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INTRODUCTION

The review of crustacean metamorphoses given in this paper contains little that will be new to carcinologists, except perhaps a few accompanying unorthodox ideas. The paper is written for students in general zoology and is recommended reading for entomologists, who commonly think of metamorphosis as a phenomenon pertaining particularly to insects. It is true that the metamorphoses of insects and of crustaceans have no relation to each other, and have little in common, but a preliminary discussion of both will help in arriving at a general understanding of the nature of metamorphosis as it occurs in the arthropods.

The first treatise on metamorphosis was written by Ovid in about the year A.D. 7, but the metamorphoses that Ovid described were mostly the transformations of members of the human species into animals, trees, or rocks, willed by the ancient gods or goddesses in revenge against some mortal that had offended them. The metamorphoses imposed on animals by nature are not punishments, extreme as they may be in some cases, but are beneficent changes of form to better accommodate the individuals of a species temporarily to a more advantageous way of living. The young butterfly, for example, transformed in the egg into a wormlike caterpillar, is not an elegant creature as are its parents, but from a practical standpoint the caterpillar is perfectly adapted to its chief function, which is that of feeding.

The metamorphoses of Crustacea differ essentially from those of insects in that they pertain to a much earlier stage of development. The young insect hatches from the egg usually with the definitive number of body segments. The insects are thus *epimorphic;* but if the young insect has taken on a metamorphosed form in its embryonic development, it appears on hatching as a creature quite different from its parents. Yet a caterpillar, for example, is actually a winged juvenile stage of the butterfly corresponding with the so-called nymphal stage of a grasshopper. The principal difference between the two is that the wings of the young grasshopper develop externally, and those of the caterpillar grow internally within pockets of the skin beneath the cuticle. Likewise, a "legless" fly maggot has legs developing in pouches of the skin covered by the cuticle. A young grasshopper goes over directly into a mature grasshopper; the caterpillar, the maggot, and others of their kind, when full grown with plenty of food stored in their bodies, must undergo a second transformation in a pupal stage to be restored to the parental form. This is the usual course of metamorphosis among the insects.

Most of the Crustacea, on the other hand, hatch at an early stage of embryonic development, though at varying periods of immaturity, when they have only a few body segments and corresponding appendages. During their development after hatching they successively add new segments and appendages until the definitive number is attained. The majority of crustaceans are thus *anamorphic* in their manner of postembryonic growth, though a few are epimorphic.

Anamorphosis involves a change of form during development, but it is merely a way of growing, common to crustaceans, diplopods, and some chilopods. It should not be confused with changes of form that have nothing to do with progressive development toward the adult; such changes constitute a true *metamorphosis*. The metamorphoses of Crustacea are changes of form that the growing animal may take on at successive stages of its anamorphic growth, including the sexually mature stage of many parasitic species. In such cases, metamorphosis has been superposed on anamorphosis. As Gurney (1942) has said, "it may be assumed that development in the Crustacea was primitively a continuous process of growth and addition of somites and limbs, as we find it to be in some branchiopods, and that abrupt changes between successive moults leading to the origin of definable phases are secondary responses to changes in the habit of life of the larva and adult." Gurney notes an apparent exception to this rule in the Euphausiacea and some Penaeidae, in which the larva and the adult lead much the same kind of life. The successive phases of development in these two groups, however, are mainly stages of anamorphic growth; their only metamorphosis is the adaptation of the larval appendages for swimming.

Insect larvae may undergo metamorphic changes of form during their growth, but with the insects this larval *heteromorphosis,* commonly called "hypermetamorphosis," affects the fully segmented young insect, and is therefore not comparable to the heteromorphic larval growth of most Crustacea. Some metamorphosed young insects transform directly into the adult, but most of them first undergo a reconstruction in a special, proimaginal pupal stage. Among the Crustacea there is no transformation stage strictly comparable to the insect pupa.

True metamorphic forms are not recapitulations of phylogenetic stages in the evolution of a species. An insect larva, though often wormlike in appearance, does not represent a worm stage in the ancestry of insects. A caterpillar has a modern insect head and mouth parts, a well-developed tracheal system, and wings growing beneath its cuticle. No worm, ancestral or otherwise, was ever thus equipped. Among the Crustacea also most juvenile forms assumed during the larval growth are temporary adaptations to a changed mode of life and are not phylogenetic recapitulations. Yet, it is true that former ancestral characters discarded somewhere along the line of evolution may appear in the ontogeny of the individual, and it is often difficult to determine what phases of development are recapitulatory and what are metamorphic aberrations. The following hypothetical example will make clear the distinction between the two, and will lead to a practical definition of metamorphosis.

If the eggs of birds regularly hatched into reptilelike creatures, which later transformed into feathered fowls, the change of form would literally be a metamorphosis; but, since birds have been derived from reptilian ancestors, it might be specifically a case of phylogenetic recapitulation. On the other hand, if there issued from the bird's egg a creature having no relation to anything in the avian line of adult evolution, but which still finally transformed into a bird, the change of form would be one of quite a different nature, and it is this kind of change that will be regarded as metamorphic in the following discussions. As here defined, therefore, *metamorphosis* is a structural change at any time in the life history of an animal that may be regarded as an aberration from the ancestral direct line of adult development which followed approximately the phylogenetic course of evolution of the species. In this case metamorphosis may affect the embryo, the larva, or the adult. Simple development without metamorphic interpolations might then be termed *orthomorphosis*.

In the higher Crustacea there is a tendency for hatching to take place at later and later stages of ontogeny, leaving a correspondingly lesser amount of development to be accomplished after the larva leaves the egg. Finally a condition is reached when body segmentation and appendage formation are complete or almost so at hatching; the animal then becomes epimorphic in its development. In an epimorphic arthropod, the embryonic development may proceed by the method of anamorphosis, or the entire body may be first laid down as a germ band.

In the second case segmentation appears later, usually progressing from before backward, suggesting that it represents a former anamorphic mode of segment formation in which the anterior segments are the oldest. Since anamorphic growth, either in the larva or the embryo, is characteristic of the annelid worms and recurs in so many of the arthropods, it was probably the primitive method of growth in the annulate animals.

The most immature larval form among the arthropods is the crustacean nauplius. For practicable purposes early hatching must be given up by terrestrial animals, unless they go back to the water to lay their eggs, as do the land crabs, frogs, and toads. The anamorphic myriapods do not quit the egg until they have acquired the adult type of structure and are equipped with a sufficient number of legs for terrestrial locomotion. The completely epimorphic spiders and insects are best fitted to cope at once on hatching with the conditions of their environment, and they have become the most successful of the land arthropods. Though some insects lay their eggs in the water and the young are aquatic, they are simply terrestrial forms that have become secondarily adapted in the larval stage for life in the water; they hatch at the same stage as their relatives on land.

The Crustacea are primarily aquatic animals; only a few have become adapted to a permanent life on land. The eggs of most species are laid in the water, and the newly hatched young must be capable of swimming; the adults can later adopt a bottom habitat if they acquire ambulatory legs. Considering the uniformity of the water environment of a swimming larva, there is relatively little inducement for a young aquatic animal to undergo adaptive metamorphoses. The metamorphoses of most crustacean larvae, therefore, are relatively simple as compared with those of insect larvae, which have a great diversity of habitats open to them. Parasitic crustaceans, however, are a conspicuous exception to this generalization.

As a rule small animals in the water are eaten by larger animals, but the small creatures have one recourse against their possible predators and that is to become parasitic on them. Parasites, however, have to be structurally adapted to a parasitic life, and consequently most parasites undergo metamorphic changes. Many of the smaller crustaceans have adopted parasitism, and the most extreme degrees of crustacean metamorphosis are found among such species, especially if the adults themselves remain parasites. Such adults in some cases have lost all resemblance to the ancestral forms of their race, even every mark of their crustacean ancestry. Moralists may cite the "degeneration" of such parasites as a warning of what parasitism may lead to, but actually parasites are highly specialized for the life they lead by a simplification of structure and the elimination of all unnecessary organs, which were indispensable to their free-living ancestors. In fact, no sympathy need be wasted on "degenerate" parasites; give them credit for having found a simple and easy way of living, though at the expense of another creature. They have discarded all useless equipment, and some of them have devised most ingenious ways of attacking the host.

The control of metamorphosis by hormones has been extensively studied in insects, but apparently no comparable studies have been made on the role of hormones in the metamorphosis of crustaceans. It is well known that hormones are produced in the eyestalks of decapods, and the source of the eyestalk hormones has usually been referred to two organs known as the *sinus gland* and the *X organ*. However, from recent investigations (see Bliss and Welsh, 1952; Passano, 1953) it is now known that the so-called sinus "gland" is not a gland but a complex of the enlarged ends of nerve fibers proceeding from the X organ and from numerous neurosecretory cells in the brain, in the ganglia of the optic lobe, and in the thoracic ganglia. The sinus "gland" is therefore a receiving and distributing center for various hormones. Functions that have been attributed to these hormones include the movement of pigment in the compound eye, regulation of chromatophore activity in the integument, control of moulting, and the rate of development of the ovaries. Knowles (1953) gives evidence that the chromatophores are activated also by neurosecretory cells in the region of the tritocerebral commissure and the postcommissural nerves. The control of moulting by lengthening the period between moults was attributed by Passano to the X organ, which is itself a neurosecretory tissue in the proximal ventral part of the medulla terminalis of the optic lobe. Removal of both sinus "glands" has no effect on moulting since the hormone can escape from the cut ends of the nerves. Panouse (1946) also, in a study of *Leander,* had claimed that the "sinus gland" produces a hormone that normally blocks the growth of tissues and thus causes a lengthening of the intermoult period and retards the maturing of the ovaries.

From later work by Gabe (1953) and Echalier (1954), however, it now appears that moulting, at least in the Malacostraca, is controlled by a pair of ductless glands in the antenno-maxillary region. These glands, discovered by Gabe, are named by him the Y organs, and were demonstrated to be present in 58 malacostracan species, ranging from *Nebalia* to the decapods and stomatopods. In species in which the excretory gland is maxillary, the Y organs are in the antennal segment; in those having antennal glands they lie in the second maxillary segment. Each gland is implanted on the epidermis by an enlarged base and is innervated from the suboesophageal ganglion; in form it is conical, lenticular, or foliaceous. From their histological structure and changes during the intermoult period, Gabe shows that the Y organs are comparable to the thoracic endocrine glands of holometabolous insects, and he suggests that they have something to do with moulting. Following this suggestion, Echalier (1954) made experimental tests by removing the organs. He found that bilateral ablation of the glands, when not made too late after they had already discharged their secretion, resulted in a very great lengthening of the intermoult period, far in excess of the usual time between moults. Echalier, therefore, contends that the Y organs are crustacean endocrine glands for the control of moulting. That they do not disappear in the adult as do the thoracic glands of insects, Gabe points out, follows from the fact that the crustaceans continue to moult in the adult stage.

I. EVOLUTION OF THE ARTHROPODS

In any discussion of arthropod metamorphosis the question of recapitulation always comes up in relation to the larval forms. If there is any ancestral recapitulation in ontogeny, it then becomes necessary to have at least a theoretical concept of the evolution of the arthropods and some idea of what ancestral forms they had that might be recapitulated in the development of the individual.

The evolutionary origin of the arthropods is hidden in remote Pre-Cambrian times, so probably we shall never know the facts from visual evidence. There is, however, ample evidence from a study of modern forms to indicate that the early progenitors of the arthropods were closely related to the progenitors of the annelid worms, and that these two groups of annulate animals had a common ancestor. The fundamental characters preserved in the annelid–arthropod organization are: an elongate segmented body, an alimentary canal extending through the length of the body, a paired ventral nerve cord with segmental ganglia, a somatic musculature, and mesodermal coelomic sacs. We may therefore visualize the primitive annulate as a very simple, wormlike creature having these features. The mode of development was anamorphic, new segments being formed in a subterminal zone of growth. From this primitive segmented worm the annelids have been directly evolved with little addition other than the development of segmental groups of lateral bristles, which in the polychaetes have been carried out on movable lateral lobes of the segments, the so-called parapodia, that serve for swimming and burrowing.

By a different type of specialization for locomotion, members of another branch from the ancestral stock developed ventrolateral, lobelike outgrowths of the body segments, and thus became walking animals. These primitive legs eventually evolved into the jointed appendages of modern arthropods, the lobelike origin of which is still recapitulated in the embryo. At the lobopod stage of evolution (fig. 1 A) the animals resembled a modern onychophoran, and are

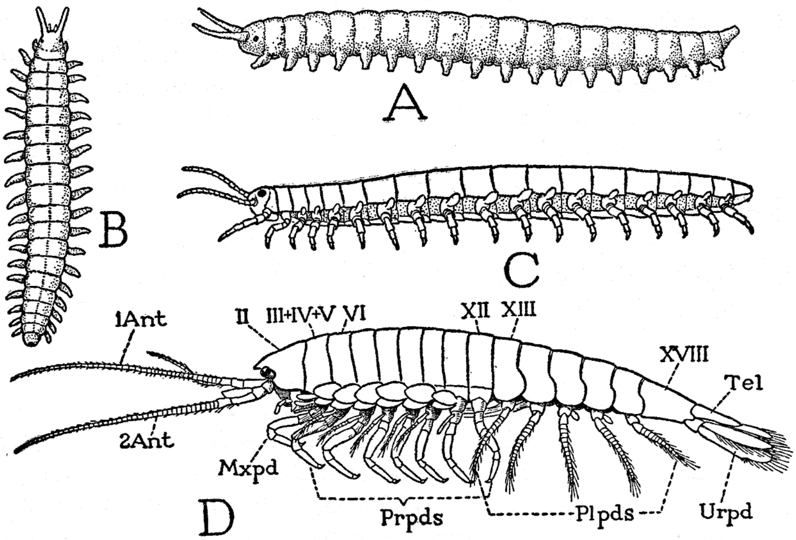

FIG. 1.—Theoretical evolutionary stages of the arthropods.

A, a primitive lobopod, common ancestral form of the Onychophora and Arthropoda. B, a derived form with longer and slenderer legs. C, a primitive arthropod with sclerotized integument, jointed legs, and gill lobes on the coxae. D, a fairly generalized modern crustacean, *Anaspides tasmaniae*.

1Ant, first antenna; *2Ant*, second antenna; *Mxpd*, maxilliped; *Plpds*, pleopods; *Prpds*, pereiopods; *Tel*, telson; *Urpd*, uropod; *II-XVIII*, body segments.

perhaps represented by such fossils as the Pre-Cambrian *Xenusion* and the Cambrian *Aysheaia*. The modern Onychophora are probably direct descendants from these early lobopods, and have structurally not progressed much beyond them. Others, however, acquired a sclerotization of the integument, which allowed the legs to become longer and slenderer (B), and finally jointed (C) for more efficient action in locomotion. These jointed-legged forms were the first true arthropods. The segmentation of the legs early took on a definite pattern, which has been preserved in both fossil and living arthropods, most of which retained the walking mode of locomotion, though some may also swim or fly.

From these early Pre-Cambrian arthropods (fig. 1 C) in which all the appendages were fully segmented ambulatory legs, the trilobites branched off by specialization of the body structure, but with no essential differentiation of the appendages. In the other derivative groups, however, the appendages took on different forms adapting them to various uses, but the number retained for walking is characteristic of the several modern arthropod groups. The myriapods use most of their postoral appendages for progression; the Malacostraca (D) use five or more pairs for walking, except where some of these have been modified for grasping; *Limulus* and the arachnids use four pairs, the insects three. That the ambulatory limbs, when limited in number, should in all cases be those of the middle part of the body, though not necessarily the same appendages, follows from the mechanical necessity of balance. The anterior appendages become sensory and gnathal in function; those of the abdomen have been modified for various purposes, such as respiration, silk spinning, copulation, egg laying, or swimming.

The modern arthropods comprise two distinct groups, the Chelicerata and the Mandibulata. In the chelicerates the first postoral appendages are a pair of pincerlike chelicerae that serve for feeding, and the ancestors of this group were probably closely related to the ancestors of the trilobites. The principal feeding organs of the mandibulates are a pair of jaws, the mandibles, formed of the second postoral appendages. The Mandibulata, including the crustaceans, the myriapods, and the insects, are certainly a monophyletic group, but their origin and their interrelationships are obscure.

Among the Crustacea the malacostracan type of organization (fig. 1 D), in which the thoracic appendages are typically ambulatory and the abdominal appendages natatory, would appear to be more primitive than the entomostracan types because it more closely conforms with the structure of other arthropods, and could be more directly derived from that of a primitive walking arthropod (C). The entomostracan forms, therefore, have been secondarily reconstructed for a purely pelagic life by a readaptation of the thoracic appendages for swimming.

If we accept the premise that the original arthropod (fig. 1 C) was a simple animal with jointed legs along the entire length of a uniformly segmented body, the crustaceans were derived from this common arthropod ancestor by specializations that established the generalized crustacean structure (D). Developmental recapitulation of adult crustacean structures, therefore, can go back only to the beginning of adult crustacean evolution. The embryo, however, starts its development from a single cell and the free larva completes development

what happens to the trochophore?

up to the adult. The embryo and the early larva, therefore, represent pre-crustacean stages of arthropod evolution. The embryo, however, must reproduce its parental form. Hence the crustacean characters appear at a very early stage of ontogeny, but the resulting embryonic or larval stages are not recapitulations of adult crustacean evolution. The crustacean characters are simply precociously imposed on the anamorphic stages of ontogeny. Finally, if the embryo is set free as a larva at an early stage of development, it must be structurally adapted to a free life, and in its subsequent growth other adaptations may be necessary. Thus it comes about that metamorphosis still further complicates the course of ontogeny. The life histories of parasitic larvae best demonstrate that larval forms are metamorphic adaptations to a way of living, since the nonparasitic adult ancestors of such species can hardly be supposed to have had the larval form. Where a specialized adult structure has arisen since the crustaceans became crustaceans, there may be a true recapitulation of an earlier adult form, as in the megalops of the crabs. A further discussion of the nature of larval forms will be given in connection with the life history of a penaeid (p. 54).

II. THE NAUPLIUS AND THE METANAUPLIUS

Since among the crustaceans the young hatch at different periods of development, the youngest larvae may have very diverse forms in the various orders, representing different ontogenetic stages according to the degree of development they undergo within the egg. The earliest hatched larval form is the *nauplius,* which is particularly characteristic of the Entomostraca, but occurs also in the Euphausiacea and Penaeidea among the Malacostraca. The nauplius is usually followed by a *metanauplius,* which is the first stage of postembryonic growth. From the metanauplius on, development may be merely a matter of regular anamorphic growth by the successive addition of new segments and appendages, but in many species the larva takes on different forms as it develops. These ontogenetic changes differ so much in the various orders that no general description can be given, hence a discussion of them will be left to the next section of this paper. Special attention, however, must be given to the nauplius and the metanauplius.

The nauplius.—The nauplius is a minute creature, highly variable in form in different species, but typically ovoid or pyriform in shape with the larger end anterior (fig. 2 A). It has a pair of uniramous antennules, or first antenna (*1Ant*), typically biramous second antennae (*2Ant*) and mandibles (*Md*), and a median eye of two or more parts.