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ART. VIII.—*Outline of a Natural Classification of the Trilobites*; by CHARLES E. BEECHER. (With Plate III.)

Introduction.

WITH the possible exception of the barnacles, no group of arthropods has received more varied treatment by specialists than the trilobites. This taxonomic uncertainty has been due mainly to a lack of knowledge of the structure, and to certain real or fancied resemblances to *Limulus*.

The early references of trilobites to the mollusks, insects, and fishes need not be noticed, for since they have been made the subject of special study, they have been commonly classed with the crustacea, and placed near the phyllopods by most observers. Quite a number of naturalists, however, still divorce the trilobites and limuloids from the crustacea and ally them with the arachnids. It is not proposed at this time to discuss the homologies of *Limulus*, but the trilobites show the clearest evidence of primitive crustacean affinities, in their protonauplius larval form, their hypostoma and metastoma, the five pairs of cephalic appendages, the slender jointed antennules, the biramous character of all the other limbs and their original phyllopodiform structure. They differ from *Limulus*, not only in most of these regards, but also in not having an operculum. From this and all other arthropods, they are distinguished by having compound eyes on free cheek pieces which apparently represent the pleura of a head segment that is otherwise lost, except possibly in some forms of stalked eyes and in the cephalic neuromeres of later forms. The most recent discussions as to the affinities of trilobites are to be found in the papers by Bernard,[7, 8, 9, 10] Kingsley,[23] Woodward,[34] and the writer,[5] where from the facts presented, their intimate relationships with the crustacea follow as a necessary corollary.

Previous Classifications.

The various schemes of classification that have been applied to the trilobites since that of Brongniart,[11] in 1822, have been enlarged and revised by various authors, until, at the present time, no particular arrangement of the families or genera can be said to be endorsed. The one which is generally recognized as manifestly faulty, that of Barrande,[3] is the one most commonly found in text-books and special memoirs. Barrande's definitions and limitations of the generic and family groups were natural and accurate, showing a most complete knowledge of generic and specific values, but in the grouping and arrangement of the families, he selected characters of secondary rank.

Of all the investigators who have attempted any classification of the families, J. W. Salter[32] seems to have had the clearest insight into the important value of certain characters, and to have approached nearest to a natural system. In zoölogical research, the study of ontogeny and the principles of morphogenesis were then scarcely recognized as having any direct application. It is quite remarkable, therefore, that Salter, as early as 1864, should have singled out, as the basis of his subdivisions, the characters which are the dominant variants in ontogeny.

It is not necessary in this place to discuss all the classifications which have been proposed. Barrande[3] gives a complete resumé down to 1850, and shows in a very satisfactory manner the weak points of each, furnishing strong reasons as to why they are unnatural and therefore untenable. The underlying principles of these early attempts at a classification are here briefly summarized. (1) The first classification of trilobites was advanced by Brongniart[11] in 1822, in which all the forms previously known as *Entomolithus paradoxus* were shown to belong to five distinct genera. (2) Dalman,[16] in 1826, made two groups based upon the presence or absence of eyes. (3) Quenstedt,[30] in 1837, recognized the number of thoracic segments and the structure of the eyes as of the greatest importance. (4) Milne-Edwards,[28] in 1840, considered the power of enrollment as of prime value. (5) Goldfuss,[20] in 1843, made three groups, depending on the presence or absence of eyes and their structure. (6) Burmeister,[12] in 1843, accepted the two divisions of Milne-Edwards, and laid stress on the nature of the pleura and the size of the pygidium. (7) Emmrich's first scheme,[17] in 1839, was founded on the shape of the pleura, the presence or absence of eyes and their structure. (8) The later classification of the same author,[18] published in 1844, was based on whether the abdomen was composed of fused or free segments, and the minor divisions depended chiefly on the structure of the eyes and the facial suture. (9) Corda,[15] in 1847, placed all trilobites in two groups, one having an entire pygidial margin, and the other with the pygidium lobed or denticulate. (10) McCoy,[25] in 1849, took the presence or absence of a facet on the pleura for a divisional character. As this is an indication of the power or the inability of enrollment, it does not differ materially from the schemes of Milne-Edwards and Burmeister.

Zittel,[35] in a historial review brought down to 1885, includes in addition the schemes of Barrande and Salter, and remarks that the basis of Barrande's general grouping, namely, the structure of the pleura, has neither a high physiological nor morphological meaning. Both Barrande and Salter recognize nearly the same families, with slight differences, and the latter adopts a division into two lines, based on the number of body rings and the size of the pygidium. These include and are themselves included in four groups, founded on the presence and form of the facial suture and the structure of the eyes.

Haeckel* has recently given the trilobites their full value in a classification of the articulates. Although he has not advanced a detailed classification, still it is desirable to review the ordinal groups which he proposes. He considers the *Trilobita* as a legion under the first class, *Aspidonia*, of the crustacea, which is characterized as being without a nauplius larval form and as having a pair of preoral antennæ. In this class is also included the legion *Merostomata*, the *Trilobita* being especially distinguished by the number and character of the legs. The writer[5] believes that it is now satisfactorily demonstrated that the protaspis, or early larval form of the trilobite, is a protonauplius, and homologous with the nauplius of higher crustacea. Therefore, the *Trilobita* cannot remain in the *Aspidonia* as here defined.

Haeckel further divides the *Trilobita* into two orders, the first, the *Archiaspides* (or *Protrilobita*), and the second, the *Eutrilobita* (or *Pygidiata*). The *Archiaspides* is represented by the families Olenida and Triarthrida, and is distinguished by the absence of a real pygidium, and by the complete homonomy of the numerous body segments and their phyllopodiform appendages. The families are themselves distinguished by the semicircular or crescent-shaped cephalon and by the presence or absence of genal spines. The *Eutrilobita* is represented by the families Asaphida and Calymenida, and is marked by the heteronomy of the body segments as expressed in the functional pygidium.

* Systematische Phylogenie der wirbellosen Thiere (Invertebrata). Zweiter Theil. 1896.

Salter, Burmeister, and Emmrich have, as previously noticed, attempted to use the comparative size and development of the pygidium for dividing the trilobites into groups larger than families, and it seems evident from the present state of knowledge that it is impossible to make this character of more than family or even generic value. Many of the genera which must naturally be included in the *Archiaspida* have pygidia that cannot be said to be rudimentary, obsolete, or wanting in function. Even those genera having pygidia with few segments, as *Mesonacis*, *Holmia*, *Paradoxides*, *Selenopeltis*, *Dicranurus*, *Bronteus*, *Harpes*, etc., show in many other more important characters that they are highly differentiated and specialized forms and that this feature is one expression of such development. The futility of the scheme is at once evident when a comparison is made between allied genera which present marked differences in the size and segmentation of the pygidium, as *Phacops* and *Dalmanites*, *Ceraurus* and *Encrinurus*, *Calymene* and *Homolanotus*, *Harpes* and *Trinucleus*, *Mesonacis* and *Zecanthoides*, *Paradoxides* and *Dikelocephalus*.

The last classification to be noticed is that of E. J. Chapman,[13] in 1889, in which four suborders or primary groups are proposed, differing considerably from any previous arrangement, and based upon arbitrary features of general structure and configuration, especially the form of the glabella, whether wide, conical, or enlarged. Twenty-seven families are recognized. In this scheme, *Trinucleus*, *Ampyx*, and *Æglina* form one section; *Paradoxides* and *Acidaspis*, together with *Phacops* and *Encrinurus*, another; all under one suborder. Omitting the Agnostidæ, there are here considered in a single suborder the most characteristic representatives of nearly all the types of trilobite structure. *Proëtus*, *Cyphaspis*, and *Arethusina* fall into three sections, under two suborders, although these genera, on account of their great similarity in essential points, are placed in a single family by most authors. A further analysis of this classification in its broader lines would be unprofitable. It is sufficient to state that the facts obtained from the study of the ontogeny of any species are completely in discordance with these classifications, and clearly demand other interpretations.

Rank of the Trilobites.

As to the rank of the trilobites in a classification of the crustacea, there is also much diversity of opinion. They have long been regarded as an order, but any attempt to include them in this way under higher groups, such as the *Entomostraca*, *Malacostraca*, or *Palæocarida*, results in such broad generalities and looseness of definition as to render these divisions of little value. Even the *Entomostraca*, as restricted to the orders Phyllopoda, Ostracoda, Copepoda, and Cirripedia, seems heterogeneous and probably polyphyletic. Milne-Edwards,[27] Gegenbaur,[19] Walcott,[33] and others have considered the trilobites as belonging to a class of arthropods intermediate between the crustacea and arachnids. Some recent authors, as Lang,[24] have attempted to overcome the difficulty by attaching them as an appendage ("Anhang") to the crustacea. Kingsley,[23] on the other hand, has placed them as a subclass of the crustacea, leaving all the other crustacea to come under a second subclass, the *Eucrustacea*. The present state of knowledge of their structure and development is in favor of giving the trilobites the rank of a subclass, but for purposes of comparison and correlation, the fullest results can be brought out by recognizing the old and well-known subclasses,—the *Entomostraca* and *Malacostraca*.

The following tabular view of the leading points of the comparative morphology of the three subclasses is introduced to show, first, the claims of the *Trilobita* as an equivalent group, and, second, the progressive differentiation of characters. In nearly every particular the trilobite is very primitive, and closely agrees with the theoretical crustacean ancestor. Its affinities are with both the other subclasses, especially their lower orders, but its position is not intermediate.

Comparative Morphology of Crustacea.

Subclass I. *Trilobita.*	Subclass II. *Entomostraca.*	Subclass III. *Malacostraca.*
1. All marine.	Marine and fresh water.	Marine and fresh water.
2. Free.	Free, parasitic, and attached.	Free and parasitic.
3. Body longitudinally triregional.	Various.	Various.
4. Larva a protonauplius.	Larva almost universally a nauplius.	Larva generally a zoea, a nauplius stage being often developed before hatching, except in *Euphausia* and *Peneus*.
5. Number of segments variable.	Number of segments variable.	Definite number of segments.
6. Cranidium of five fused segments.	Head of five fused segments to which, rarely, a thoracic segment is added.	Head of five fused segments to which one or more, or all of the thoracic segments may unite, forming a more or less complete cephalothorax.
7. Ocelli rarely present.	Ocelli present throughout life.	Ocelli absent in adult forms.
8. Paired compound sessile eyes on cheek pieces usually present.	Paired compound eyes usually present; stalked or sessile. Absent in adult Cirripedia and some Copepoda.	Paired compound eyes usually present; stalked or sessile.

Subclass I. *Trilobita.*	Subclass II. *Entomostraca.*	Subclass III. *Malacostraca.*
9. Thorax distinct; number of segments variable, all free.	Thorax with variable number of segments.	Thorax with eight segments, some of which are generally united with the head.
10. Abdomen distinct; variable number of fused segments.	Abdomen with variable number of separate segments.	Abdomen of seven generally free segments; eight in Leptostraca.
11. All segments of cranidium, thorax, and abdomen, except the anal segment, carry paired appendages.	Some segments without appendages.	All segments usually carry appendages except the last one or two.
12. All appendages biramous except antennules	Some appendages are modified and have lost biramous structure.	Some appendages have lost biramous structure.
13. Appendages typically phyllopodiform. Exopodite a swimming leg; endopodite modified into a crawling leg.	Appendages generally greatly changed in most orders; phyllopodiform in young forms and throughout life in Phyllopoda.	Appendages typically phyllopodiform, but greatly modified in all but the lowest order (*Nebalia*).
14. All appendages of the head except antennules pediform.	Some appendages of the head modified into rowing organs, mandibles, or suckers.	Some appendages of the head modified into mandibles, or organs for seizing food.
15. Thoracic appendages ambulatory and swimming.	Thoracic appendages ambulatory, swimming, and seizing.	Thoracic appendages ambulatory, swimming, and seizing.
16. Abdominal limbs on all segments except the anal, phyllopodiform.	Abdominal limbs generally wanting.	Abdominal limbs often reduced except the last pair, which with telson frequently form a caudal fin. Chiefly branchial in some groups.
17. Coxal elements of all limbs forming gnathobases, which become manducatory organs on the head.	Coxal elements seldom forming gnathobases except on the head.	Coxal elements seldom forming gnathobases except on the head; never on the abdomen.
18. Respiration cuticular and by fringes on exopodites.	Respiration mainly cuticular and by the limbs and gill appendages.	Respiration cuticular and by the limbs and epipodites.

The more primitive characters of the trilobites as drawn from the foregoing table may be summarized as follows: (1) They are all free marine animals; (2) the animal has a definite configuration; (3) the larva is a protonauplius-like form; (4) the body and abdomen are richly segmented, and the number of segments is variable; (5) the head corresponds to the typical crustacean; (6) the thorax and abdomen are always distinct, the number of segments in each being variable; (7) all segments except the anal bear paired appendages; (8) all appendages are typically phyllopodiform; and (10) the coxal elements of all limbs form gnathobases, which become organs of manducation on the head.

It may be questioned by some whether the present state of knowledge of the ventral structure of trilobites warrants such general assertions as to details of organization. In the first place, it must be granted that there is a remarkable uniformity in the features of the dorsal crust, which naturally reflects to a degree the differentiation and variation of the organs and appendages of the ventral side. Furthermore, the actual appendages have been observed in such diverse and characteristic genera as *Trinucleus*, *Triarthrus*, *Asaphus*, *Ceraurus*, and *Calymene*, and found to conform closely to a single type, so that it seems safe to assume a like agreement throughout.

Morphology of the Cephalon.

The structure of the trilobite head suggests homologies which should be noticed here, and if these correlations are based upon true structural likenesses, they serve not only to emphasize the primitive character of the trilobite, but also aid in interpreting certain organs and structures in the higher crustacea.

The five fused somites of the crustacean head are generally believed to correspond to the third, fourth, fifth, sixth, and seventh neuromeres, leaving the first and second unrepresented either by distinct segments or appendages. These two neuromeres commonly constitute most of the cerebral mass above the œsophagus, and enervate the ocelli and paired eyes. In some, the antennæ are enervated from supra-œsophageal ganglia, while in other forms their ganglia are infra-œsophageal. It was formerly supposed that the stalked eyes of the higher crustacea represented appendages of a head segment, but this belief has been abandoned on account of the derivation of stalked out of sessile organs, as in *Peneus*, and also because the eyes do not always have a relatively fixed position, but may pertain to the first, second, or third head segments. Their structural position in the trilobites, however, is invariable, and it seems probable that in some families of higher crustacea, the eyes are in exact correlation, and may be similarly interpreted.

The writer[5] has previously discussed this question, and adduced reasons for considering the free cheeks in trilobites as "the pleura of an occuliferous head segment." In many species (*Dalmanites*, *Æglina*, etc.), the free cheeks are continuous, forming one piece extending around the front of the head, between the cranidium and the hypostoma, while in others there is a separate piece, the epistoma, between the proximal ends of the cheek pieces holding a like position. These structures occupy the exact position of a true segment, and since, upon theoretical grounds, additional head segments are to be accounted for, the only satisfactory correlation is to consider them as such. Furthermore, the free cheeks are distinctly separated from the cranidium by an open suture, and may be wholly converted into eyes, as in *Æglina armata* Barr., or the unfacetted portion may be reduced to almost nothing, as in *Deiphon*. In such cases, the parallelism is exact with true movable eyes. Bernard[7] concludes from his studies of *Apus* that the hypostoma is homologous with the annelid prostomium. This would make the hypostoma represent the first, and the free cheeks the second of the obsolete segments. Thus the trilobite cephalon would fulfil the demand for additional evidences of primitive head segments, and account for the development of eyes separate from the cephalothorax as commonly restricted.

Supposed evidences of free cheeks or of facial sutures have been recognized in *Limulus*, *Hemiaspis*, and *Bunodes*, but these seem really to correspond to the lines on the dorsal surface of the cephalon of *Harpes* and some *Trinucleus*, running from the glabella to the eye spots and to the margin, and are not the sutures marking the limits of the free cephalic elements, as in *Asaphus* and *Proëtus*. *Limulus*, however, has a suture comparable to that in *Harpes* and *Trinucleus*, extending around the ventral border of the cephalothorax nearly to the posterior angles, and partly separating the ventral plate. In the process of moulting, this suture opens and enables the animal to free itself from its former test.

These interpretations may be employed to some advantage in correlating the segmentation of the trilobite cephalon. As previously stated, the recognized plan in the nervous system of a generalized crustacean requires that there should be a brain or supra-œsophageal ganglion enervating (a) the unpaired eye, (b) the frontal sensory organs and stalked eyes, and (c) the anterior antennæ; then a ventral nervous chord consisting of a succession of double ganglia enervating, respectively, the second pair of antennæ, the mandibles, the first pair of maxillæ, the second pair of maxillæ, and lastly each of the paired thoracic and abdominal appendages. Altogether, there are seven neuromeres pertaining to the head, and on the basis that each neuromere corresponds to an original segment, as on the post-cephalic region, there would need to be this number accounted for. The anterior segment, or number one in the trilobites, would be represented by the hypostoma; the second segment, by the paired eyes, free cheeks, and epistoma; the third, by the anterior lobe of the glabella and the first antennæ; the fourth, by the second lobe of the glabella and the second pair of antennæ; the fifth, by the third lobe of the glabella and the mandibles; the sixth, by the fourth lobe of the glabella and the first maxillæ; and the seventh, by the neck lobe, or occipital ring, and the second pair of maxillæ. The five annulations, or lobes, of the axis of the cranidium, since they primarily carry fulcra for the attachment of muscles supporting or moving the appendages, could thus be interpreted in terms of the ventral structure, making the first lobe the antennulary, the second the antennary, the third the mandibular, the fourth the first maxillary, and the fifth the second maxillary.

No other group of crustacea furnishes such constant and well-developed structures representing the second theoretical head segment, which is obscure or obsolete in all the living groups, excepting probably the stalked eyes of some crustacea and the movable occular segment of the Stomatopods. For this reason, in addition to the many other important differences previously noted in the table of comparative morphology, the trilobites are regarded as a subclass, and the relative denomination and structural relations of this second segment, along with other characters, are considered as of sufficient physiological and morphological importance to determine the ordinal divisions.

Principles of a Natural Classification.

Most satisfactory and conclusive results have already come from the application of the law of morphogenesis, or the recapitulation theory, to various groups of animals, by means of which their natural classification and phylogenetic relations have been determined. Hyatt[21] says on this point (1889): "We have endeavored to demonstrate that a natural classification may be made by means of a system of analysis in which the individual is the unit of comparison, because its life in all its phases, morphological and physiological, healthy or pathological, embryo, larva, adolescent, and old (ontogeny), correlates with the morphological and physiological history of the group to which it belongs (phylogeny)." It is also interesting to note that Agassiz[1] recognized in ontogeny a standard of classification. One of his strongest statements is as follows: "Embryology [=ontogeny] will in the end furnish us with the means of recognizing the true affinities among all animals, and of ascertaining their relative standing and normal position in their respective classes with the utmost degree of accuracy and precision."

These principles can be best applied in a group of animals which has a geological history more or less complete, and which is not wholly parasitic or greatly degenerated. It is of the greatest importance, also, to study the ontogeny of primitive and non-specialized species, because without very complete paleontological evidence, the development of a much later derived form may be so involved with larval adaptations and accelerated characters as to be misleading.

The trilobites lend themselves to this treatment in fulfilling most of the necessary conditions. They have a known geological history stretching through the entire paleozoic, from the beginning of the Cambrian to the Permian. Their structure is generalized and quite uniform, and no sessile, attached, parasitic, land or fresh water species are known. The ontogeny of all the principal groups has been studied, including Cambrian, Ordovician, Silurian, and Devonian types.

The trilobites necessarily furnish little information of the stages of growth which may be classed as embryonic. The early embryonic stages are not preserved as fossils, and therefore may be omitted. In this category are the *protembryo*, or the ovum in its unsegmented and segmented stages (the so-called "eggs of trilobites" may of course represent any stage of embryonic development before the escape of the young); the *mesembryo*, or blastosphere; the *metembryo*, or gastrula; the *neoembryo*, or planula-like stage; and the *typembryo*, when the first distinctive features make their appearance. The first embryonic stage recognized in the trilobites can be referred to the *phylembryo* as defined by Jackson,[22] when the animal may be clearly referred to its proper class. Since this period is distinctive for each class of animals and usually bears a separate name, it has been termed by the writer[5] the *protaspis* stage of trilobites. It closely approximates the protonauplius form, or the theoretical, primitive, ancestral larval form of the crustacea. Like the homologous nauplius of modern higher crustacea, it is the characteristic larval type common to the class. The nauplius is therefore considered as a derived larva modified by adaptation.

The post-embryonic stages of ontogeny have received the names *nepionic*, for the infantile or young; *neanic*, for the immature or adolescent; *ephebic*, for the mature or adult; and *gerontic*, for the senile or old. When especially applied to trilobites, the nepionic stages may include the animal when the cephalon and pygidium are distinct and the thorax incomplete. There would thus be as many nepionic stages as the number of thoracic segments. The neanic stages would be represented by the animal with all parts complete, but with the average growth incomplete. Final progressive growth and development of the individual would fall under the ephebic stage. Lastly, general evidences of senility would be interpreted as belonging to the gerontic stage.

Application of Principles for Ordinal Divisions.

In other classes of animals above the lower cœlenterates, the phylembryonic stage is the starting point from which correlations are made, and out of which all the higher groups are developed by a series of changes along certain lines. The protoconch represents this period in the cephalopods and gastropods; the prodissoconch, in the pelecypods; the protegulum, in the brachiopods, and the protechinus, in the echinoids. In the trilobites, the protaspis, as already stated, has the value of the phylembryo, and in its geological history and the metamorphoses it undergoes to produce the perfect trilobite, accurate information can be gained as to what the primitive characters are, and the relative values of other features acquired during the long existence of the class.

The simple characters possessed by the protaspis are the following, as drawn from the study of this stage in all the principal groups of trilobites: Dorsal shield minute, not more than ·4 to 1^{mm} in length; circular or ovate in form; axis distinct, more or less strongly annulated, limited by longitudinal grooves; head portion predominating; axis of cranidium with five annulations; abdominal portion usually less than one-third the 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 visible, narrow and marginal. Examples, Plate III, figs. 1, 5.

During this stage, several moults took place before the complete separation of the pygidium or the introduction of thoracic segments. These brought about various changes, as the stronger annulation of the axis, the appearance of the free cheeks on the dorsal side, and the growth of the pygidium by the introduction of new appendages and segments, as indicated by the additional grooves on the axis and limb. A full representation of the variety and succession of these early protaspis stages is presented in the writer's paper on the "Larval Stages of Trilobites."[5] Some of the conclusions and discussions in that paper are made use of here.

In the earliest or Cambrian genera, the protaspis stage is by far the simplest expression of this period to be found. In the higher and later genera, the process of acceleration or earlier inheritance has pushed forward certain characters until they appear in the protaspis, thus making it more and more complex.

Taking the early protaspis stages in *Solenopleura*, *Liostracus*, or *Ptychoparia*, it is found that they agree exactly with the foregoing diagnosis in its most elementary sense. Since they are the characters shared in common by all the larvæ at this stage, they are taken as primitive and accorded that value in dealing with adult forms possessing homologous features. Therefore, any trilobite with a large elongate cephalon, eyes rudimentary or absent, free cheeks ventral or marginal, and glabella long, cylindrical, and with five annulations, would naturally be placed near the beginning of any genetic series or as belonging to a very primitive stock.

Next must be considered the progressive addition of characters during the geological history of the protaspis, and in the ontogeny of the individual during its growth from the larval to the mature condition. It was shown in the paper already referred to, that there was an exact correlation to be made between the geological and zoölogical succession of first larval stages and adult forms, and therefore both may be reviewed together.

The first important structures not especially noticeable in all stages of the protaspis are the free cheeks, which usually manifest themselves in the meta- or para-protaspis stages, though sometimes even later. Since they bear the visual areas of the eyes, when they are present, 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. When first discernible, they are very narrow, and in *Ptychoparia* and *Sao* include the genal angles. In *Dalmanites* and *Cheirurus*, however, the genal angles are borne on the fixed cheeks. If, as Bernard[7] concludes, the crustacean head has been formed by the bending under, to the ventral side, of the anterior segments of an ancestral carnivorous annelid, this furnishes a means of further determining and also of satisfactorily correlating the prime significance and importance of the free cheeks.

Since the free cheeks are ventral in the earliest larval stages of all but the highest trilobites, and as this is an adult feature among a number of genera which on other grounds are very primitive, this is taken as generally indicative of a very low rank. It seems to mean that the second segment remains where it was mechanically placed, and retains its full somitic nature, though from the necessities of such a condition, true ventral segments must soon disappear through modification into other structures or through disuse as segments. The genera *Harpes*, *Agnostus*, *Trinucleus*, and their allies agree in having well-developed, continuous, ventral free cheeks, and constitute a natural group. As they possess one expression or type of the genesis of an important common character, based upon facts of development, it should stand as an ordinal character, and as such it is here taken. For this group, the name *Hypoparia* is proposed. It is fully defined, and its limitations established in the proper place in the classification.

The remaining genera of trilobites present two distinct types of head structure, dependent upon the extent and character of the free cheeks. In both, the free cheeks make up an essential part of the dorsal crust of the cephalon, being continued on the ventral side only as a doublure or infolding of the edge, similar to that of the free edge of the cranidium, the ends of the thoracic pleura, and the margin of the pygidium. They may be separated only by the cranidium, as in *Ptychoparia*, or by the cranidium and epistoma, as in *Illænus* and *Homalonotus*, or they may be united and continuous in front, as in *Æglina* and *Dalmanites*. One type of structure is distinguished by having the free cheeks include the genal angles, thus cutting off more or less of the pleura of the occipital segment. The genera belonging to this group constitute the second order, the *Opisthoparia*.

The third and last type of structure includes forms in which the pleura of the occipital segment extend the full width of the base of the cephalon, embracing the genal angles. The free cheeks are therefore separated from the cranidium by sutures cutting the lateral margins of the cephalon in front of the genal angles. Genera having this structure are here placed in the order *Proparia*.

Several genera, as *Calymene* and *Triarthrus*, have been described as having the facial sutures beginning at or cutting the apex of the genal angle, thus making it indeterminate whether they should be classed with the Opisthoparia or Proparia. It will be found, however, that some species of these genera leave no doubt as to the anterior or posterior position of the suture. The small genal spines of *Calymene callicephala* Green are situated on the ends of the fixed cheeks, while similar but larger spines in *Triarthrus spinosus* Billings are on the free cheeks, making the former belong to the Proparia and the latter to the Opisthoparia.

Application of Principles for Arrangement of Families and Genera.

The remaining characters to be noticed have chiefly family and generic values, and naturally follow the preceding discussions. They are of great assistance, both in determining the place of a family in an order, and the rank and genetic position of a genus in a family.

There is very satisfactory evidence that the eyes have migrated from the ventral side, first forward to the margin and then backward over the cephalon to their adult position. The most primitive larvæ should therefore present no evidence of eyes on the dorsal shield. Just such conditions are fulfilled in the youngest larva of *Ptychoparia*, *Solenopleura*, and *Liostracus*. 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. A study of the genera of trilobites shows that this is a very archaic feature, chiefly characteristic of Cambrian genera, and only appearing in the primitive genera of higher and later groups or as an evidence of degeneration. It first develops in the later larval stages of certain genera (*Ptychoparia*, etc.); next in the early larval stages (*Sao*); then disappears from the adult stages (*Triarthrus*); and finally is pushed out of the ontogeny (*Dalmanites*).

In *Ptychoparia*, *Solenopleura*, *Liostracus*, *Sao*, and *Triarthrus*, the eyes are first visible on the margin of the dorsal shield after the protaspis stages have been passed through, and later than the appearance of the eye lines; but in *Proëtus*, *Acidaspis*, *Arges*, and *Dalmanites*, 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. Progression in these characters may be expressed, and in so far taken for general application among adult forms to indicate rank, as follows: (1) absence of eyes; (2) eye lines; (3) eye lines and marginal eyes; (4) marginal eyes; (5) submarginal eyes; (6) eyes near the pleura of the neck segment.

The changes in the glabella are equally important and interesting. Throughout the larval stages, the axis of the cranidium shows distinctly by the annulations that it is composed of five fused segments, 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* and *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* and *Acidaspis*). From these simple types of simple pentamerous glabellæ, all the diverse forms among species of various genera have been derived, through changes affecting any or all the lobes. The modifications usually consist in the progressive obsolescence of the anterior annulations, finally producing a smooth glabella, as in *Illænus* and *Niobe*. The neck segment is the most persistent of all, and is rarely obscured. The third, or mandibular, segment is frequently marked by two entirely separate lateral lobes, as in *Acidaspis*, *Conolichas*, *Chasmops*, etc. Likewise, the fourth annulation carrying the first pair of maxillæ is often similarly modified in the same genera, also in all the Proëtidæ, and in *Cheirurus*, *Crotalocephalus*, *Sphærexochus*, *Ampyx*, *Harpes*, etc. Here again, among adult forms, the stages of progressive differentiation may be taken as indicating the relative rank of the genera.

The comparative areal growth of the free cheeks is expressed by the gradual moving of the facial suture toward the axis. As the free cheeks become larger, the fixed cheeks become smaller. In the most primitive protaspis stages, and in *Agnostus*, *Harpes*, and *Trinucleus*, the dorsal surface of the cephalon is wholly occupied by the axis and the fixed cheeks, while in the higher genera, the area of the fixed cheeks becomes reduced until, as in *Stygina* and *Phillipsia*, they form a mere border to the glabella. Therefore, the ratio between the fixed and free cheeks furnishes another means of assisting in the determination of rank.

The pleura from the segments of the glabella are occasionally visible, as in the young of *Olenellus*, but usually the pleura of the neck segments are the first and only ones to be distinguished on the cephalon, the others being so completely coalesced as to lose all traces of their individuality. The pleura of the pygidium appear soon after the earliest protaspis stage, and in some genera (*Sao*, *Dalmanites*) are even more strongly marked than in the adult state and much resemble separate segments. The growth of the pygidium is very considerable through the protaspis stage. At first, it is less than one-third the length of the dorsal shield, but by 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, all of which are added during the nepionic stages. An interpretation of these facts, to apply in valuing adult characters, would indicate that a very few segments, both in thorax and pygidium, may be evidence of arrested development or degeneration. On the other hand, the apparently unlimited multiplication of thoracic and especially of abdominal segments in some genera is also to be considered as a primitive character expressive of an annelidan style of growth. Genera like *Asaphus*, *Phacops*, etc., having a constant number of thoracic segments accompanied by other characters of a high order, undoubtedly represent the normal trilobite type.

These analyses and correlations clearly 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 larvæ. Thus, the larvæ of *Dal-*

manites 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 come in their adult stages. Evidently such modifications have been acquired by the action of the law of earlier inheritance, or tachygenesis.

In a classification of trilobites, for the purpose of illustrating the principles here enunciated, the ontogenies of *Sao* and *Dalmanites*, Plate III, figs. 1–8, are selected. *Sao* belongs to the ancient family Olenidæ of the order Opisthoparia, and naturally may be expected to furnish very clear evidence as to the relations of many lower and older genera. *Dalmanites*, also, with its simple head structure, will give similar data regarding the Proparia.

The early protaspis stage of *Sao*, Plate III, fig. 1, has no dorsal development of the free cheeks, and with the elongate form of the cephalic portion may be compared with the cephala of *Agnostus* and *Microdiscus*, and therefore correlates with the Hypoparia. The cephalon, at a later period of development, when the animal has two free thoracic segments, Plate III, fig, 2, shows the narrow marginal free cheeks and distinct eye lines. Here the resemblance to the cephala of *Atops* and *Conocoryphe*, Plate III, figs. 14, 15, is very marked, and indicates that the Conocoryphidæ is genetically the first family of the Opisthoparia. When *Sao* has eight thoracic segments, Plate III, fig. 3, the characters of the cephalon accord closely with *Ptychoparia* and *Olenus*, showing that these genera should precede it in arranging the genera of the family Olenidæ. Evidence is thus furnished for the proper position of the first two families of the order. Now, if the relative values of the differentiation of the glabella, the position of the eyes, and the size of the free cheeks are considered in the light of the preceding analyses of these features, the remaining families of the order, as represented in their typical genera, naturally arrange themselves as indicated in Plate III, figs. 18–23. There results (1) the Conocoryphidæ (represented by *Atops* and *Conocoryphe*, figs. 14, 15); (2) the Olenidæ (*Ptychoparia* and *Olenus*, figs. 16, 17); (3) the Asaphidæ (*Asaphus* and *Illænus*, figs. 18, 19); (4) the Proëtidæ (*Proëtus*, fig. 20); (5) the Bronteidæ (*Bronteus*, fig. 21); (6) the Lichadidæ (*Lichas*, fig. 22); and (7) the Acidaspidæ (*Acidaspis*, fig. 23).

For the Proparia, similar results are brought out by the study of the ontogeny of *Dalmanites*, and by comparisons with the characters governing the sequence of families in the Opisthoparia. The narrow marginal free cheeks place the Encrinuridæ and Calymenidæ as primitive. The small or obsolete eyes and the larval form of the glabella in the former further show that this family should be placed at the beginning. The nepionic *Dalmanites*, with seven thoracic segments, has a head structure very similar to the adult *Cheirurus* (*Eccoptocheile*), fig. 28, thus making the Cheiruridæ precede the Phacopidæ. The arrangement of families under the Proparia accordingly will be (1) the Encrinuridæ (*Placoparia* and *Encrinurus*, Plate III, figs. 24, 25); (2) the Calymenidæ (*Calymene* and *Dipleura*, figs. 26, 27); (3) the Cheiruridæ (*Cheirurus* (*Eccoptocheile*), fig. 28); and (4) the Phacopidæ (*Dalmanites*, *Chasmops*, *Acaste*, *Phacops*, figs. 29–33).

The sequence of families in the most primitive order, Hypoparia, may now be easily disposed of. The genera are so aberrant and offer such conspicuous differences from ordinary trilobites, that it was considered better to delay their disposition until the variations in structure governing the arrangement of families in the higher orders were clearly shown. The degree of specialization of the glabella, of the form and character of the fixed cheeks, and the great range in the number of segments in the thorax and pygidium are strong evidence that we are dealing with the terminal genera of the order which must have attained its normal development in pre-Cambrian times. *Agnostus* and *Microdiscus* have so many protaspidian and larval characters that they must be considered more primitive than the other genera, although in some respects they show a high degree of specialization and even degeneration, as will be noticed under the family Agnostidæ. Moreover, *Harpes*, in its elongate cephalon, persistent ocelli, and many thoracic segments, is also quite primitive. *Trinucleus*, with ocelli only present in larval stages, a transverse cephalon, and genal spines belonging to the free cheeks, is considerably higher and properly comes last in the order, thus making the arrangement of families as follows: (1) Agnostidæ (*Agnostus*, *Microdiscus*, Plate III, figs. 9, 10); (2) Harpedidæ (*Harpes*, fig. 11); and (3) Trinucleidæ (*Trinucleus*, *Ampyx*, figs. 12, 13).

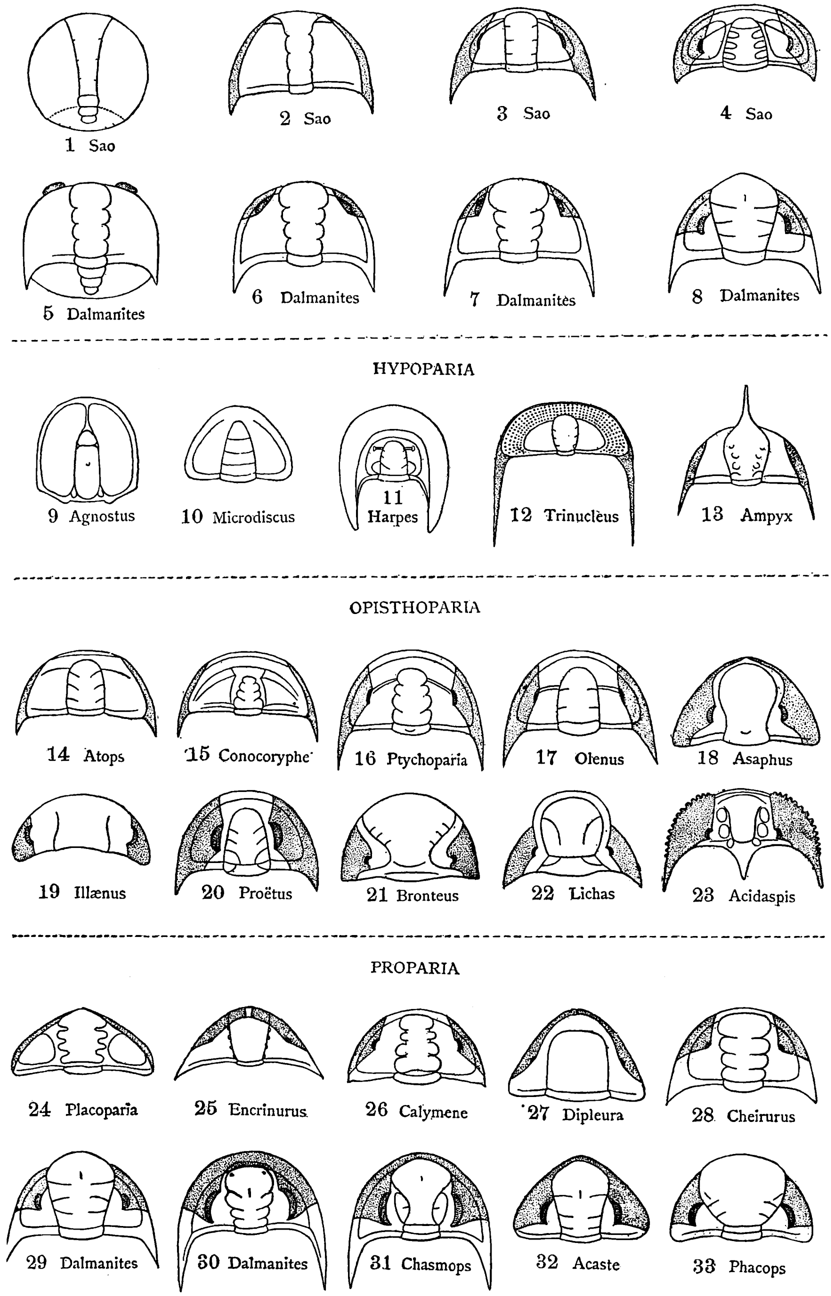
Diagnoses and Discussions.

Subclass Trilobita.

Marine crustacea, with a variable number of metameres; body covered with a hard dorsal shell or crust, longitudinally trilobate from the defined axis and pleura; head, thorax, and abdomen distinct. Head covered with a cephalic shield composed of a primitively pentamerous middle piece, the cranidium, and two side pieces, or free cheeks, which may be separate or united in front, and carry the compound sessile eyes, when present; cephalic appendages pediform, consisting of five pairs of limbs, all biramous, and functioning as ambulatory and oral organs, except the simple antennules, which are purely sensory. Upper lip forming a well-developed hypostoma; under lip present. Somites of the thorax movable upon one another, varying in number from two to twenty-nine. Abdominal segments variable in number, and fused to form a caudal shield. All segments, thoracic and abdominal, carry a pair of jointed biramous limbs. All limbs have their coxal elements forming gnathobases, which become organs of manducation on the head. Respiration integumental and by branchial fringes on the exopodites. Development proceeding from a protonauplius form, by the progressive addition of segments at successive moults.

Heretofore it has been impossible to give an adequate diagnosis of the *Trilobita*, owing to the absence of information regarding certain important characters, and the obscurity of the information relating to some other features. It is believed that enough is now known to frame a definition of the class, which, in accuracy and completeness, will compare favorably with any based upon living groups. Such a definition brings out the fact that the differences between the trilobites and other large groups are clearly recognizable, and do not consist of a statement of anomalous characters whose real significance is unknown.

[To be continued.]



Classification of Trilobites. Beecher.