Intertidal invertebrates of central California coast,* by permission, University of California Press, publ.]

The endopods of thoracic and abdominal limbs are modified to perform various functions: locomotion, respiration, food-gathering, cleansing, defense, reproduction, and sensory perception. The planktonic types of crustaceans have long feathered setae and antennae enabling them to float (Fig. 37, *3-4*). If an animal is predatory, the chelae (or subchelae in stomatopods) of one or more thoracic limb pairs are specialized and enlarged for capturing and tearing food (Fig. 25, 26, 30). Burrowers have slender bodies to aid in burrowing and slipping into crevices (Fig. 38,*1-2*).

Deep-sea forms usually are blind or nearly so, but free-swimmers living near the surface have well-developed eyes and other sense organs. Certain types have phosphorescent or luminous organs called photophores which emit light and may be used for illumination in searching for food and detecting enemies. Those that have become terrestrial have special organs for respiration; the vascular lining of the carapace performs this function in land crabs, whereas in wood lice (Isopoda) breathing is accomplished through invaginations of the abdominal limb integuments.

Parasitic and commensal forms have prehensile devices for attachment, structures modified for piercing skin of the host, and sucking organs, and may lose appendages for locomotion (Fig. 38,*3*).

Cephalocarida and Mystacocarida are exclusively benthonic marine crustaceans living from the intertidal zone to depths of 300 meters. They are diminutive deposit-feeders, living in the loose, organic-rich sediment of the subtidal zone and are unable to swim.

Most Branchiopoda inhabit fresh to brackish and slightly alkaline water in lakes and temporary ponds among weedy vegetation, although *Artemia* is found in salt lakes and briny pools (Fig. 37,*2*). *Triops* survives periods of desiccation; in fact, the eggs normally require a drying-out period prior to hatching. Branchiopods swim, crawl, or burrow in muddy substrates, feeding on algae and diatoms. Notostracan branchiopods occur commonly in temporary lakes and ponds and even alkaline pools, crawling on bottom and feeding on detritus including parts of larger organisms. Eggs in mud distributed by birds and in dried mud may be viable even after 15 years. Transported hermaphroditic populations possibly explain geographic distribution of species.

Copepoda are prevalent in all open-ocean areas, as well as fresh-water environments (Fig. 20); many forms are pelagic, but most are benthonic (Fig. 37,*3,4*). Cyclopoid and harpacticoid species may construct cysts for survival during anaerobic periods. Ostracoda thrive in virtually all kinds of aquatic environments, ranging from streams, lakes, temporary ponds, and brackish estuaries or lagoons to shallow seas and intermediate and abyssal depths in oceans. In the fossil record a preponderant majority of ostracode species consist of shallow marine bottom-dwellers.

Cirripedia are marine animals except for a few which live in brackish water. They attach themselves to rocks, seaweed, hulls of ships and floating objects, some forms exhibiting parasitism on larger animals, and some are commensal with fishes and whales (Fig. 21, 22).

Among Malacostraca the numerous varied groups exhibit adaptations to many different environments and modes of life. The Phyllocarida are predominantly marine, Leptostraca being strong swimmers but also adapted for burrowing in the mud in shallow coastal waters (Fig. 19,*8*). Phyllocarids are found in depths ranging to 6,000 meters, although some (e.g., *Caryocaris*) are planktonic; most are bottom-dwellers. Eocarids (Fig. 17,*2-3*) were marine scavengers probably living in coastal lagoons and swamps. Extant Syncarida inhabit fresh water (Fig. 18,*3-4*), although many fossil species were marine. They are nektonic to benthonic, microphagous to carnivorous, as shown by variations in development of eyes and maxillipeds. Most groups of Peracarida are predominantly marine, occurring at all depths; many are benthonic detritus-feeders burrowing and building tubes in the substrate.

Dominantly pelagic malacostracans include the carnivorous or detritus-feeding Mysidacea (Fig. 18,*1-2,11*) and Euphausiacea (Fig. 24,*4*), which are main food sources of many marine fishes and whales. The Cumacea (Fig. 18,*5*) and Tanaidacea (Fig.

18,*9*) are mainly crawlers and burrowers in shallow sea-bottom mud, but many range to abyssal depths. A majority of the Isopoda (Fig. 19,*2;* 23,*1-11*) and Amphipoda (Fig. 19,*7*) also are marine (e.g., *Limnoria,* a ubiquitous isopod wood-borer) and found at most depths. Both of these groups include fresh-water and terrestrial members, however. Some degenerate isopods infest other crustaceans as parasites (Fig. 33, *2*) and are vicious enemies of fishes; likewise, amphipods include such ectoparasites as the whale louse *Paracyamus* (Fig. 38,*6*). Ability to live in the water of hot springs and in underground waters is a feature of the Thermosbaenacea. Mimicry and concealment are illustrated by such isopods as the slender-bodied *Idotea* (Fig. 38,*5*), which orient themselves parallel to seaweed stems and assume coloration identical with them.

Only the Isopoda rival the Decapoda in variety of effective adaptation to living habits and habitats. Decapods may be strong swimmers (Fig. 17,*1;* 24,*2,5-8;* 25,*1-2,6;* 26,*4*) and many are able to burrow swiftly to moderate depths in sea-bottom or fresh-water sediment (Fig. 25,*3-5;* 26,*1,5,7,11*) or on land, along streams, or on shores (e.g., *Callianassa,* Fig. 38,*1-2*). Numerous crabs can scuttle over the earth surface and robber crabs are adept at climbing trees. The hermit crabs (Fig. 37,*1*) are peculiarly specialized for using empty snail shells for protection, with the naked abdomen twisted into coils of the shell interior. Fiddler crabs (Fig. 36,*1-2*) and pistol shrimps (Fig. 38,*4*) are examples of unusual adaptations, the first for effective burrowing and the second seemingly for offensive-defensive protection. Long persistence of acquired adaptive characters is illustrated by the stout-shelled lithodid crabs (Fig. 37,*6*), which have abandoned an ancestral mode of life like that of hermit crabs and become suited to a free existence, while retaining asymmetry of the abdomen inherited from shell-inhabiting predecessors.

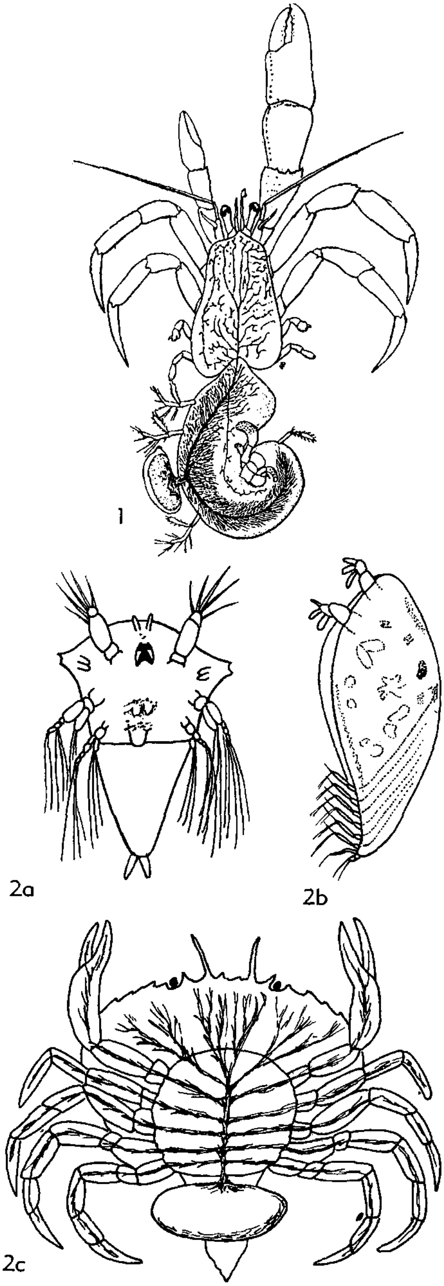


FIG. 39. Crustacean parasites illustrated by rhizocephalan cirripeds preying on crabs.——*1. Peltogaster pagurus* (rhizocephalan) on hermit crab, *Pagurus bernhardus,* saclike body of parasite containing viscera and eggs visible on left side of crab's twisted naked abdomen, with food-gathering roots permeating its host's abdomen and thorax, ×0.7 (from Paul Krüger in H. G. Bronn, *Klassen und Ordnungen des Tierreichs,* by permission, Akademische Verlagsgesellschaft, publ.).——*2. Sacculina carcini; 2a,b,* nauplius stage (dorsal) and cypris stage (lateral) larvae, much enl; *2c,* ventral view of crab with attached adult female rhizocephalan distinguished by saclike body and roots penetrating interior and appendages of crab, ×0.7 (from Stempell).

COMMENSALISM AND PARASITISM

Only one genus of Branchiopoda, the cladoceran *Anchistropus,* is known to be parasitic (on *Hydra*). Certain ostracodes are parasitic on fishes and other crustaceans. Caligoid copepods are parasitic or commensal on fish, attached by the head, the mouth being modified for sucking and hooklike mandibles adapted to pierce the skin of the host. Lernaeopodoid copepods, the so-called fish maggots, are ectoparasites, which as larvae bury themselves in the walls of the mouth cavity or gill chamber of salmon and other fishes to feed on body fluids. Some copepods embed themselves in the eyes or other organs of fishes, hard-shelled mollusks, nudibranchs, and in other crustaceans, and may live their entire life cycle on or within the host. Those that live on marine annelid worms have degenerated to become limbless, being attached by a tubular branched structure within the host. Branchiuran argulids are external parasites which fasten themselves by means of powerful discs; their antennae are equipped with hooks and spines to further grip the surface of fishes (Fig. 38,*3*).

Cirripedia contain several parasitic orders, the Acrothoracica being content to occupy shells of other barnacles, corals, snails, clams and other animals after boring into them. The Ascothoracica are external or internal parasites of echinoderms or coelenterates obtaining sustenance from the body of the host. The highly parasitic Rhizocephala are world-wide in distribution (Fig. 39). They infest other crustaceans, principally Decapoda, and have no appendages or typical crustacean features, but consist of a thin-walled sac enclosing a visceral mass containing reproductive organs. They penetrate the abdomen of the host by means of a threadlike root which branches in all directions to absorb nourishment (Fig. 39, *1,2c*). The crustacean nature of these parasites is affirmed by their larval development which passes through nauplius and cypris stages (Fig. 39,*2a,b*). The larvae hatch out and settle on another decapod host, where the life cycle is repeated.

Epicaridean isopods (Fig. 33,*2*) are ectoparasitic on other crustaceans (copepods, ostracodes, mysidaceans, euphausiaceans, isopods, amphipods, parasitic cirripeds, and decapods). Caprellidean amphipods (Cyamidae) are ectoparasites on whales (Fig. 38,*6*). Decapods are commensal with mollusks, sponges, echinoderms, and ascidians.

CLASSIFICATION

In older classification, as previously noted, all crustaceans were divided into groups termed Entomostraca and Malacostraca. The first included a heterogeneous assemblage of mostly small forms now included in classes (or subclasses) named Cephalocarida, Branchiopoda, Ostracoda, Copepoda, Branchiura, Euthycarcinoida, Mystacocarida, and Cirripedia. The category of crustaceans consisting of so-called entomostracans has long been abandoned. The Malacostraca, on the other hand, persist in classification. They contain most of the larger crustaceans with a thorax of eight somites and an abdomen containing seven or eight somites. A majority of the higher crustaceans grouped in the Malacostraca are medium-sized to large marine forms.

The development of crustacean classification, with notice of the numerous divergent arrangements advocated by authors, is not outlined in this chapter. Instead, it is judged sufficient to summarize here the classification adopted in the *Treatise* with statement of the stratigraphic occurrence of suprageneric taxa and record of numbers of genera and subgenera contained in them as given by *Treatise* authors.

It should be explained that a very large number of extant genus-group taxa unknown as fossils are not included in systematic descriptions of *Treatise* chapters on crustacean groups and these necessarily are omitted from tabulation. The magnitude of such omissions can be indicated by very incomplete information on numbers of extant genera of the Mysidacea and Isopoda.

Tattersall & Tattersall (1951) have described 40 genera of British mysidaceans and Tattersall (1951) has recorded genera of the same group known from North America, the latter including numerous forms found also in Britain, as well as 24 additional genera. The total of 64 genera is only part of the mysidacean fauna of the world. The *Treatise* contains no description and illustration of an extant mysidacean. Including fossil forms, the *Treatise* lists 29 genera of isopods (Trias.-Rec.), only a few of which are represented by living species from any part of the world. By way of contrast, Richardson (1905) described 128 genera of North American isopods and Van Name (1936) added 72 genera to the isopod fauna of the same continent. Many of these 190 forms are fresh-water and terrestrial.

OUTLINE OF TREATISE CLASSIFICATION OF CRUSTACEA

An outline of classification of crustaceans adopted in the *Treatise* is given in the following tabulation, which shows supra-generic taxa down to subfamily rank, accompanied by records of geologic occurrence and numbers of included genera. The last-mentioned data provide information on numbers of subgenera additional to nominotypical ones which are differentiated in some family groups, as well as numbers of doubtfully recognized genera. For example, the notation "(41+?20;3)" indicates recognition of 41 genera, 20 doubtfully recognized genera, and 3 subgenera other than nominotypical ones.

Totals include only genus-group taxa for which systematic descriptions are given in the *Treatise*. Suprageneric taxa recorded as ranging to the Recent contain an unspecified number (generally large) of additional Recent genera not listed in the *Treatise*.

Treatment of the Crustacea as a super-class and its main divisions as classes has been discussed adequately by Manton in a preceding chapter (p. *R*3). Here it is desirable merely to add that complexity of the taxonomic hierarchy above the genus-group rank in the Malacostraca, for example, furnishes intrinsic justification for recognizing categories designated as super-orders within a subclass, infraorders within a suborder, and sections within an infra-order. Either family or superfamily may be the next lower-rank assemblage within an order, suborder, infraorder, or section.

Main Divisions of Crustacea Exclusive of Ostracoda

- Crustacea *(superclass)* (833+?20;46). *Cam.-Rec.*
- Cephalocarida *(class)* (2). *Rec.*
  - Brachypoda *(order)* (2). *Rec.*
    - Hutchinsoniellidae (1). *Rec.*
    - Lightiellidae (1). *Rec.*
- Branchiopoda *(class)* (99+?20;3). *L.Dev.-Rec.*
  - Calmanostraca *(subclass)* (10). *L.Dev.-Rec.*
    - Notostraca *(order)* (2). *U.Carb.-Rec.*
      - Triopsidae (2). *U.Carb.-Rec.*
    - Kazacharthra *(order)* (7). *L.Jur.*
      - Ketmeniidae (7). *L.Jur.*
    - Acercostraca *(order)* (1). *L.Dev.*
      - Vachonisiidae (1). *L.Dev.*
  - Diplostraca *(subclass)* (75+?20:3). *L.Dev.-Rec.*
    - Conchostraca *(order)* (56+?20;3). *L.Dev.-Rec.*
      - Laeviscaudata *(suborder)* (1). *L.Cret.-Rec.*
        - Lynceidae (1). *L.Cret.-Rec.*
      - Spinicaudata *(suborder)* (55+?20;3). *L.Dev.-Rec.*
        - Limnadioidea *(superfamily)* (7+?5). *Carb.-Rec.*
          - Limnadiidae (5+?5). *Carb.-Rec.*
            - Limnadiinae (2). *Rec.*
            - Estheriininae (3+?5). *Carb.-L.Cret.*
          - Cyclestheriidae (1). *Rec.*
          - Leptestheriidae (1). *Rec.*
        - Cyzicoidea *(superfamily)* (18+?11;2). *L.Dev.-Rec.*
          - Cyzicidae (6+?9;2). *L.Dev.-Rec.*
          - Asmussiidae (12+?2). *L.Dev.-U.Cret.*
            - Asmussiinae (9). *L.Dev.-U.Cret.*
            - Torgalykiinae (3+?2). *Dev.-U.Jur.*
        - Estherielloidea *(superfamily)* (4+?1;1). *U.Carb.-L.Cret.*
          - Estheriellidae (4+?1;1). *U.Carb.-L.Cret.*
            - Estheriellinae (3;1). *U.Carb.-L.Cret.*
            - Monoleiolophinae (1+?1). *Penn.-L.Cret.*
        - Leaioidea *(superfamily)* (13). *M.Dev.-L.Cret.*
          - Leaiidae (13). *M.Dev.-L.Cret.*
        - Vertexioidea *(superfamily)* (13+?3). *L.Carb.-Rec.*
          - Vertexiidae (6). *L.Carb.-U.Trias.*
          - Limnadopsidae (3+?2). *L.Carb.-Rec.*
          - Pemphilimnadiopsidae (1). *Penn.*
          - Ipsiloniidae (3+?1). *Dev.-L.Cret.*
    - Cladocera *(order)* (19). *Oligo.-Rec.*
      - Eucladocera *(suborder)* (18). *Oligo.-Rec.*

- Sidoidea *(superfamily)* (1). *Rec.*
  - Sididae (1). *Rec.*
- Daphnioidea *(superfamily)* (15). *Oligo.-Rec.*
  - Daphniidae (1). *Oligo.-Rec.*
  - Chydoridae (13). *Rec.*
    - Chydorinae (12). *Rec.*
    - Eurycercinae (1). *Rec.*
  - Bosminidae (1). *Rec.*
- Polyphemoidea *(superfamily)* (2). *Rec.*
  - Polyphemidae (2). *Rec.*
- Haplopoda *(suborder)* (1). *Rec.*
  - Leptodoridae (1). *Rec.*
- Sarsostraca *(subclass)* (14). *L.Dev.-Rec.*
  - Anostraca *(order)* (13). *L.Dev.-Rec.*
    - Artemiidae (1). *Pleist.-Rec.*
    - Branchipodidae (4). *?U.Carb., ?Eoc., Rec.*
    - Branchinectidae (1). *Rec.*
    - Chirocephalidae (2). *Rec.*
    - Polyartemiidae (1). *Rec.*
    - Streptocephalidae (1). *Rec.*
    - Thamnocephalidae (1). *Rec.*
    - Gilsonicarididae (1). *L.Dev.*
    - Uncertain family (1). *U.Carb.*
  - Lipostraca *(order)* (1). *M.Dev.*
    - Lepidocarididae (1). *M.Dev.*
- Mystacocarida *(class)* (1). *Rec.*
  - Mystacocaridida *(order)* (1). *Rec.*
    - Derocheilocarididae (1). *Rec.*
- Euthycarcinoidea *(class)* (2). *L.Trias.-M.Trias.*
  - Euthycarcinida *(order)* (2). *L.Trias.-M.Trias.*
    - Euthycarcinidae (2). *L.Trias.-M.Trias.*
- Copepoda *(class)* (2). *Mio.-Rec.*
  - Calanoida *(order)*. *Rec.*
  - Cyclopoida *(order)* (1) *Mio.-Rec.*
    - Genus undetermined (1). *Mio.*
  - Harpacticoida *(order)* (1). *Mio.-Rec.*
    - Cletodidae (1). *Mio.-Rec.*
  - Caligoida *(order)*. *Rec.*
  - Notodelphyoida *(order)*. *Rec.*
  - Lernaeopodoida *(order)*. *Rec.*
  - Monstrilloida *(order)*. *Rec.*
- Branchiura *(class)* (4). *Rec.*
  - Arguloida *(order)* (4). *Rec.*
    - Argulidae (4). *Rec.*
- Cirripedia *(class)* (107;29). *U.Sil.-Rec.*
  - Acrothoracica *(order)* (12). *Carb.-Rec.*
    - Pygophora *(suborder)* (7). *Rec.*
      - Lithoglyptidae (6). *Rec.*
      - Cryptophialidae (1). *Rec.*
    - Apygophora *(suborder)* (1). *Carb.-Rec.*
      - Trypetesidae (1). *Carb.-Rec.*
    - Suborder uncertain (4). *Trias.-Plio.*
      - Rodgerellidae (1). *M.Jur.-L.Plio.*
      - Zapfellidae (3). *Trias.-Plio.*
  - Rhizocephala *(order)* (11). *Rec.*
    - Kentrogonida *(suborder)* (5). *Rec.*
      - Peltogastridae (1). *Rec.*
      - Sacculinidae (1). *Rec.*
      - Lernaeodiscidae (1). *Rec.*
      - Clistosaccidae (1). *Rec.*
      - Sylonidae (1). *Rec.*
    - Akentrogonida *(suborder)* (5). *Rec.*
    - Uncertain affinities (1). *Rec.*
  - Ascothoracica *(order)* (12). *Cret.-Rec.*
    - Synagogidae (3). *Rec.*
    - Lauridae (3). *Rec.*
    - Petrarcidae (1). *Rec.*
    - Dendrogastridae (3). *Rec.*
    - Uncertain family (2). *U.Cret.*
  - Thoracica *(order)* (72;29). *U.Sil.-Rec.*
    - Lepadomorpha *(suborder)* (38;9). *U.Sil.-Rec.*
      - Cyprilepadidae (1). *U.Sil.*
      - Praelepadidae (1). *M.Carb.*
      - Scalpellidae (17;3). *U.Trias.(Rhaet.)-Rec.*
      - Heteralepadidae (2). *Rec.*
      - Iblidae (1). *Rec.*
      - Koleolepadidae (1). *Rec.*
      - Lepadidae (4;2). *?U.Trias., M.Eoc.-Rec.*
      - Malacolepadidae (1). *Rec.*
      - Oxynaspididae (1). *M.Eoc.-Rec.*
      - Poecilasmatidae (3;4). *U.Eoc.(Barton.)-Rec.*
      - Stramentidae (3). *Cret.(Alb.-Senon.).*
      - Uncertain family (3). *Rec.*
    - Verrucomorpha *(suborder)* (3;4). *U.Cret. (?Cenoman.-U.Senon.)-Rec.*
      - Verrucidae (3;4). *U.Cret.(?Cenoman.-U.Senon.)-Rec.*
    - Brachylepadomorpha *(suborder)* (2). *U.Jur. (Tithon.)-U.Mio.(Helvet.).*
      - Brachylepadidae (2). *U.Jur.(Tithon.)-U.Mio. (Helvet.).*
    - Balanomorpha *(suborder)* (29;16). *U.Cret. (U.Senon.)-Rec.*
      - Chthamalidae (9;2). *U.Cret.(U.Senon.)-Rec.*
      - Balanidae (20;14). *M.Eoc.-Rec.*
        - Balaninae (9;11). *M.Eoc.(Auvers.)-Rec.*
        - Tetraclitinae (1;2). *Oligo.-Rec.*
        - Chelonibiinae (1). *L.Mio.-Rec.*
        - Coronulinae (8;1). *U.Mio.-Rec.*
        - Emersoniinae (1). *U.Eoc.*
- Malacostraca *(class)* (586;14). *L.Cam.-Rec.*
- Phyllocarida *(subclass)* (52). *L.Cam.-Rec.*
  - Leptostraca *(order)* (4). *U.Perm.-Rec.*
    - Nebaliidae (4). *U.Perm.-Rec.*
  - Hymenostraca *(order)* (1). *?L.Cam., M.Cam.-L.Ord.*
    - Hymenocarididae (1). *?L.Cam., M.Cam.-L.Ord.*
  - Archaeostraca *(order)* (22). *L.Ord.-U.Trias.*
    - Ceratiocarina *(suborder)* (15). *L.Ord.-U.Trias.*
      - Ceratiocarididae (4). *L.Ord.-L.Dev., ?Carb., ?U.Perm.*
      - Austriocarididae (2). *M.Dev.-U.Trias.*
      - Echinocarididae (5). *L.Dev.-L.Miss.*
        - Echinocaridinae (3). *L.Dev.-L.Miss.*
        - Montecaridinae (2). *?L.Dev., M.Dev.-U.Dev.*
      - Pephricarididae (1). *U.Dev.*
      - Aristozoidae (3). *?M.Ord., U.Sil.-M.Dev.*
    - Rhinocarina *(suborder)* (7). *?Sil., L.Dev.-M.Penn., ?U.Perm.*
      - Rhinocarididae (6). *?Sil., L.Dev.-M.Penn., ?U.Perm.*

- Ohiocarididae (1). *U.Dev.*
- Uncertain order and family (25). *L.Cam.-L.Carb., L.Perm.*
- *Nonphyllocarid and uncertain genera formerly attributed to Phyllocarida*
  - Forms referred to order Discinocarina (3). *L.Cam.-U.Trias., ?L.Jur.*
    - Discinocarididae (1). *M.Ord.-U.Trias., ?L.Jur.*
    - Peltocarididae (2). *?L.Cam.-?M.Cam., ?L. Ord., U.Ord.-U.Sil., ?U.Perm.*
  - Uncertain genera (19). *M.Cam.-U.Trias.*
- Eumalacostraca *(subclass)* (534;14). *M.Dev.-Rec.*
- Eocarida *(superorder)* (14). *M.Dev.-Perm.*
  - Eocaridacea *(order)* (6). *M.Dev.-Penn.*
    - Eocarididae (2). *M.Dev.*
    - Palaeopalaemonidae (1). *U.Dev.-L.Miss.*
    - Anthracophausiidae (3). *Miss.-Penn.*
  - Pygocephalomorpha *(order)*. (8). *Miss.-Perm.*
    - Tealliocarididae (2). *L.Carb.*
    - Pygocephalidae (4). *Miss-Penn.*
    - Notocarididae (2). *Perm.*
- Syncarida *(superorder)* (20). *U.Miss.-Rec.*
  - Palaeocaridacea *(order)* (6). *U.Miss.-Perm.*
    - Palaeocarididae (3). *U.Miss.-Perm.*
    - Uronectidae (1). *L.Perm.*
    - Acanthotelsonidae (1). *Penn.*
    - Pleurocarididae (1). *Penn.*
  - Anaspidacea *(order)* (5). *Trias.-Rec.*
    - Anaspididae (3). *Trias.-Rec.*
    - Koonungidae (2). *Rec.*
  - Bathynellacea *(order)* (5). *Rec.*
    - Bathynellidae (5). *Rec.*
  - Stygocaridacea *(order)* (3). *Perm-Rec.*
    - Stygocarididae (2). *Rec.*
    - Clarkecarididae (1). *Perm.*
    - Uncertain order and family (1). *Trias.*
- Peracarida *(superorder)* (47). *Perm.-Rec.*
  - Mysidacea *(order)* (5). *Trias.-Rec.*
    - Lophogastrida *(suborder)* (1). *Rec.*
    - Mysida *(suborder)* (2). *Trias.-Rec.*
      - Uncertain family (2). *Trias-U.Jur.*
    - Uncertain suborder and family (3). *M.Jur.*
  - Thermosbaenacea *(order)* (2). *Rec.*
    - Thermosbaenidae (2). *Rec.*
  - Spelaeogriphacea *(order)*. *Rec.*
  - Cumacea *(order)* (1). *U.Perm.-Rec.*
    - Uncertain family (1). *M.Jur.*
  - Tanaidacea *(order)* (2). *Perm.-Rec.*
    - Monokonophora *(suborder)* (1). *Perm.-Rec.*
      - Uncertain family (1). *U.Perm.-M.Jur.*
    - Dikonophora *(suborder)*. *Rec.*
    - Uncertain suborder and family (1). *L.Jur.*
  - Isopoda *(order)* (29). *Trias.-Rec.*
    - Gnathiidea *(suborder)*. *Rec.*
    - Anthuridea *(suborder)*. *Rec.*
    - Flabellifera *(suborder)* (15). *Trias.-Rec.*
      - Cirolanidae (1). *?Mio., Rec.*
      - Sphaeromatidae (10). *Trias.-Rec.*
        - Sphaeromatidae Hemibranchiatae group (2). *?Mio., Rec.*
        - Uncertain group (8). *Trias.-Pleist.*
      - Archaeoniscidae (1). *Jur.*
      - Serolidae. *Rec.*
      - Uncertain family (3). *M.Trias.-Plio.*
    - Valvifera *(suborder)* (2). *Oligo.-Rec.*
      - Idoteidae (2). *Oligo.-Rec.*
        - Mesidoteinae (2). *Oligo.-Rec.*
    - Asellota *(suborder)*. *Rec.*
    - Oniscoidea *(suborder)* (6). *Eoc.-Rec.*
      - Trichoniscidae (1). *U.Eoc.-Rec.*
        - Trichoniscinae (1). *Eoc.-Rec.*
      - Oniscidae (1). *U.Eoc.-Rec.*
        - Oniscinae (1). *U.Eoc.-Rec.*
      - Porcellionidae (2). *U.Eoc.-Rec.*
      - Armadillidiidae (2). *Mio.-Rec.*
    - Phreatoicidea *(suborder)* (3). *Perm.-Rec.*
      - Amphisopidae (1). *Trias.-Rec.*
      - Palaeophreatoicidae (2). *Perm.*
    - Epicaridea *(suborder)*. *?U.Jur., Rec.*
    - Uncertain suborder (1). *Jur.-Cret.*
      - Urdidae (1). *Jur.-Cret.*
    - Doubtful genera (2). *Jur.*
  - Amphipoda *(order)* (6). *U.Eoc.-Rec.*
    - Gammaridea *(suborder)* (6). *U.Eoc.-Rec.*
      - Gammaridae (6). *U.Eoc.-Rec.*
    - Caprellidea *(suborder)*. *Rec.*
      - Caprellidae. *Rec.*
      - Cyamidae. *Rec.*
    - Hyperiidea *(suborder)*. *Rec.*
    - Ingolfiellidea *(suborder)*. *Rec.*
    - Uncertain suborder. *Dev.*
  - Anthracocaridacea *(order)* (2). *Miss.*
    - Anthracocarididae (2). *Miss.*
- Eucarida *(superorder)* (421;14). *Permotrias.-Rec.*
  - Euphausiacea *(order)* (4). *Rec.*
    - Bentheuphausiidae (1). *Rec.*
    - Euphausiidae (3). *Rec.*
  - Decapoda *(order)* (417;14). *Permotrias.-Rec.*
    - Dendrobranchiata *(suborder)* (15). *Permotrias.-Rec.*
      - Penaeidea *(infraorder)* (15). *Permotrias.-Rec.*
        - Penaeoidea *(superfamily)* (14). *Permotrias.-Rec.*
          - Penaeidae (12). *Permotrias.-Rec.*
          - Uncertain family (2). *U.Cret.*
        - Sergestoidea *(superfamily)* (1). *Rec.*
          - Sergestidae (1). *Rec.*
    - Pleocyemata *(suborder)* (396;14). *Permotrias.-Rec.*
      - Stenopodidea *(infraorder)* (1). *Rec.*
        - Stenopodidae (1). *Rec.*
      - Uncinidea *(infraorder)* (1). *L.Jur.*
        - Uncinidae (1). *L.Jur.*
      - Caridea *(infraorder)* (14). *M.Jur.-Rec.*
        - Atyidae (2). *Tert.-Rec.*
        - Oplophoridae (2). *?U.Jur., ?U.Cret., Rec.*
        - Palaemonidae (5). *Tert.-Rec.*
        - Udorellidae (1). *U.Jur.*
        - Uncertain family (4). *M.Jur.-U.Cret.*
      - Astacidea *(infraorder)* (31,2). *Permotrias.-Rec.*
        - Erymidae (11;1). *Permotrias.-U.Cret., ?Paleoc.*

- Eryminae (5;1). *L.Jur.-U.Cret., ?Paleoc.*
- Clytiopsinae (6). *?Permotrias., L.Trias.-U.Trias.*
- Platychelidae (2). *U.Trias.*
- Nephropidae (13;1). *M.Jur.-Rec.*
  - Nephropinae (4). *U.Cret.-Rec.*
  - Homarinae (3;1). *Cret.-Rec.*
  - Neophoberinae (3). *M.Jur.-Rec.*
  - Uncertain subfamily (3). *?M.Jur., U.Jur.-U.Cret.*
- Astacidae (2). *U.Jur. or L.Cret.-Rec.*
- Parastacidae (2). *Pleist.-Rec.*
- Austroastacidae (1). *Rec.*
- Palinura *(infraorder)* (37;2). *?L.Trias., M.Trias.-Rec.*
  - Glypheoidea *(superfamily)* (11;1). *?L.Trias., M.Trias.-L.Tert.*
    - Glypheidae (4;1). *?L.Trias., M.Trias.-L.Tert.*
    - Mecochiridae (5). *M.Trias.-U.Cret.*
    - Pemphicidae (2). *M.Trias.*
  - Eryonoidea *(superfamily)* (11). *U.Trias.-Rec.*
    - Tetrachelidae (1). *U.Trias.*
    - Coleiidae (2). *L.Jur.-L.Cret.*
    - Eryonidae (4). *L.Jur.-L.Cret.*
    - Polychelidae (4). *M.Jur.-Rec.*
  - Palinuroidea *(superfamily)* (15;1). *L.Jur.-Rec.*
    - Palinuridae (9;1). *L.Jur.-Rec.*
    - Cancrinidae (1). *U.Jur.*
    - Scyllaridae (5). *L.Cret.-Rec.*
- Anomura *(infraorder)* (43). *L.Jur.-Rec.*
  - Thalassinoidea *(superfamily)* (12). *L.Jur.-Rec.*
    - Thalassinidae (1). *?Pleist., Rec.*
    - Axiidae (5). *L.Jur.-Rec.*
    - Laomediidae (2). *Mio.-Rec.*
    - Callianassidae (4). *U.Jur.-Rec.*
      - Callianassinae (2). *U.Cret.-Rec.*
      - Protocallianassinae (1). *?L.Cret., U.Cret.-Paleoc.*
      - Upogebiinae (1). *U.Jur.-Rec.*
  - Paguroidea *(superfamily)* (16). *L.Jur.-Rec.*
    - Pylochelidae (1). *Rec.*
    - Paguridae (12). *Jur.-Rec.*
      - Pagurinae (2). *L.Cret.-Rec.*
      - Diogeninae (6). *U.Cret.-Rec.*
      - Uncertain subfamily (4). *Jur., ?L.Cret.-?U.Cret.*
    - Coenobitidae (1). *?L.Mio., Rec.*
    - Lithodidae (1). *Rec.*
    - Lomidae (1). *Rec.*
  - Galatheoidea *(superfamily)* (12). *M.Jur.-Rec.*
    - Galatheidae (9). *M.Jur.-Rec.*
      - Galatheinae (4). *L.Cret.-Rec.*
      - Munidopsinae (1). *Rec.*
      - Uncertain subfamily (4). *M.Jur.-U.Cret.*
    - Aeglidae (1). *Rec.*
    - Porcellanidae (2). *U.Cret.-Rec.*
  - Hippoidea *(superfamily)* (3). *Tert.-Rec.*
    - Albuneidae (2). *Tert.-Rec.*
    - Hippidae (1). *Rec.*
- Brachyura *(infraorder)* (269;10). *L.Jur.-Rec.*
  - Dromiacea *(section)* (41;2). *L.Jur.-Rec.*
    - Dromioidea *(superfamily)* (33;2). *L.Jur.-Rec.*
      - Eocarcinidae (1). *L.Jur.*
      - Prosopidae (13;2). *M.Jur.-Cret., Rec.*
        - Prosopinae (4). *M.Jur.-L.Cret.*
        - Pithonotinae (7;2). *M.Jur.-U.Cret.*
        - Homolodromiinae (2). *Rec.*
      - Dromiidae (3). *Paleoc.-Rec.*
      - Dynomenidae (10). *U. Jur.-Rec.*
      - Uncertain family (6). *U.Jur.-U.Cret., ?Paleoc.*
    - Homoloidea *(superfamily)* (5). *U.Jur.-Rec.*
      - Homolidae (5). *U.Jur.-Rec.*
    - Dakoticancroidea *(superfamily)* (3). *U.Cret.*
      - Dakoticancridae (3). *U.Cret.*
  - Oxystomata *(section)* (59;2). *L.Cret.(Alb.)-Rec.*
    - Dorippoidea *(superfamily)* (8). *L.Cret.(Alb.)-Rec.*
      - Dorippidae (8). *L.Cret.(Alb.)-Rec.*
        - Dorippinae (3). *L.Cret.(Alb.)-Rec.*
        - Tymolinae (5). *L.Cret.(Alb.)-Rec.*
    - Calappoidea *(superfamily)* (34). *L.Cret.-Rec.*
      - Calappidae (19). *L.Cret.-Rec.*
        - Calappinae (15). *L.Cret.-Rec.*
        - Matutinae (4). *?L.Cret., M.Tert.-Rec.*
      - Leucosiidae (15). *?L.Eoc., M.Eoc.-Rec.*
    - Raninoidea *(superfamily)* (17;2). *L.Cret.(Alb.)-Rec.*
      - Raninidae (17;2). *L.Cret.(Alb.)-Rec.*
  - Oxyrhyncha *(section)* (30;2). *?U.Cret., Eoc.-Rec.*
    - Majidae (24). *?U.Cret., Eoc.-Rec.*
      - Majinae (6). *?U.Cret., Eoc.-Rec.*
      - Micromaiinae (3). *Eoc.-Oligo.*
      - Inachinae (6). *U.Eoc.-Rec.*
      - Pisinae (6). *Mio-Rec.*
      - Acanthonychinae (3). *Plio-Rec.*
    - Parthenopidae (5;2). *Eoc.-Rec.*
      - Parthenopinae (4;2). *M.Eoc.-Rec.*
      - Eumedoninae (1). *Rec.*
    - Uncertain family (1). *Mio.*
  - Cancridea *(section)* (9). *Eoc.-Rec.*
    - Corystidae (1). *Rec.*
    - Atelecyclidae (4). *Eoc.-Rec.*
    - Cancridae (4). *M.Eoc.-Rec.*
      - Cancrinae (3). *Mio.-Rec.*
      - Lobocarcininae (1). *M.Eoc.-U.Eoc.*
  - Brachyrhyncha *(section)* (118;4). *Cret.-Rec.*
    - Portunoidea *(superfamily)* (22;2). *U.Cret.-Rec.*
      - Portunidae (17;2). *Eoc.-Rec.*
        - Portuninae (6;2). *Eoc.-Rec.*
        - Macropipinae (2). *Oligo.-Rec.*
        - Carcininae (4). *L.Eoc.-Rec.*
        - Psammocarcininae (3). *L.Eoc.-L.Oligo.*
        - Podophthalminae (2). *Oligo.-Rec.*
      - Carcineretidae (5). *U.Cret.*
    - Xanthoidea *(superfamily)* (85;2). *U.Cret.-Rec.*
      - Xanthidae (46). *U.Cret.-Rec.*
      - Potamidae (1). *U.Tert.-Rec.*
      - Geryonidae (4;2). *Eoc.-Rec.*
      - Goneplacidae (21). *?U.Cret., Paleoc.-Rec.*
        - Goneplacinae (3). *Eoc.-Rec.*
        - Carcinoplacinae (11). *Paleoc.-Rec.*

Prionoplacinae (3). *Oligo.-Rec.*
Hexapodinae (3). *?U.Cret., Eoc.-Rec.*
Uncertain subfamily (1). *Mio.*
Pinnotheridae (3). *Eoc.-Rec.*
Grapsidae (8). *M.Eoc.-Rec.*
Grapsinae (2). *Oligo.-Rec.*
Varuninae (3). *?M.Eoc.,U.Eoc.-Rec.*
Sesarminae (1). *U.Oligo. or L.Mio.-Rec.*
Uncertain subfamily (2). *M.Eoc.-U.Eoc., ?Oligo.*
Gecarcinidae (2). *Plio.-Rec.*
Ocypodoidea *(superfamily)* (7). *M.Eoc.-Rec.*
Ocypodidae (6). *M.Eoc., Mio.-Rec.*
Ocypodinae (2). *Plio.-Rec.*
Macrophthalminae (2). *Mio.-Rec.*
Uncertain subfamily (2). *M.Eoc., L.Mio.*
Retroplumidae (1). *M.Eoc.-Rec.*
Uncertain superfamily (4). *?L.Cret.-U.Cret., ?M.Eoc., Rec.*
Palicidae (4). *?L.Cret.-?U.Cret., ?M.Eoc., Rec.*
Brachyura of uncertain status (12)
Decapoda of uncertain status (4).
Genera questionably assigned to Decapoda (2)
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CEPHALOCARIDA

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[Chapter submitted January, 1962]

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MORPHOLOGY

GENERAL FEATURES

The body (Fig. 40) consists of a horseshoe-shaped cephalon, an eight-somite thorax, and a 12-somite abdomen (including the telson). Both the cephalon and thorax bear flat pleura, which are directed somewhat backward on the thoracic somites. On the cephalon the pleural lobes are continuous with each other anteriorly. Pleural lobes are reduced to posteriorly directed spines on the abdominal somites.

On the middle of the ventral surface of the cephalon is a conspicuous **labrum** which projects distinctly ventrally and posteriorly past the mouth, forming the floor of the **atrium oris.** There are five pairs of cephalic appendages: two pairs of antennae, a pair of mandibles, and two pairs of maxillae (Fig. 40).

Each thoracic somite bears a limb, except in *Lightiella,* where they are absent on the eighth. The first abdominal somite has a pair of reduced limbs which form genital appendages. The telson bears a well-developed caudal furca. The other abdominal somites lack appendages.

(On facing page.)

Fig. 40. Morphology of adult cephalocarid, *Hutchinsoniella macracantha* Sanders, ventral view, showing striking similarity of maxillae and all thoracic limbs, ×64 (9).