THE LARVAL STAGES OF TRILOBITES.

BY

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(Plates VIII–X.)

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I. INTRODUCTION.

It is now generally known that the youngest stages of trilobites found as fossils are minute ovate or discoid bodies, not more than one millimetre in length, in which the head portion greatly predominates. Altogether they present very little likeness to the adult form, to which, however, they are traceable through a longer or shorter series of modifications.

Since Barrande[2] first demonstrated the metamorphoses of trilobites, in 1849, similar observations have been made upon a number of different genera by Ford,[22] Walcott,[34, 35, 36] Matthew,[26, 27, 28] Salter,[32] Callaway,[13] and the writer.[4, 5, 7] The general facts in the ontogeny have thus become well established and the main features of the larval form are fairly well understood.

Before the recognition of the progressive transformation undergone by trilobites in their development, it was the custom to apply a name to each variation in the number of thoracic segments and in other features of the test. The most notable example of this is seen in the trilobite now commonly known as *Sao hirsuta* Barrande. It was shown by Barrande[3] that Corda[17] had given no less than ten generic and eighteen specific names to different stages in the growth of this species alone.

The changes taking place in the growth of an individual are chiefly: the elongation of the body through the gradual addition of the free thoracic segments; the translation of the eyes, when present; the modifications in the axis of the glabella; the growth of the free-cheeks; and the final assumption of the mature specific characters of pygidium and ornamentation.

In the present paper the larval stages of several species are described and illustrated for the first time, and a review is under-taken of all the known early larval stages thus far described. This work would have no special interest in itself were it not for the fact, that, with our present understanding of trilobite morphology, it is possible to reach some conclusions of general importance, which have a direct bearing on the significance and interpretation of several of the leading features of the trilobite carapace, and incidentally upon the structure and relations of the nauplius of the higher Crustacea.

II. The Protaspis.

Barrande[3] recognized four orders of development in the trilobites, as follows:

		Types.
I.	Head predominating, incomplete. Thorax nothing or rudimentary. Pygidium nothing.	*Sao hirsuta.*
II.	Head distinct, incomplete. Thorax nothing. Pygidium distinct, incomplete.	*Trinucleus ornatus*, and all *Agnostus*.
III.	Head complete. Thorax distinct, incomplete. Pygidium distinct, incomplete.	*Arethusina konincki.*
IV.	Head complete. Thorax complete. Pygidium distinct, incomplete.	*Dalmanites hausmanni.*

A study of these groups shows at once that they form a progressive series in which the first alone is primitive. The others are more advanced stages of development, as shown by the larger size of the individuals, and their having characters which appear successively in the ontogeny of a species belonging to the first order of development. To attain the stage which is represented by actual specimens, they must have passed through earlier stages, which as yet have not been found. Furthermore, it is evident that Barrande did not consider the orders after the first as primitive, and characteristic of the genera cited, for, in some remarks under the third order, he says[3]: "Il est très-vraisemblable, que la plupart des Trilobites de cette section, si ce n'est tous, devront être un jour transférés dans la première, par suite de la dècouverte probable d'embryons sans segmens thoracique."

The geological conditions necessary for the fossilization of the minute larval forms of trilobites are such, that only in comparatively rare instances are any of the immature stages preserved. Larval specimens are doubtless often overlooked or neglected by collectors, but generally the sediments are too coarse for the preservation of these small and delicate organisms. In certain horizons and rocks, however, such remains are quite abundant, and complete ontological series may be obtained. Yet, it is not strange that series of equal completeness have not been found in all Paleozoic horizons.

The abbreviated or accelerated development of many of the higher Crustacea has resulted in pushing the typical free-swimming, larval nauplius so far forward in the ontogeny that this stage is either eliminated or passed through while the animal is still within the egg, so that when hatched it is much advanced. Although the trilobites show distinct evidence of accelerated development through the earlier inheritance of certain characters which will be taken up later, yet it is not believed that the normal series or periods of transformation were to any degree disturbed, since both the simplest and most primitive genera whose ontogeny is known and the most highly specialized forms agree in having a common early larval type. This would be expected from their great antiquity, their comparatively generalized and uniform structure, and from the fact that no sessile, attached, parasitic, land, or fresh-water species are known. These conditions by introducing new elements into the ontogeny would tend to modify or abbreviate it in various ways, especially among the higher genera.

Before discussing any of the various philosophical and theoretical problems involved in an attempt to correlate the larval forms of Crustacea, a brief consideration of the known facts relating to the larvæ of trilobites will be presented.

Minute spherical or ovoid fossils associated with trilobites have been described as possible trilobite eggs, by Barrande[3] and Walcott,[33] but nothing is known, of course, of the embryonic stages of the animals themselves. The smallest and most primitive organisms which have been detected, and traced by means of series of specimens through successive changes into adult trilobites, are, as stated above, little discoid or ovate bodies not more than one millimeter in length, as shown on plates VIII and IX. It is fair to assume that we have here a general exhibition of trilobite larval stages, since the ten species represented are from various geological horizons, belonging to the Cambrian, Ordovician and Silurian sediments, with

Devonian types, and showing the simple as well as the highly specialized forms.

All the facts in the ontogeny of trilobites point to one type of larval structure. This is even more noticeable than among recent Crustacea, in which the nauplius is considered as the characteristic larval form. It is desirable to give a name to this early larval type apparently so characteristic of all trilobites, and among different genera varying only in features of secondary importance. This stage may therefore be called the *protaspis* (πρῶτος, *primus*: ἀσπὶς, *scutum*).

The principal characters of the protaspis are the following: Dorsal shield minute, varying in observed species from .4 to 1 mm. in length; circular or ovoid in form; axis distinct, more or less strongly annulated; head portion predominating; glabella with five annulations; abdominal portion usually less than one-third the whole length of the shield, axis with from one to several annulations; pleural portion smooth or grooved; eyes when present anterior, marginal or submarginal; free-cheeks when present very narrow, marginal.

Several moults took place during this stage before the complete separation of the pygidium or the introduction of thoracic segments. When such moults are recognized, they may be considered as early, middle and late protaspis stages, and designated respectively as anaprotaspis, metaprotaspis and paraprotaspis. They introduced various changes, such as the stronger annulation of the axis, the beginning of the free-cheeks, and the growth of the pygidial portion from the introduction of new appendages and segments as indicated by additional grooves on the axis and pleura. Similar ecdyses occur during the nauplius stage of many living Crustacea before a decided transformation is brought about. Certain of these later stages have received a distinctive name, and are called the metanauplius.

It is believed that the protaspis is homologous with the nauplius or metanauplius of the higher Crustacea. Most of the reasons for this belief will appear later in the present paper; some which may be stated now are as follows:

(1) The size of the protaspis does not differ greatly from that of many nauplii, and represents as large an animal as could be hatched from the bodies considered as the eggs of trilobites.

(2) Some of the sediments carefully examined by the writer could preserve smaller larval trilobites were such originally present and provided with a chitinous test, as shown by the abundance of minute ostracodes, and the perfection of detail in these and other fossils.

(3) The protaspis can be shown to be structurally closely related to the nauplius, and in a more marked degree possesses some characters required in the theoretical crustacean ancestor.

III. Review of Larval Stages of Trilobites.

Matthew[27, 28] has carefully described several early larval (protaspis) stages of trilobites from the Cambrian rocks of New Brunswick, which are very simple and primitive, and will be noticed first.

Solenopleura robbi Hartt; plate VIII, figure 1; from the Cambrian of New Brunswick; after Matthew.[27] This larva is very minute and circular in outline; the glabella is obscurely annulated and extends to the anterior margin, where it is expanded; the neck ring is the only one well defined; the abdominal portion is less than one-third the whole length, and is limited by a slight transverse furrow; no traces of eyes or free-cheeks discernible.

Liostracus onangondianus Hartt; plate VIII, figure 2; from the Cambrian of New Brunswick; after Matthew.[27]. This form is similar to the preceding, though larger, and with the glabella more rapidly expanding in front. The neck segment is the only one which is distinct.

It should be mentioned that most of the larval specimens here described and figured are preserved in fine shales and slates, as casts of the interior of the dorsal shield, so that some features are not as emphatic as on the exterior of the test. When well preserved, the axis always shows the typical five annulations on the cephalon.

Ptychoparia linnarssoni Walcott; plate VIII, figures 3 and 4; from the Cambrian of New Brunswick; after Matthew.[28] The earliest stage is slightly more elongate than the preceding forms. The axis is narrow, expanding in front and obscurely annulated, five annulations belonging to the cephalon, and one to the pygidium, which is very short and separated from the cephalon by a distinct groove.

The second stage (figure 4) is decidedly more elongate; the axis is more distinctly annulated; the occipital pleura defined; and the pygidium is larger and has an additional segment.

Ptychoparia kingi Meek; plate VIII, figures 5, 6 and 7; from the Cambrian of Nevada and Utah. Figure 5 represents a cast of the protaspis, and shows a defined occipital ring, with the axis slightly expanded and undefined in front; pygidium truncate behind. Figure 6, which is referred to a later stage (metaprotaspis) of the same species, shows the inception of several characters that have not as yet appeared in the previous larvæ. The axis is very strongly annulated; the anterior lobe is nearly as long as the four posterior annulations of the cephalon, and on each side there is a furrow representing the eye-line of the adult; the free-cheeks are present as narrow marginal plates, including the genal spines; the pygidium shows two segments separated by a furrow.

An adult *Ptychoparia kingi* is shown in figure 7 and may be taken as representing the sum of the changes passed through in the development of larvæ like the preceding, belonging to the genera *Solenopleura*, *Liostracus* and *Ptychoparia*. The introduction and growth of the segments of the thorax are perhaps the most marked changes, but other points of importance to be noted are: the comparatively smaller size of the cephalon and its transverse form; the limitation and recession of the glabella, which is now rounded in front, and only extends about two-thirds the length of the cephalon; the growth of the eyes and free-cheeks at the expense of the fixed-cheeks; the increased segmentation of the abdomen, shown in the axial and pleural grooves on the pygidium.

Sao hirsuta Barrande; plate VIII, figures 8, 9, 10 and 11; from the Cambrian of Bohemia; after Barrande.[3] The specimens of this species are preserved as casts, and several of the features are therefore somewhat subdued. The earliest or anaprotaspis stage, represented in figure 8, is quite as primitive in most respects as any of the preceding. It is circular in outline, the annulations of the axis are distinctly shown only in the neck segment and pygidial portion, and the eye-line is present. In figure 9 of the metaprotaspis, quite an advance is seen in the development of the free-cheeks and the more pronounced annulation of the glabella, together with pleural grooves from the neck segment and those of the pygidium. The next stage (figure 10) probably represents the close of the protaspis stage (paraprotaspis) and the inception of the nepionic condition, when the cephalon and pygidium are distinct and before the development of the free thoracic segments.

In considering the changes necessarily passéd through by these larvæ previous to attaining their adult characters (figure 11) the most notable, aside from increase in size and addition of the sixteen thoracic segments, are: the appearance and translation of the eyes *pari passu* with the growth of the free-cheeks; the growth of the border in front of the glabella, which now narrows anteriorly, and terminates about one-third the length of the cephalon within the margin; the less distinct annulation of the glabella; and the development of the spines and tubercles ornamenting the test.

Triarthrus becki Green; plate VIII, figures 12, 13, and 14; from the Ordovician, Utica slate, near Rome, N. Y. A larval form of this species was figured by the writer[5] in 1893. At this time, the eye-line was confused with the anterior annulation of the axis, making the cephalon appear to have six instead of five annulations. A recent examination of a large number of specimens shows that five is the invariable number, as here represented. Two protaspidian stages of this species have been noticed, differing chiefly in the size of the pygidium. Both agree in showing a strongly annulated axis, not expanded in front and terminating some distance within the margin. From the first annulation, a slightly elevated ridge on each side indicates the eye-line, and extends to the marginal eye-lobe. The adult form (figure 14) shows in addition to several characters noted in the previous species, the nearly complete loss of the two anterior annulations of the glabella; the disappearance of the eye-line; and the development of a row of nodes along the axis, from the neck segment to the proximal segment of the pygidium.

Acidaspis tuberculata Conrad; plate IX, figures 1, 2 and 3; from the Lower Helderberg group, Albany county, New York.[4] Several of these remarkable larvæ have been found perfectly silicified in a limestone from which they have been freed by etching. In general form, they resemble the second larval stage of *Sao* (plate VIII, figure 9), but the pygidium is shorter and the glabella does not expand and terminate in the anterior margin. No eye-line is present, but the eye-lobes may be seen a little within the margin. The glabella has the characteristic number of annulations; margin provided with a row of denticles; genal angles extended into spines; pygidium with four spines.

The adult condition (figure 3) shows that the eyes have moved inwards and backwards to near the neck segment. The glabella has lost its annulations and is broken up into a median lobe with two smaller ones on each side, while the neck ring is projected into a spine. The changes noted here are much more profound than in any of the preceding genera, since *Acidaspis* is one of the most highly specialized of trilobites in its glabellar structure and elaborate ornamentation. The protaspis, too, partakes of this specialization, and, although the general form of the shield and the annulation of the axis are as primitive as in *Triarthrus*, yet the characteristic spinosity of the genus appears even at this early stage and is a marked instance of acceleration of development.

Arges consanguineus Clarke; plate IX, figure 4; from the Lower Helderberg group, Albany county, New York. A single larval form of this type has been found and at first was provisionally referred to *Phaëthonides*.[4] The recent publication by Clarke,[14] of *Arges consanguineus* from the same horizon, and a comparison of the larva with the description and with considerable additional material, renders it now possible to determine definitely the relations of this interesting form. As the main details of structure in *Acidaspis* and *Arges* are so similar, the transformations undergone by the larva are much alike in each case. The young *Arges* likewise shows the same acceleration in the development of the spines and surface ornamentation, and the retention of the primitive features of the glabella. The specimen seen in figure 4 represents a late larval stage (paraprotaspis), as shown by the transverse form of the cephalon and the large size of the pygidium.

Proëtus parviusculus Hall; plate IX, figures 5, 6 and 7; Utica slate, near Rome, New York. Two larval stages of this species have been found. The younger (figure 5) is smooth, broadly ovate, .72 mm. long, and widest in front; axis distinctly annulated, cylindrical on the cephalon, tapering on the pygidium; eyes nearly transverse to the axis, very large and prominent, situated on the anterior margin, separated only by the axis. The specimen represented in figure 6 is in the paraprotaspis stage, and measures .96 mm. in length. It shows an advance over the other in its size, its larger pygidium with grooved pleura, and the beginning of the recession of the eyes.

The adult of this small species is shown in outline enlarged two diameters, in figure 7. The principal changes from the larva which should be noticed are: the loss of the four anterior annulations of the glabella, the neck segment being the only one wholly defined, although the basal lobes represent remnants of the next anterior; the translation of the eyes backward as far as the pleura of the neck segment, and the change from a transverse to a parallel position with respect to the axis.

In the original description of this species,[23] no mention was made of fine undulating striæ ornamenting the entire dorsal surface of the test, nor of the basal lobes of the glabella. Both these features are present in the type specimen, which is from Cincinnati, Ohio, as well as in all the specimens from the Utica slate, near Rome, New York. With these additional characters, the species is very closely related to *Proëtus decorus* Barrande.

Dalmanites socialis Barrande; plate IX, figures 8-11; from the Ordovician of Bohemia; after Barrande.[3] A nearly complete series of the growth stages of this species is given by Barrande. The earliest, or anaprotaspis, stage found (figure 8) exhibits an outline and axis similar to *Acidaspis*. The eyes are quite large and situated, as in the same stage of *Proëtus*, transverse to the axis, on the anterior border. Genal angles present, but in this case not produced by the free-cheeks as in *Sao* and *Ptychoparia;* glabella strongly annulated, increasing in diameter anteriorly, although not expanding at the frontal margin as in *Sao*, etc. In the two following stages (figures 9, 10), the pygidium increases in size, and the pleura are defined. To reach maturity (figure 11), eleven segments are developed in the thorax, the glabella becomes more prominently developed in front, but the five annulations are maintained. The eyes have travelled in and back as far as the third head segment, and their longer axes have swung around into a position parallel with the axial line, as in *Proëtus*. The pygidium has added many new segments, and the extremity is prolonged into a spine.

Before proceeding further in the discussion of the protaspis, it is necessary to notice a number of forms of young trilobites which have heretofore been referred to the embryonic and larval stages, but which are now believed to belong to stages later than the protaspis.

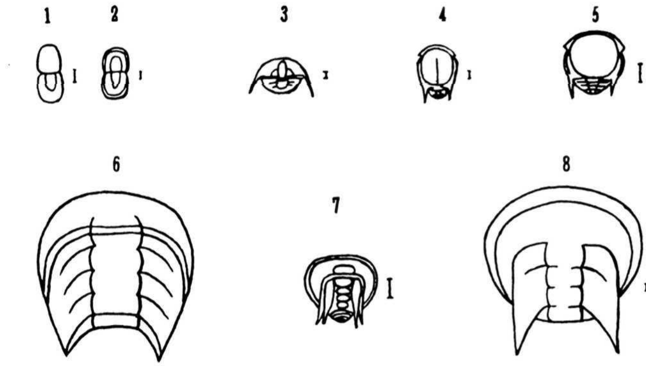


FIGURE 1. *Agnostus nudus* Beyr.; after Barrande.
FIGURE 2. *Agnostus rex* Barr.; after Barrande.
FIGURE 3. *Trinucleus ornatus* Sternb.; after Barrande.
FIGURE 4. *Hydrocephalus saturnoides* Barr.; after Barrande.
FIGURE 5. *Hydrocephalus carens* Barr.; after Barrande.
FIGURE 6. *Olenellus* (*Mesonacis*) *asaphoides* Emmons; Ford collection; original. x 30.
FIGURE 7. *Olenellus* (*Mesonacis*) *asaphoides* Emmons: after Ford.
FIGURE 8. *Olenellus* (*Mesonacis*) *asaphoides* Emmons; after Walcott.

Besides the truly elementary forms described by Barrande and already noticed (*Sao hirsuta* and *Dalmanites socialis*), there are others which he referred to his second, third and fourth orders of development.[3] Among these *Agnostus* may be taken first. The youngest forms of *Agnostus nudus* and *A. rex* (figures 1, 2) measure respectively 2 and 1.3 mm. in length, and the adults 13 and 15 mm. The earliest stages of the genera shown on plates VIII and IX measure less than 1 mm., while the adults are more than 25 mm., with the exception of *Proëtus parviusculus*, which is seldom more than 10 mm. long, though this species has a protaspis .72 mm. in length. The cephalon and pygidium of the youngest known *Agnostus* are quite separate and distinct, which is not the case with the typical protaspis stage. It therefore seems probable that on account of the comparatively large size and advanced structure of the youngest stages observed, the elementary forms of this genus are as yet unknown, and possibly the extreme tenuity of the test in the protaspis has prevented their preservation. In the same way the young of *Trinucleus* (figure 3) show a separate cephalon and pygidium, and the specimens are in a much more advanced stage of development than the protaspis of *Proëtus*, shown on plate IX, figure 5. An evidence of age is furnished, also, in the transverse shape of the head, which, in typical elementary forms, is longer than wide, instead of wider than long.

The youngest specimens of *Arethusina koninckii*, figured by Barrande,[3] are 2 mm. or upwards in length and have seven or more free thoracic segments, with the cephalon wider than long. The facts of ontogeny show that younger stages must be admitted in which the number of segments diminishes to nothing, continuing down to a form agreeing with the protaspis of other genera.

It has already been suggested[4] that the species described by Barrande[3] under the generic name of *Hydrocephalus* are probably the young of *Paradoxides*. This conclusion receives further support from the undoubted young of *Olenellus*, a related genus, which in its immature stages bears a strong resemblance to *Hydrocephalus*. The youngest examples of the latter have a distinct pygidium, a well-developed cephalon, and large eye-lobes at the sides of the glabella, as in adult forms. Free-cheeks were evidently present though not generally preserved. See figures 4 and 5.

The young of *Olenellus asaphoides*, described and illustrated by Ford[22] and Walcott,[35, 36] also present a number of features considerably in advance of a typical protaspis. The immature characters are mainly the large size of the cephalon and the distinct annulation of the axis. The post-protaspidian characters are the distinct and separate pygidium, the adult position of the eyes, and the apparently well-developed free-cheeks. In figure 7, after Ford,[22] the outer pair of spines belongs to the free-cheeks, the other pair being formed by the pleural extensions of the glabella, which were called the interocular spines. See also figures 6 and 8.

The young specimen of *Ptychoparia monile* Salter sp., figured and noticed by Callaway,[13] is 1.5 mm. in length, and agrees, as far as can be determined without seeing the original, with what is known of other species of the same genus. It probably belongs to a stage later than the protaspis.

Matthew[26] has carefully described some small cephala of *Ctenocephalus* (*Hartella*) *matthewi* and *Conocoryphe* (*Bailiella*) *baileyi*, from the Cambrian of New Brunswick. The fact of their being separate cephala, transverse in form, and from 2 to 3 mm. in length, is sufficient to show that they do not represent the youngest stages of these species.

The immature examples of *Agnostus*, *Trinucleus*, *Arethusina*, *Paradoxides*, *Olenellus*, *Ctenocephalus* and *Conocoryphe*, here briefly noticed are of great interest in a study of the ontogeny of the various species to which they pertain. In the present paper, however, it is intended chiefly to establish the primary larval characters of the trilobites, and therefore only the earliest stages are considered. Under the genera just mentioned, the writer has endeavored to show that as yet their ontogeny cannot be traced as far back as the stage which has been defined as the *protaspis*. Therefore, any general notions of first larval forms must at present be based on the genera *Solenopleura*, *Liostracus*, *Ptychoparia*, *Sao*, *Triarthrus*, *Acidaspis*, *Proëtus* and *Dalmanites*.

IV. Analysis of Variations in Trilobite Larvæ.

After taking a general survey of the earliest known larval stages of trilobites figured on plates VIII, IX, it is evident that an accurate and detailed description of any one would not apply to any other except in certain broad characters. To formulate a definition of the protaspis applicable to all, as has been done previously (p. 169), it is necessary to neglect or eliminate some rather striking characters which should now be mentioned. A few features thus omitted are considered as very primitive larval characters, while others are modifications introduced in higher or later genera through the operation of the law of earlier inheritance.

From the best evidence now obtainable, the eyes have migrated from the ventral side, first forward to the margin and then backward over the cephalon to their adult position, thus agreeing with Bernard's conclusions.[12] Therefore, the most primitive larvæ should present no evidence of eyes on the dorsal shield, and naturally there would be no free-cheeks visible. Just such conditions are satisfied in the youngest larva of *Ptychoparia*, *Solenopleura* and *Liostracus*, which are the most primitive genera whose protaspis is known. The eye-line is present in the later larval and adolescent stages of these genera, and persists to the adult condition. In *Sao* it has been pushed forward to the earliest protaspis, and is also found in the two known larval stages of *Triarthrus*. *Sao* retains the eye-line throughout life, but in *Triarthrus* the adult has no traces of it, and none of the higher and later genera studied has an eye-line at any stage of development. Matthew has considered this feature as especially characteristic of most of the Cambrian genera, and now it is further shown to be a character first appearing in the later larval stages of certain genera (*Ptychoparia*, etc.), next in the larval stages (*Sao*), then disappearing from adult stages (*Triarthrus*), and finally pushed out of the ontogeny altogether (*Acidaspis*, *Dalmanites*, etc.). The eyes are visible on the margin of the dorsal shield after the paraprotaspis stage, later than the eye-line in *Ptychoparia*, *Solenopleura*, *Liostracus*, *Sao* and *Triarthrus;* but in the other genera through acceleration they are present in all the protaspis stages, and persist to the mature, or ephebic, condition, moving in from the margin to near the sides of the glabella.

The changes in the glabella are equally important and interesting. Throughout the larval stages, the axis of the cephalon is five-segmented or annulated, indicating the presence of as many paired appendages on the ventral side. In its simplest and most primitive state, it expands in front, joining and forming the anterior margin of the head (larval *Ptychoparia*, *Sao*). During later growth it becomes rounded in front and terminates within the margin. In higher genera through acceleration it is rounded and well-defined in front even in the earliest larval stages and often ends within the margin (larval *Triarthrus*, *Acidaspis*). From these common types of simple, pentamerous glabellæ, all the diverse forms among adult individuals of various genera have been derived, through changes affecting any or all of the lobes. The modifications usually take place in the anterior lobes first, and gradually involve the others, though rarely disturbing the neck segment which is the most persistent of all. Six lobes are occasionally found in the glabellæ of some species. They do not indicate an additional pair of limbs, for the extra lobe is produced (*a*) by division of the anterior lobe through the greater or less extent of the eye-line across the axis, as in *Olenellus*, *Paradoxides* and *Ogygia*: or (*b*) by the marked development of muscular fulcra, which are supposed to be connected with the hypostoma.

The next structures not especially noticeable in all stages of the protaspis are the free-cheeks, which usually manifest themselves in the meta- or paraprotaspis stages, though sometimes even later. Since they bear the visual areas of the eyes, their appearance on the dorsal shield is practically simultaneous with these organs; and before the eyes have travelled over the margin, the free-cheeks must be wholly ventral in position. They are very narrow when first discernable (plate VIII, figures 6, 9 and 10), and in *Ptychoparia*, *Sao*, etc., include the genal angles, but in *Dalmanites* they extend only a short distance below the eyes.

The remaining features of the protaspis which here require notice are the pleural furrows and the pygidium. The pleura from the anterior segments of the glabella are occasionally shown, as in the young of *Olenellus* (figure 6), but usually the pleura of the neck segment are the first and only ones to be distinguished on the cephalon, the others being so intimately coalesced as to lose all traces of their individuality. This makes the cranidium, or head shield, exclusive of the free-cheeks, consist of the fused lateral extensions or pleura of the head segments, as already noticed by Bernard.[12] The possible pleural or segmental nature of the free-cheeks will be noticed later.

The distinct pleura of the pygidium appear soon after the anaprotaspis stage, and in some genera (*Sao*, *Dalmanites*) are even more marked than in the adult state, much resembling separate segments. The growth of the pygidium is very considerable through the protaspis stages. At first it is less than one-third the length of the dorsal shield, but by the successive addition of segments, it soon becomes nearly one-half as long. In some genera it is completed before the appearance of the free thoracic segments, though usually new segments are added during the adolescence of the animal.

A number of genera present adult characters, which agree closely with some of the larval features noticed in this section, and are important in a phylogenetic study of the trilobites. The main features of the cephalon in the simple protaspis forms of *Solenopleura*, *Liostracus* and *Ptychoparia*, are retained to maturity in such genera as *Carausia* and *Acontheus*, which have the glabella expanded in front, joining and forming the anterior margin. They are also without eyes or eye-line. *Ctenocephalus* retains the archaic glabella nearly to maturity, and likewise shows eye-lines and the beginnings of the free-cheeks (larval *Sao*). *Conocoryphe* and *Ptychoparia* are still further advanced in having the glabella rounded in front, and terminated within the margin (larva of *Triarthrus*). These facts and others of a similar nature show that there are characters appearing in the adults of later and higher genera, which successively make their appearance in the protaspis stage, sometimes to the exclusion or modification of structures present in the most primitive larva. Thus the larvæ of *Dalmanites* or *Proëtus*, with their prominent eyes, and glabella distinctly terminated and rounded in front, have characters which do not appear in the larval stages of ancient genera, but which may appear in their adult stages. Evidently such modifications have been acquired by the action of the law of earlier inheritance, or tachygenesis. Altogether it seems that we have represented on plates VIII and IX a progressive series of first larval stages in exact correlation with adult forms, the latter also constituting a progressive series, structurally and geologically.

A summary of the features added to the dorsal shield of the anaprotaspis stage of acceleration during the evolution of the class, from the simpler forms of Cambrian times to the later and more highly differentiated *Dalmanites*, *Proëtus* and *Acidaspis*, would include: the free-cheeks; the eyes; the more strongly lobed glabella, rounded in front; the transient eye-line; the genal angles; and the ornaments of the test.

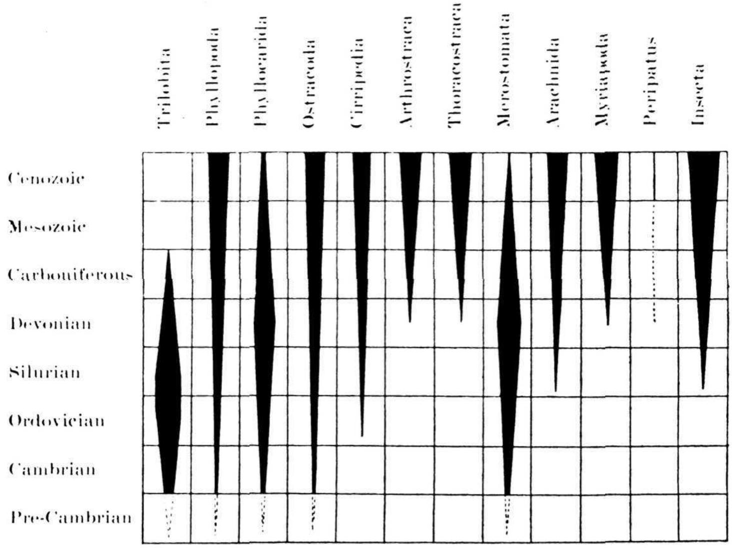
These additions, as may be seen by reference to plates VIII and IX, considerably complicate and modify the primitive protaspis, but, as previously mentioned, it does not lose any of its essential structures. Besides, it is possible to trace the origin and significance of the acquired characters, and thus to assign to each its true value.

V. Antiquity of the Trilobites.

The superlative age of the trilobites has been generally recognized, and is too well known to require more than a passing notice. Even in the earliest Cambrian, they bear evidence of great antiquity in their diversified form, their larval modifications, and their polymerous head and caudal shield, all of which features show that trilobite phylogeny must reach far back into pre-Cambrian times.

Not only are the smallest species found in the Cambrian (*Agnostus*), but also many of the largest (*Paradoxides*). There is a great range of variation in the number of free thoracic segments, varying from two in *Agnostus* to twenty in *Paradoxides*. The pygidium likewise shows extreme variation of from two to upwards of ten ankylosed segments. The eyes may be absent as in *Agnostus* and *Microdiscus*, or very large as in *Paradoxides*, though both in this respect and in the number of somites, free or fused, the Cambrian genera are exceeded in later deposits. In ornamentation and spiniform processes, the Cambrian species show considerable development though not as great as others since that time. However, the wide variations they do present in this particular indicates differentiation and specialization considerably removed from the beginning of the trilobite phylum.

The acquisition of distinct larval stages could only have been reached through a long series of changes in ancestral forms. The composition of the cephalon and caudal shield indicates a derivation from some primitive form, probably annelidan, in which, through adaptation to special requirements, certain polar segments became fused, forming very distinct terminal body regions. Furthermore, the tribolites are the only large division of the Arthropoda which has become extinct. The Merostomata and Phyllocarida, culminated a little later, though still represented by living species, but all the other divisions apparently have continued to increase since their inception during Paleozoic time. The only known arthropod contemporaries of the trilobites in the Cambrian are the Merostomata, Ostracoda, Phyllopoda, and Phyllocarida, all of the higher forms apparently having developed since that time. A more graphic view of the geological range and distribution of the arthropods is represented in the following table:



Having thus far reviewed the features of the primitive protaspis and some of the characters it acquired through earlier inheritance, together with the comparative age of the different groups of arthropods, it must be conceded, that, in interpreting crustacean phylogeny from the facts of ontogeny, the trilobites, so far as they show structure, are entitled to first place. Moreover, since the appendages are quite fully known and from them the trilobite proves to be a most generalized and primitive crustacean, still greater reliance can be placed on deductions based upon a study of this type. The recent discoveries of the antennæ and the exact details of trilobite structure, together with the larval homologies here made and the concordance of trilobites with the theoretical original crustacean leave almost no doubt as to their true crustacean affinities. Woodward,[37] from another point of view, reaches the same opinion by saying: "The trilobita, being certainly amongst the earliest forms of crustacea with which we are acquainted, cannot be removed from that class without destroying its ancestral record."

VI. Restoration of the Protaspis.

At first thought, the attempt to reconstruct the ventral side of the trilobite protaspis may seem a little hazardous or premature, but a careful consideration of all the data leads the writer to undertake this with some confidence.

The genus *Triarthrus* is taken for the basis of this restoration, as it is to-day the best known of all the trilobites, and its ventral structure has been ascertained to a degree of perfection of detail which compares favorably with many of the recent crustaceans.[6, 7, 8, 9] The writer has studied the structure of many adult and immature specimens some of them not more than 5 mm. in length, so that fortunately the appendages are known at many stages of growth. Especially are the young and rudimentary limbs near the extremity of the pygidium in adolescent individuals of considerable morphological interest, for they agree closely with the phyllopodiform trunk appendages in the metanauplius of *Apus*, and protozoëa of *Euphausia*, or in a general way, with the still more rudimentary trunk limbs in the nauplius stages of these and other forms.

It has been definitely ascertained that the cephalon in trilobites bears five pairs of jointed appendages or limbs.[9] In larval or immature specimens, and in adults in which the glabella retains its primitive structure, this number is indicated on the dorsal shield by the five lobes or annulations of the glabella, including the neck ring. These may therefore be taken as representing, in so far, the original segmentation of the head, and agree with what is generally accepted as the primitive structure in modern true Crustacea. The head portion of the protaspis clearly shows this pentasomitic structure, and evidently carried a corresponding number of paired limbs on the ventral side. It has also been demonstrated that the annulations on the axis of the pygidium correspond to the number of paired limbs beneath, exclusive, of course, of the anal segment. Here, too, it is possible to tell from the pygidial portion of the protaspis the number of limbs present during life. The protaspis of *Triarthrus*, represented in plate VIII, figure 13, on this basis had five pairs of limbs attached to the head portion and two pairs to the pygidium.

Next, as to the composition and form of these elementary protaspis limbs, it is safe to assume that the anterior pair, corresponding to the antennules, must be uniramous since they are so during all the young and adult stages observed, and since this form is common to all nauplius stages of modern Crustacea, and is recognized as primitive and elementary for the class. There is apparently a greater similarity in the larval antennules than between any other appendages, and as *Apus* and *Euphausia* have these in a very generalized form, they are taken as types of the first pair of limbs of the trilobite protaspis, as shown in plate X, figure 1 (1). It should be noted, too, that the antennules of the trilobites arise from the sides of the upper lip or hypostoma, as in the nauplius.

The other head appendages are typically branched, though in many of the recent Crustacea they lose this character after the larval stages. Especially is this true of the third pair of limbs, which become modified into the mandibles. In trilobites the primitive biramous structure of the head limbs persists to adult stages, occurring also in limbs of all the posterior segments where they become more and more phyllopodiform.[8] In the restoration of the protaspis it seems only necessary to append this archaic type of limb to each segment, agreeing as it does in form and structure with the rudimentary limbs of older stages and with the nauplius and metanauplius stages of *Apus*.

It cannot be doubted that the protaspis had five pairs of limbs on the head portion and one or more on the pygidium, and although these are the main points necessary to prove the argument in the next section, on the nauplius, yet it seems perfectly warrantable and better for graphic purposes to attach the required number of elementary limbs to the ventral side of the protaspis, as represented in plate X, figure 1.

There are other organs and structural details occurring in the nauplius and in adult trilobites, which deserve recognition in a restoration of the protaspis stage. First among these is the labrum, or upper lip. Nowhere is this plate so well developed and so striking a ventral feature as among the trilobites. There can be no hesitation, therefore, in accepting this as characteristic of the protaspis.

The trilobites and most recent crustaceans have a metastoma, or lower lip. This is already developed in the nauplius stage of some Crustacea, as *Euphausia* and *Peneus*, and probably represents an early larval character. It usually appears as a median plate divided into two small plates, or lappets, on each side of the median line, posterior to the mouth, and is thus represented in the restored protaspis. As it occurs on a segment bearing also a pair of legs and has no separate neuromere, it cannot well be considered as representing a somite.

An anal opening is found in most nauplii, especially in those of the non-parasitic Crustacea, and in those in which this stage is normal and free-swimming. The protaspis, as representing a free-swimming larval stage of trilobites, therefore, probably possessed an anal opening.

The only character represented in the restoration which is accepted purely from analogy is the median unpaired eye. This organ is almost universally present in the nauplius, and is regarded as a very primitive character wherever found.

The next and last structures to be noticed are the free-cheeks and the beginnings of the paired eyes, as shown in plate X, figure 1 (*g, oc*). Their existence has already been indicated in the descriptions and observations of the protaspis and its derived characters, and need not be repeated here. Apparently the nauplius presents nothing homologous, unless possibly the frontal sensory organs of *Apus, Balanus, Peneus*, etc., may be taken as such. The paired eyes and frontal sensory organs are close together and seem to have some intimate connection, for, as the paired eyes develop, the latter dwindle and disappear. Likewise in the trilobites the free-cheeks bear the visual areas, and may be almost wholly converted into eyes as in *Æglina (Cyclopyge)*.

The greater or less separation of the cerebral ganglia in the chætopods and in some of the lower crustacea leads to the idea that the free-cheeks in trilobites are the pleura of an oculiferous head segment, which otherwise is lost. If the hypostoma is homologous with the annelid prostomium, as urged by Bernard[11], then the free-cheeks may be considered as representing the second procephalic segment, which is the number required on the supposition that each neuromere corresponds to a somite. There is a separate neuromere to each mesodermic metamere posterior to the head, and from analogy we should expect that each neuromere in the head would represent an original segment, especially as it can be demonstrated that the head is composed of consolidated or fused segments (Kingsley[24]).

Having thus shown the probable ventral structure of the protaspis, we are prepared to make some general observations on the larval type of modern Crustacea known as the *Nauplius*. Before doing this it is well to emphasize again that there is very positive evidence, amounting virtually to certainty, that the protaspis had five pairs of limbs attached to the cephalic portion, behind which was an abdominal portion containing the formative elements out of which all the posterior somites and appendages were developed.

VII. The Crustacean Nauplius.

The name *Nauplius* was first used by O. F. Müller[29] to designate a minute crustacean believed to represent an adult animal. Afterwards it was found to be a larval stage of *Cyclops*, but because it agreed in structure with the larvae of many other Crustacea the name was retained for that type of larval form and is now in general use. Primarily it is supposed to represent the first free-swimming stage after the escape of the animal from the egg. However, many species are quite fully developed when leaving the egg, and undergo comparatively slight subsequent metamorphoses, and in these and other species there may be developed in the egg an embryo having some of the characters of the nauplius. Therefore, the term is also applied to all cases where a certain assemblage of nauplian characters occurs in the development of any crustacean. Thus it may be considered as a stage of development not restricted to a definite period of ontogeny.

The adult *Apus* possesses so many nauplian features, and in its development passes through such simple metamorphoses, that it has been aptly considered by Bernard[11] as a nauplius grown to maturity. Balfour[1] also states that the chief point of interest in the development of *Apus* "is the fact of the primitive Nauplius form becoming gradually converted without any special metamorphoses into the adult condition."* This form, together with the nauplii of other crustaceans and the study of the larval and adult characters of the trilobites, ought to afford definite knowledge of the characters possessed by the ancestral forms of the Crusateea.

Before farther examining the nauplius it may be well to state the characters, which, on the grounds of comparative anatomy and phylogeny, are believed to represent the primitive adult crustacean. It will be seen that, in many respects, the trilobite

*The adult *Apus* properly has five pairs of cephalic limbs. A sixth pair of appendages has been correlated as maxillipedes, though from their innervation they seem to be metastomic and homologous with the chilaria of *Limulus*.

recalls this type, but, as already suggested, is removed some distance from the prototype, although in itself a most primitive crustacean. Lang[25] gives a very comprehensive description of the racial form, as follows: "The original Crustacean was an elongated animal, consisting of numerous and tolerably homonomous segments. The head segment was fused with the 4 subsequent trunk segments to form a cephalic region, and carried a median frontal eye, a pair of simple anterior antennæ, a second pair of biramose antennæ and 3 pairs of biramose oral limbs, which already served to some extent for taking food. From the posterior cephalic region proceeded an integumental fold which, as dorsal shield, covered a larger or smaller portion of the trunk. The trunk segments were each provided with one pair of biramose limbs. Besides the median eye there were 2 frontal sensory organs. The nervous system consisted of brain, œsophagael commissures and segmental ventral chord, with a double ganglion for each segment and pair of limbs. The heart was a long contractile dorsal vessel with numerous pairs of ostia segmentally arranged. In the racial form the sexes were separate, the male with a pair of testes, the female with a pair of ovaries, both with paired ducts emerging externally at the bases of a pair of trunk limbs. The excretory function was carried on by at least 2 pairs of glands, the anterior pair (antennal glands) emerging at the base of the second pair of antennæ, the posterior (shell glands) at the base of the second pair of maxillæ. The mid-gut possibly had segmentally arranged diverticula (hepatic invaginations)."

The characters ascribed to the typical nauplius have been selected mainly on the principle of general average. They do not satisfy the theoretical demands resulting from a comparative morphological study nor are they consistent with the accepted requirements of an ancestral type of the Crustacea. Claus[16] urges that the nauplius is a modified or secondary larval form, and the writer now hopes to farther substantiate this view, and partly to reconstruct the nauplius from internal evidence and from its more primitive representative, the protaspis of the trilobites.

The usual fetaures attributed to the nauplius are: three pairs of appendages, afterwards forming two pairs of antennæ and the mandibles: the first pair is uniramous and sensory in function; the second and third pairs are biramous, swimming appendages; body usually unsegmented; anteriorly there is a single median eye, and a large labrum, or upper lip; an alimentray canal bent anteriorly, and ending in an anus near the posterior end of the body; a dorsal shield; the second pair of antennæ are innervated from a sub-œsophageal ganglion. Frontal sense organs and a rudimentary metastoma are sometimes present. The trunk and abdominal regions are not generally differentiated.

Balfour[1] remarks of the nauplius that: "In most instances it does not *exactly* conform to the above type, and the divergences are more considerable in the Phyllopods than in most other groups." This variation is indeed quite marked among nearly all the groups besides the phyllopods and furnishes the facts for the conclusion, that the hexapodous condition is not primitive.

On plate X are represented some of the leading types of nauplius structure, taken chiefly from the excellent compilation by Faxon.[2] Bearing in mind the typical and average characters of this larva, some of the variations will be briefly reviewed.

The nauplius of *Apus*, represented in plate X, figure 2, shows the rudiments of five trunk segments, which in a later stage (figure 3) develop phyllopodiform appendages belonging to sixth, seventh, and eighth pairs of limbs. They are the anterior trunk appendages and appear at a time when the fourth cephalic pair is a mere rudiment while the fifth is entirely undeveloped. The fourth and fifth pairs of head appendages evidently must have some existence, though undeveloped in the nauplius. The physical conditions of nauplius life probably do not require them, and they therefore remain for a time quiescent or undeveloped.

In figures 4, 5, 8, and 6, respectively, of *Branchipus*, *Artemia*, *Leptodora*, and *Limnaida*, the first pair of appendages becomes progressively shortened, until, in the last, they almost disappear. *Leptodora* (figure 8) and *Lepidurus* (figure 7) also have rudimentary trunk segments and appendages (*g*). Figures 9 and 10, of *Daphnia* and *Moina* (from summer eggs), show how rudimentary the nauplius appendages may become when this stage is passed within the egg. Even a more marked reduction is exhibited in the embryos of *Palæmon* and *Astacus* (figures 25 and 26). *Cyclops* is a very normal form, though even here in a second nauplius stage (figure 12), a fourth pair of limbs is developed.

Examples have been cited showing the reduction and obsolescence of the anterior antennæ, or first pair of nauplius limbs, and some cases will now be cited in which the third pair also becomes reduced and rudimentary. *Achtheres* (figure 14) and *Mysis* (figure 22) afford instances of this variation. The former is of additional interest, as showing that the appendages from the fourth to the eighth, may be developed, while the third remains quiescent, and that the second pair, typically biramous, is here unbranched. Similarly, in *Mysis*, *Nebalia* (figure 19), and especially in *Cypris* (figure 18), the nauplius limbs are simple. The embryo of *Lucifer* (figure 24) and a late nauplius stage of *Euphausia* (figure 21) are also of moment, in showing the beginnings of the metastoma (*mt*) with the two maxillæ and first maxillipedes.

It appears from the foregoing facts, that enough has been shown to prove the marked variations in the number and state of development of the nauplius appendages, and to reach the conclusion, that potentially five pairs of cephalic appendages are present. The two posterior pairs are the ones usually not developed until after some of the trunk limbs appear. Very satisfactory explanations have been offered as to why the first three pairs have been selected by the larva, although it does not seem to have been recognized that the fourth and fifth have been more or less suppressed during the evolution of the class. Lang[25] accounts for the three pairs of nauplian limbs by saying that: "In a young larva which, like the *Nauplius*, is hatched early from the egg, only a few of the organs most necessary for independent life and independent acquisition of food can be developed. The 3 most anterior pairs of limbs, which serve for swimming may be described as such most necessary organs. The third pair perhaps belongs to this category, because as mouth parts, generally provided with masticatory processes, they serve not only witn the others for locomotion, but also for conducting food to the oral aperture."

Another point in favor of the original pentamerous composition of the cephalic portion of the nauplius or protonauplius is the dorsal shield which is present in many forms, and is considered (*vide* Bernard[11]) as a dorsal fold of the fifth segment. So that in reviewing the nauplius structures, we find here and there evidences of the entire series of head segments.

Now, since the protaspis fulfils the rquirements by having five well-developed cephalic segments, and is besides the oldest crustacean larva known, it is believed that, in so far, at least, it represents the primitive ancestral larval form for the class. The nauplius, therefore, is to be considered as a derived larva modified by adaptation.

Other variations in the characters of the nauplius occur, but as they have clearly originated (*a*) from the parasitic habits of the adult, (*b*) from embryonic conditions, or (*c*) from earlier inheritance, they need not enter into consideration here. Such, for example, are (*a*) the absence of an intestine in *Sacculina*, (*b*) the absence of the median eye in *Daphnia* and *Moina*, and (*c*) the bivalve shell in *Cypris*. The larval stages of other, and especially later and higher groups of arthropods, offer more considerable differences and need not enter into this discussion, which is aimed chiefly to establish the genetic relationship between the protaspis of trilobites and the nauplius of recent Crustacea.

VIII. Summary.

Barrande first demonstrated the metamorphoses of trilobites in 1849, and recognized four orders of development, which are now shown to be stages of growth of a single larval form.

A common early larval form is recognized and called the *protaspis*.

The protaspis has a dorsal shield, a cephalic portion composed of five fused segments and a pygidial portion consisting of the anal segment with one or more fused segments.

The simplest protaspis stage is found in the Cambrian genera of trilobites. During later geological time it acquired additional characters by earlier inheritance and became modified, though retaining its pentamerous glabella and small abdominal portion.

Some of these acquired characters of the dorsal shieid are the free-cheeks, the eyes, the eye-line, the genal angles and the ornaments of the test. The free-cheeks and eyes moved to the dorsum from the ventrum.

The history of the acquired characters is traced by means of comparisons between larval and adult trilobites, through paleozoic time, and a progressive series of larval forms established in exact correlation with adult forms, which themselves constitute a progressive series, chronologically and structurally.

The antiquity of trilobites is indicated by their remains in the oldest Paleozoic rocks, and especially by the fact that in the early Cambrian they are already much specialized and differentiated in number of genera. The age of the trilobite or crustacean phylum is further shown from the distinct larval stages of trilobites and their having a head and pygidium of consolidated segments.

Since the trilobites are among the oldest and most generalized of Crustacea, their ontogeny is of considerable importance in interpreting crustacean phylogeny.

The protaspis in its segmentation shows that the cephalon had five pairs of appendages as in the adult.

The crustacean nauplius is shown to be homologous with the protaspis and to have potentially five cephalic segments bearing appendages, which should therefore be taken as characteristic of a protonauplius.

The nauplius is a modified crustacean larva. The protaspis more nearly represents the primitive ancestral larval form for the class, and approximates the protonauplius.

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X. Explanation of Plates.

Plate VIII.

Figure 1. *Solenopleura robbi* Hartt: after Matthew. Anaprotaspis stage: showing obscurely annulated axis. x30. St. John group, Cambrian, New Brunswick.

Figure 2. *Liostracus onangondianus* Hartt: after Matthew. Anaprotaspis stage: the neck lobe is the only one distinctly marked. x23. Cambrian, New Brunswick.

Figure 3. *Ptychoparia linnarssoni* Walcott: after Matthew. Anaprotaspis stage: axis slender, slightly annulated: pygidium defined by transverse furrow. x30. Cambrian, New Brunswick.

Figure 4. *Ptychoparia linnarssoni* Walcott: after Matthew. Protaspis representing a later moult than the preceding, and showing stronger annulations on the axis, with an additional one on the pygidium. x25. Cambrian, New Brunswick.

Figure 5. *Ptychoparia kingi* Meek. Anaprotaspis or early stage; showing obscurely defined characters, partly due to the fact that the specimen is a cast. x45. Cambrian, Nevada.

Figure 6. *Ptychoparia kingi* Meek. A later stage (metaprotaspis): showing the strongly annulated axis, the eye-line, the free-cheeks including the genal angles, and two segments on the pygidium. x45. Cambrian, Nevada.

Figure 7. *Ptychoparia kingi* Meek: after Walcott. An adult specimen. This and the other figures of adult individuals are represented in outline, with the free-cheeks shaded, to bring out more strongly the changes in the structure of the cephalon. x1/2. Cambrian, Utah.

Figure 8. *Sao hirsuta* Barrande: after Barrande. Anaprotaspis stage; showing obscurely the limits of the pygidium, the eye-line, and the nearly cylindrical glabellar axis, expanding on the frontal margin. This and the two following specimens are preserved as casts. x30. Cambrian, Bohemia.

FIGURE 9. *Sao hirsuta* Barrande: after Barrande. A later moult, probably near the end of the metaprotaspis stage: showing the annulated axis expanded in front: free cheeks narrow and marginal: pygidium of four segments, with pleura distinctly marked and grooved. x30. Cambrian, Bohemia.

FIGURE 10. *Sao hirsuta* Barrande: after Barrande. A more advanced stage at or after the close of the paraprotaspis, in which the pygidium is complete, but before the first free thoracic segment is developed. x30. Cambrian, Bohemia.

FIGURE 11. *Sao hirsuta* Barrande. An adult individual combining the characters as shown in several of Barrande's figures of this species. x½. Cambrian, Bohemia.

FIGURE 12. *Triarthrus becki* Green. Anaprotaspis: showing the annulated axis, terminating before reaching the anterior margin: the eye lines extending from the first segment to the marginal eye lobes: pygidium defined by a slight groove, and including two segments of the axis. x45. Ordovician, Utica Slate, near Rome, New York.

FIGURE 13. *Triarthrus becki* Green. Protaspis at a later moult: showing slight increase in size and the addition of a segment to the pygidium. x45. Utica Slate near Rome, New York.

FIGURE 14. *Triarthrus becki* Green. An adult individual of this species. x½. Utica Slate, New York.

PLATE IX.

FIGURE 1. *Acidaspis tuberculata* Conrad. Anaprotaspis: showing denticulate margin and spines on cephalon: axis strongly annulated: eyes submarginal. x20. Lower Helderberg, Albany Co., New York.

FIGURE 2. The same: profile, slightly oblique. x20.

FIGURE 3. *Acidaspis tuberculata* Conrad. An adult individual, restored from fragments and an entire enrolled specimen. Natural size. Lower Helderberg, Albany Co., New York.

FIGURE 4. *Arges consanguineus* Clarke. Dorsal view of a larva at or after the close of the paraprotaspis stage: showing the form and ornamentation. x20. Lower Helderberg, Albany Co., New York.

FIGURE 5. *Proëtus parviusculus* Hall. Anaprotaspis: showing strongly annulated axis, with grove at each side: large prominent anterior eyes: pygidial pleura indicated by faint grooves. x45. Ordovician. Utica Slate, near Rome, New York.

FIGURE 6. *Proëtus parviusculus* Hall. A later moult, near the close of the paraprotaspis stage: showing the larger pygidium which, however, is still incomplete, and the slight backward movement of the eyes. The right side of the specimen is restored. x45. Ordovician, Utica Slate, near Rome, New York.

FIGURE 7. *Proëtus parviusculus* Hall. An adult individual. x2 Ordovician, Utica Slate, near Rome, New York.

FIGURE 8. *Dalmanites socialis* Barrande: after Barrande. Anaprotaspis stage: showing the large strongly annulated axis: the prominent anterior marginal eyes: mucronate genal angles: pygidium of three segments. x30.

FIGURE 9. *Dalmanites socialis* Barrande: after Barrande. Meta protaspis stage: showing the stronger definition of the pleura of the pygidium. x30. Ordovician. Bohemia.

FIGURE 10. *Dalmanites socialis* Barrande: after Barrande. The specimen probably represents the close of the paraprotaspis stage, and shows four segments in the pygidium and the first evidence of the backward movement of the eyes, which now indent the margin. x30. Ordovician. Bohemia.

FIGURE 11. *Dalmanites socialis* Barrande: after Barrande. Outline of an adult individual. x½. Ordovician. Bohemia.

PLATE X.

The Roman numerals indicate the appendages in their consecutive order.

I. 1st pair of appendages, or antennules.

II. 2d pair of appendages, or antennæ.

III. 3d pair of appendages, or mandibles.

IV. V, etc., maxillæ, maxillipeds, swimming feet, etc.

Oel, unpaired eye: *oc*, paired eyes: *lb*, labrum.

FIGURE 1. *Triarthrus becki*. A restoration of the ventral side of the protaspis stage in accordance with the best evidence at present attainable, as explained in the text. The VIth and the VIIth pairs of appendages belong to the abdomen, which is marked off by a transverse line: *mt*, metastoma: *g*. free-cheeks.

FIGURE 2. *Apus cancriformis*: after Claus (from Faxon). *Phyllopoda*. Nauplius larva, just hatched: ventral side. Behind the mandibles (III) are indications of five thoracic somites, *g*.

FIGURE 3. *Apus cancriformis*: after Claus (from Faxon). *Phyllopoda*. Second larval stage (metanauplius): ventral side. The second maxilla, V, is wanting: *f*. frontal sense organs.

FIGURE 4. *Branchipus stagnalis*: after Claus (from Packard). *Phyllopoda*. Nauplius stage.

FIGURE 5. *Artemia gracilis*: after Packard. *Phyllopoda*. Nauplius stage: showing obscure segmentation.

FIGURE 6. *Limnadia hermanni*: after Lereboullet (from Packard). *Phyllopoda*. Nauplius: dorsal side: first pair of appendages obsolescent: labrum, *lb*, greatly developed.

FIGURE 7. *Lepidurus productus*: after Brauer (from Bernard). *Phyllopoda*. Nauplius with obscure segmentation of the trunk, *g*.

FIGURE 8. *Leptodara hyalina*: after Sars (from Balfour and Bronn). *Phyllopoda*, *Cladocera*. Nauplius larva from winter egg: *g*, rudimentary feet.

FIGURE 9. *Daphnia longispina*: after Dohrn (from Claus). *Phyllopoda*, *Cladocera*. Nauplius stage of embryo, with rudimentary appendages.

FIGURE 10. *Moina rectirostris*: after Grobben (from Faxon). *Phyllopoda*, *Cladocera*. Embryo from the summer egg in the nauplius stage, developed in the brood-cavity of the parent: appendages rudimentary.

FIGURE 11. *Cyclops tenuicornis:* after Claus (from Balfour). *Copepoda, Natantia.* Nauplius, first stage. This and the next are the original forms described as *Nauplius*, by O. F. Müller, and believed at that time to be adult.

FIGURE 12. *Cyclops tenuicornis:* after Claus (from Balfour). *Copepoda, Natantia.* Nauplius, second stage: IV, maxilliæ.

FIGURE 13. *Cetochilus septentrionalis:* after Grobben (from Faxon). *Copepoda, Natantia.* Nauplius, just hatched: ventral view.

FIGURE 14. *Achtheres percarum:* after Claus (from Faxon). *Copepoda, Parasitica.* Larva at the time it leaves the egg, with only two anterior unbranched pairs of appendages of the typical nauplius present. Under the skin are the rudiments of six pairs of appendages: III, mandibles; IV, maxillæ: V, VI, maxillæ: VII, VIII, swimming feet.

FIGURE 15. *Balanus balanoides:* after Hoek (from Faxon). *Cirripedia.* Nauplius.

FIGURE 16. *Lernaeodiscus porcellanae:* after F. Müller (from Faxon). *Cirripedia, Rhizocephala.* Nauplius, ventral side: showing outline of dorsal shield.

FIGURE 17. *Sacculina purpurea:* after F. Müller (from Huxley and Balfour). *Cirripedia, Rhizocephala.*

FIGURE 18. *Cypris ovum:* after Claus (from Faxon). *Ostracoda.* First larval (nauplius) stage, with bivalve shell and unbranched second and third pairs of appendages.

FIGURE 19. *Nebalia geoffroyi:* after Metschnikoff (from Faxon). *Leptostraca.* Side view of the so-called nauplius stage of the embryo within the egg. Rudiments are present of the two pairs of antennæ, I, II, the mandibles, III.

FIGURE 20. *Euphausia:* after Metschnikoff (from Faxon). *Schizopoda.* Nauplius, just hatched.

FIGURE 21. *Euphausia:* after Metschnikoff (from Faxon). *Schizopoda.* Nauplius at a later stage: ventral view: *mt*, metastoma: IV, V, maxillæ: VI, maxilliped. In the next, or Protozoëa, stage, the appendages, IV, V, VI, are true phyllopodiform feet.

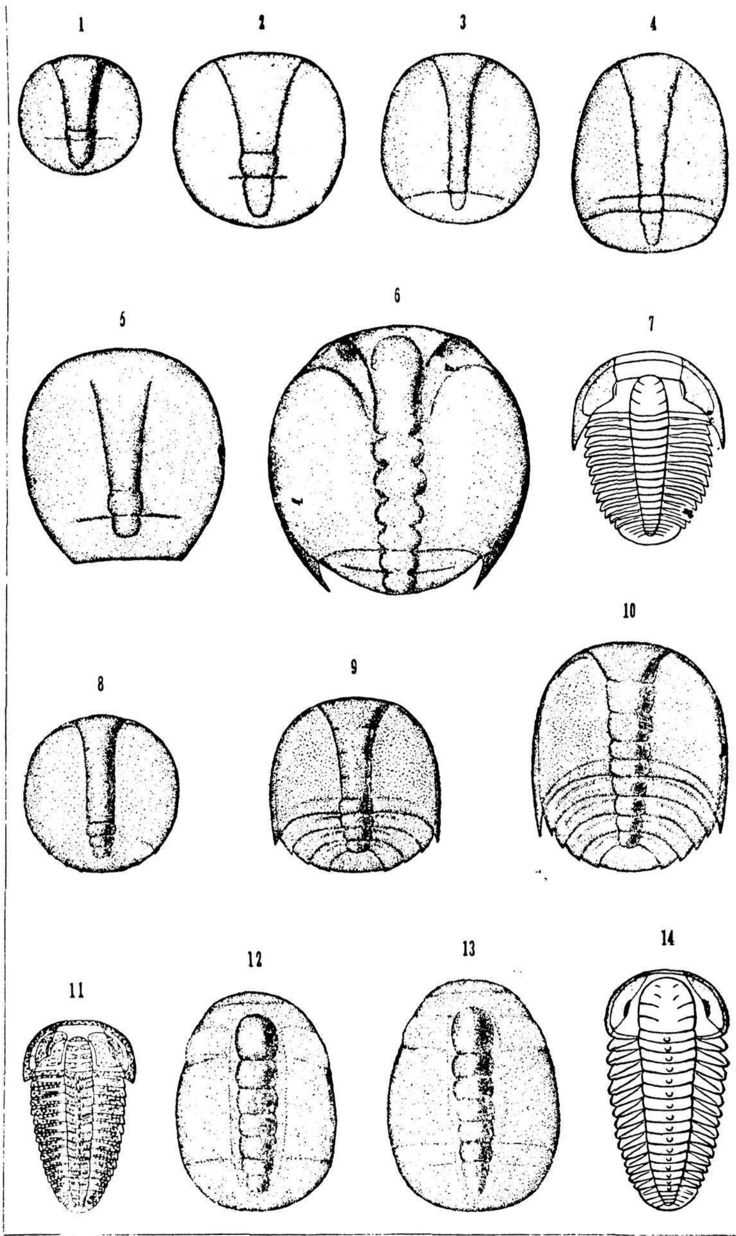
FIGURE 22. *Mysis ferruginea:* after Van Beneden (from Faxon). *Schizopoda.* Nauplius-like embryo: side view. The appendages are unsegmented, and the third pair quite rudimentary. A number of later metamorphoses are undergone in the nauplius skin, until the full number of appendages is developed.

FIGURE 23. *Peneus:* after F. Müller (from Faxon). *Decapoda, Macroura.* Nauplius: from dorsal side.

FIGURE 24. *Lucifer:* after Brooks (from Faxon). *Decapoda, Macroura.* Ventral view of embryo artificially removed from the egg: IV, V, VI, buds representing the two pairs of maxillæ and first pair of maxillipeds of the adult.

FIGURE 25. *Palæmon:* after Bobretzky (from Faxon). *Decapoda, Macroura.* Nauplius stage of embryo within the egg.

FIGURE 26. *Astacus fluviatilis:* after Reichenbach (from Faxon). *Decapoda, Macroura.* Nauplius stage of embryo.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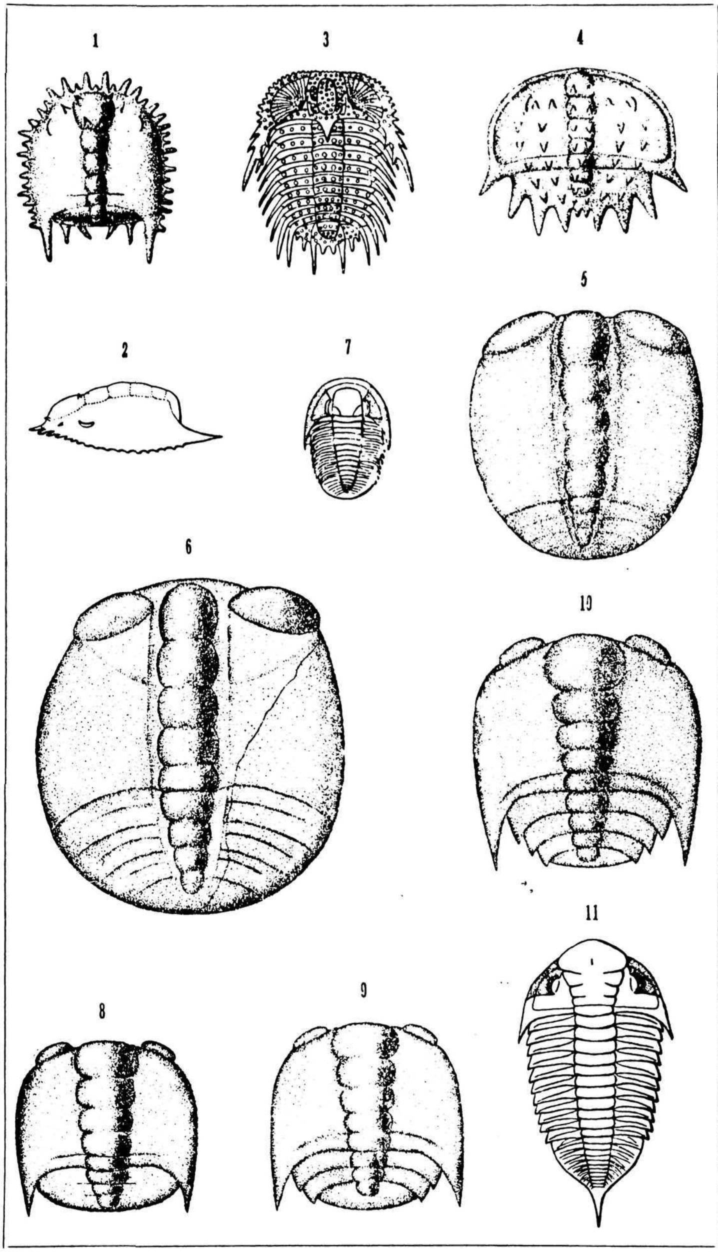
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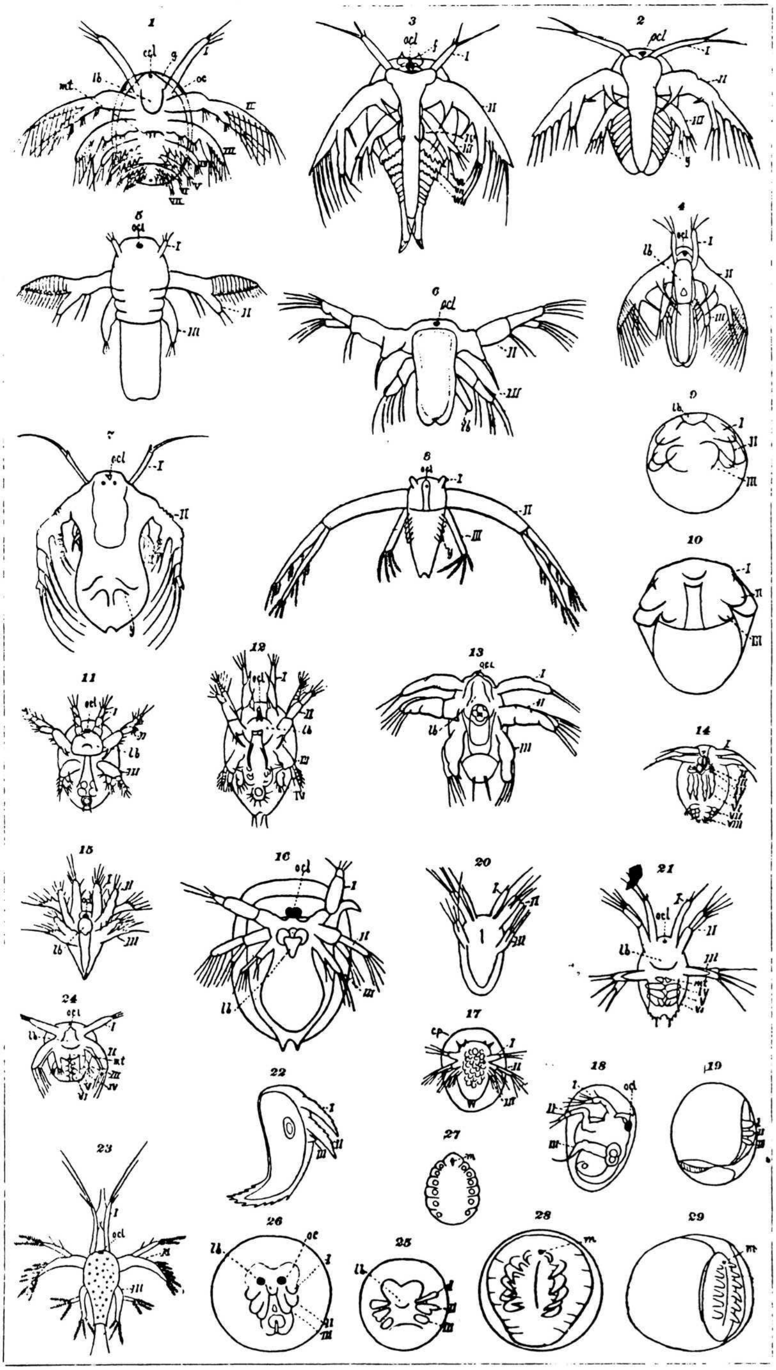
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FIGURE 27. *Limulus polyphemus*: after Kingsley. *Xiphosura.* Ventral view of embryo: showing the budding of the legs.

FIGURE 28. *Limulus polyphemus:* after Packard (from Balfour). *Xiphosura.* Ventral view of embryo in the egg: showing the rudiments of six pairs of legs: *m.* mouth.

FIGURE 29. *Limulus polyphemus:* after Packard (from Balfour.). *Xiphosura.* Oblique side view of embryo, with the mouth and rudimentary limbs on the ventral plate.

The figures of embryonic *Limulus* are introduced for comparison. They are so different from the nauplius that detailed notice seems unnecessary.