

LIFE-FORMS OF THE PAST AND PRESENT.

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[PLATES XC. and XCI.]



ONE of the most interesting results at which the naturalist arrives in extending his researches from the living present far back into the remote periods of geological time, is that he finds existing between the life-forms of the past and present, not merely accidental likenesses or analogies, but actual homologies and relationships. There is, in fact, no ground whatever for the old, and to some extent, still prevalent dogma, that the several faunas and floras, which in past ages successively peopled and clothed the surface of the earth, had no direct relationship, either with each other, or with existing types.

Indeed, so strong was this feeling in the minds of nearly all the earlier observers, that they hesitated to compare extinct organisms with living forms, and were content to accept the dictum of those geologists who taught that each series of fossiliferous deposits was a distinct creation, being separated by a universal cataclysm alike from the preceding and subsequent life-periods. It is less than twenty years since the modern doctrine of continuity of life on the earth began to be received and adopted as the basis of all sound palæontological reasoning; and notwithstanding the numerous breaks that still exist, it is nevertheless possible, by reviewing the life-history of any particular class or order, to demonstrate that a real continuity does exist from the earliest representative down to the forms of to-day.

I propose to take, by way of illustration, a few examples from a class which offers perhaps the widest geographical and geological range, combined with the greatest diversity of detail in organisation, of any among the Invertebrate kingdom, namely the Crustacea; confining myself mainly to two of the most ancient orders, the Merostomata and the Trilobita.

In tracing a group like the Crustacea further and yet

further back in past time, we find that our enquiry is greatly facilitated, not merely by reason of the reduction of our field of observation to a smaller accessible area of fossiliferous deposits, but also because the objects themselves become more and more reduced, not merely in numbers, but in diversity of forms, until at last we arrive at rocks in which the whole class is included in some two or three orders or families.

Thus in the rocks of Tertiary age Crabs (*Decapoda-Brachyura*) are apparently as abundant as in our recent seas.

But in the Secondary strata we perceive a visible diminution in the short-tailed forms, the earliest of which are, at present, only known in rocks of Oolitic age.*

Lobsters (*Decapoda-Macrura*), however, are abundant in the Oolitic series, and extend back into primary or palæozoic times, the first being found in the Coal-measures.†

Through all these formations we find representatives of the principal living genera, with the exception only of those soft-bodied forms which could not be preserved in a fossil state, such as the "Brine-shrimp," *Artemia salina*; *Cheirocephalus*; and the parasitic *Lerneonema*, *Argulus*, *Nicothoe*, and other specialised forms.

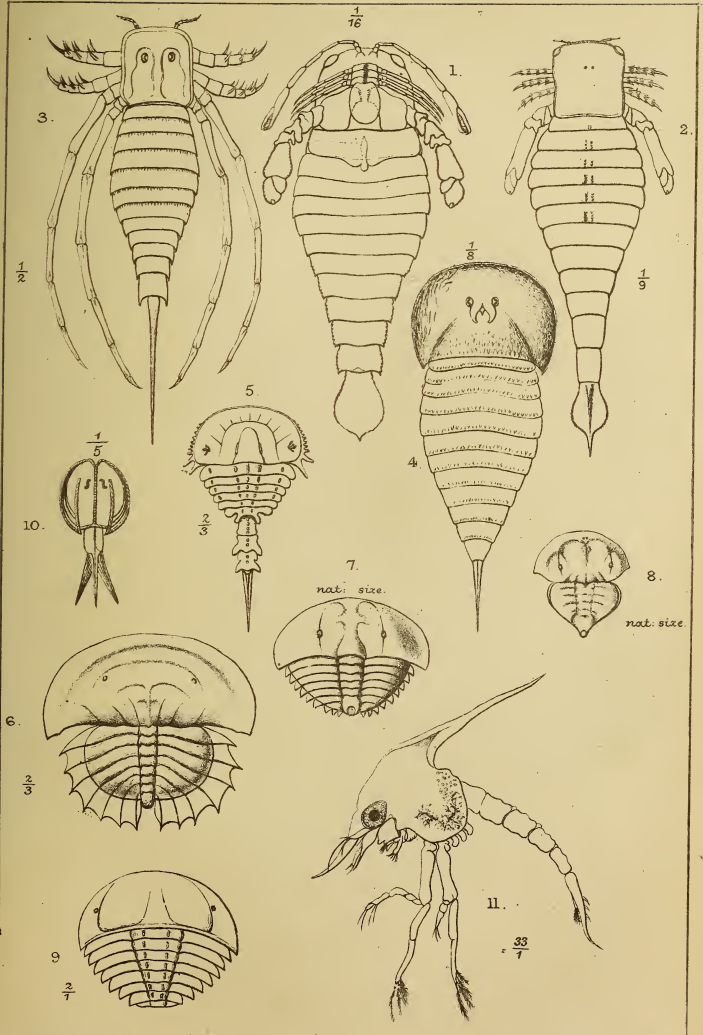
As we scan the record of these old Carboniferous rocks, so rich in organic remains, we seem to stand on some lofty beacon-hill, whence we can cast our glance upwards and downwards along the stream of time. Beneath our feet lie buried the last representatives of those aboriginal races now quite extinct, the Trilobita and the Eurypterida, whose ancient hosts peopled the seas of Devonian and Silurian ages, and reached far away into the Cambrian epoch. Beside them lie the earliest representatives known of our modern Decapods, Stomapods, and Isopods, then but few and feeble, but now the dominant races of the Crustacean class.

Is this, then, the barrier-reef between the Palæozoic and Neozoic life-periods? Do we indeed find here the beginning of all modern forms of Crustacea, and the ending of all ancient ones? By no means; nor is there, as we have already observed, any period in the whole geological record at which a hard and fast line can be drawn dividing the class into recent and extinct families.

Certain groups, such as the Entomostraca, are represented *throughout*. Others, like the Amphipoda, may perhaps extend

* Oldest known British Crab, *Palæinachus longipes*, H. Woodward, Forest Marble, Malmesbury, Wilts. See "Quart. Journ. Geol. Soc.," 1866, Vol. XXII. p. 493.

† *Anthrapalæmon Grossartii*, Salter, Coal Measures, Lanarkshire. See "Quart. Journ. Geol. Soc.," 1861, Vol. XVII. p. 531.





into Silurian times; * or, like the Isopoda, may reach back to the Devonian epoch.† The Cirripedia, a most aberrant group of Crustacea (represented abundantly in the seas of to-day by the pedunculated *Lepas* ("Ship Barnacle") and the sessile *Balanus* (or "Acorn Shell"), so common on the bottoms of ships which have been long at sea, and upon the piles of piers, and on sea-walls, and rocks washed by the tide), carry back their history, the latter through the Tertiary rocks to the Upper Chalk,‡ the former to the earliest Secondary rocks, whilst a single form is found in the Wenlock shale of Dudley (Upper Silurian).§

The King-Crabs, next to the Entomostraca, undoubtedly enjoy the most extended range in time; occurring in considerable numbers in the Lithographic stone of Solenhofen, with characters scarcely, if at all, differing from those species now found living on the east coast of North America and in the seas of China and Japan. About seven species occur in the Coal-measures (See Plate XC., figs. 6, 7, 8,) and one actually in the Silurian (See Plate XC., fig. 9) of Lesmahagow in Lanarkshire;|| these palæozoic forms closely resemble the larval stages of the living *Limulus* (See Plate XCI., figs. 21-24).

The accompanying Table will best exhibit the successive appearance of the chief orders of Crustacea, and beside them are placed the Arachnida, the Myriapoda, and the Insecta, with their representatives in palæozoic strata; thus giving the range of the entire sub-kingdom of the ARTHROPODA in time.

But omitting the solitary instances, already referred to, of those higher forms which have left traces of their existence in palæozoic times, it is evident that, from the Carboniferous strata downwards, we have to deal for the most part with three great groups of Crustacea, namely the Merostomata, the Trilobita, and the Entomostraca.

The first of these, the Merostomata (or thigh-mouthed

* I believe the form I have described under the generic name of *Necrogammarus*, from the Lower Ludlow, to be an Amphiphod. See "Trans. Woolhope Club, Hereford," 1870, p. 271.

† I have described a part of a giant Crustacean, which I believe to be an Isopod, under the name of *Præarcturus gigas*, from the Devonian of Herefordshire. See "Trans. Woolhope Club, Hereford," 1870, p. 266.

‡ *Pyrgoma cretacea*, H. Woodward, "Geol. Mag.," 1868, Vol. V. p. 258, pl. xiv. figs. 1, 2, 3. From the Upper Chalk near Norwich is at present the oldest.

§ *Turrilepas Wrightii*, H. Woodward, "Quart. Journ. Geol. Soc.," 1865, Vol. XXI. p. 486, pl. xiv. figs. 1-6.

|| *Neolimulus falcatus*, H. Woodward, "Geol. Mag.," 1868, Vol. V. p. 1, pl. i. fig. 1.

Crustacea), are divided into two sub-orders, the Eurypterida and the Xiphosura. These may not inaptly be compared with the higher Decapoda, which are divided into Brachyura (short-tailed) and Macrura (large or long-tailed); for in the Eurypterida the segments of the body are distinct and well developed (See Plate XC., figs. 1, 2, 3, 4), whilst in the Xiphosura or "King-crabs," they are coalesced and cephalised (Plate XC., figs. 6, 7, 8, 9). In both, however, the details of their organisation are arranged upon a common pattern.

In the Crab and Lobster the compound eyes are placed on movable eye-stalks; the antennæ, the mouth-organs and the organs of prehension, locomotion, and respiration, are all constructed on a common plan.* But the body-segments in the Crab are reduced to a minimum size, and merely subserve, in the female, as a cradle or marsupium for the eggs before hatching, while in the male they are quite rudimentary. In the Lobster, on the other hand, the body-segments in both sexes are well developed, and serve as a most powerful swimming organ, by which the animal can by a sudden jerk propel itself through the water with great velocity.

All the Merostomata have large compound sessile eyes, or, if pedunculated, the stalk is immovably fixed to the carapace. The larval eye-spots, or ocelli, are usually distinctly seen. The appendages are not specialised and set apart for separate duties, as in the higher forms of Crustacea, but alike fulfil all the functions of locomotion, prehension, and mastication, and for this purpose are arranged around the mouth (see Plate XC., fig. 1). The branchiæ and organs of reproduction are borne upon a series of lamelliform plates, which are in fact the modified pairs of limbs, attached to the under surface of the thoracic segments; there being as many as six plates in *Limulus*, five of which are branchiferous, and probably only two, or at the most three, in *Pterygotus*. The remaining segments are destitute of appendages.

In the Eurypterida the body-segments are largely developed for swimming (as in the Lobster); whilst in the Xiphosura they are reduced to a minimum size (as in the Crab). Lastly, it is the long-tailed division in each order which is the oldest group, the more cephalised type in each being also the more modern.

We have thus seen that *Limulus* and *Pterygotus* are as intimately related as Crabs and Lobsters are to each other at the present day; but nevertheless the type of *Pterygotus* is a very abnormal type. Let us see what we have like it among living forms.

* See an article on the Lobster, by Mr. St. George Mivart, F.L.S., in the "Popular Science Review," 1868, Vol. VII. p. 345, pl. xxii.

If we glance for a moment at the larval stage of that most specialised and highly developed of modern Crustacea the Crab, depicted on our plate (Pl. XC., fig. 11), we find that in its zooid state it has sessile eyes, a long body, destitute of any appendages; it has no walking legs, but it is a free-swimming form, performing its locomotion with its maxillipeds or jaw-feet, which are greatly developed, serving as a pair of long oars similar to those with which *Stylonurus Logani* is furnished. (Pl. XC., fig. 3).

Indeed the larva of this highest form is the most apt illustration of our ancient order the *Merostomata*.

Limulus is living to-day to represent his great ancestor in the Silurian epoch, but we find that the palæozoic King-crabs are still more closely and successfully represented, not by the adult, but by the larval stages of the living King-crab, represented in our illustration (compare figs. 6, 7, 8, and 9, on Plate XC., with figs. 21, 23, and 24 on Plate XCI).

We thus arrive at another interesting deduction, namely, that the stages of development of the individuals of to-day are a reflection of the life-history of the class in past geological time. It is worthy of notice, when speaking of the *Merostomata*, to point out that we have intermediate forms affording characters between the long-bodied *Pterygotus* and the short-bodied *Limulus*, namely the genus *Hemiaspis* (see Plate XC., fig. 5). There are also three Russian forms named *Pseudoniscus aculeatus*, *Exapinurus Schrenkii*, and *Bunodes lunula*, in which the hinder segments of the body are sensibly diminished in size and reduced in number.

A similar group of irregular forms (the Anomoura) exists among the living Decapoda.

When we turn to the Phyllopoda and Ostracoda, among the Entomostraca, we find numerous forms in the palæozoic rocks, which are readily comparable with those now existing, and differing chiefly in their greater size as compared with living types.

The one figured on our engraving (Plate XC., fig. 10), *Dithyrocaris Scouleri*, McCoy, will serve as an apt illustration of a palæozoic phyllopod, reminding one strongly of the recent *Apus* and *Nebalia*.

The Entomostraca were probably as abundant in past times, as at the present day, their remains often forming almost entire strata.

We do not propose to treat of them in the present article, but merely to point out that they are the most persistent group among the Crustacea, being found from the Cambrian period to the seas of to-day; lowness or simplicity in organisation, with great powers of vitality and reproduction superadded,

being the most satisfactory explanation by which to account for their longevity.

The group which has attracted perhaps the greatest amount of attention, and upon which vast labour has been bestowed with little or no result commensurate therewith, is that of the Trilobites.

This is a truly palæozoic group, and, so far as we are aware, an extinct group, although this is always a difficult point to be dogmatic upon.

Look, for example, at the Limulidæ. We have living King-crabs as far apart as on the east coast of North America and along the coasts of China and Japan, &c. We find them again in the Oolitic beds of Solenhofen in Bavaria. Again in the Coal-measures of England and Illinois; again in the Upper Silurian of Scotland.

We cannot doubt the continuity, but the gaps are enormous.

Nor can we, by the same rule, positively assert that the Trilobita are a strictly palæozoic type, and will *never* be found in neozoic strata.

In taking a general review of this great family or order, so widely distributed through the older sedimentary deposits, one is naturally struck by the immense amount of *variation of form*, brought about simply by the modification of a single plastic type, and that, apparently, a very elementary one. Yet by means of diverse ornamentation, in the way of spines, warts, and tubercles, by compression in one direction, by elongation in another, by adding to the normal number of segments of the body, or by subtracting therefrom; by enlargement or reduction of the eyes (the only organs seen upon the dorsal aspect of the body), we obtain—as with one of those amusing human faces in vulcanite india-rubber that children delight to contort—all those endless modifications of expression of form possible to the frame of the highest vertebrate organism.

In the present state of our knowledge it is very difficult to speak at all positively of the organisation of this group, but I incline to the belief that they conceal beneath their apparently simple structures evidence of more than one order.

For instance: they indicate, in some points, a close relationship to the Phyllopoda. We find in both the articulated labrum; and although we have not as yet obtained clear evidence of the maxillæ in the Trilobita, we are justified in concluding from analogy that they possessed such organs.* Again,

* See note on the "Palpus and other Appendages of a Trilobite," by H. Woodward; and a paper on the "Supposed Legs of Trilobites," by E. Billings; "Quart. Journ. Geol. Soc." 1870, Vol. XXVI. See also H. Woodward "On the Structure of Trilobites," "Geol. Mag." 1871, Vol. VIII. p. 289, Pl. VIII.

in both the Trilobites and Phyllopods we find genera in which a greater number of segments is attained than the normal number in the Crustacean type. Thus in *Conocephalus* there are sixteen (reckoning only one each for the head-shield and pygidium), in *Paradoxides* twenty to twenty-two, in *Arethusina* twenty-two, and in *Harpes* twenty-eight; and if we look upon the head-shield and tail-plate as composed of several body-rings united together—which seems certainly to be the correct view—we have forms presented to us in which the multiplication of segments like each other is one of its peculiar features, illustrating that form of growth which Professor Owen has most aptly described as a vegetative repetition of parts.

Barrande, who has made a special study of this group, when writing recently upon the divisions of the body, divides them into four groups:

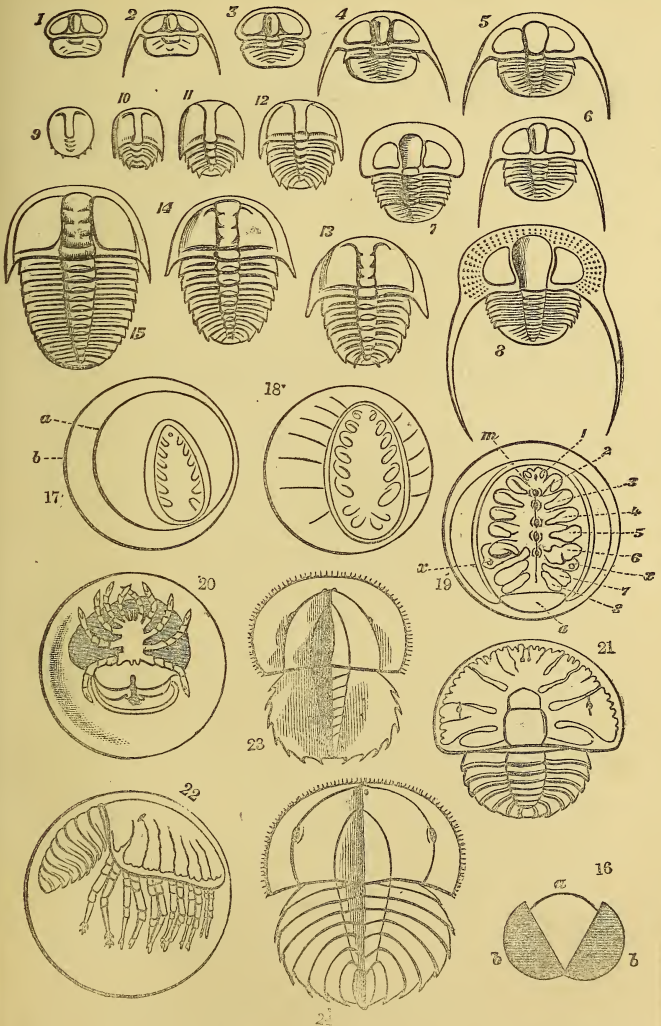
The first with from	1 to 4	free and movable thoracic segments,				containing 2 genera.
The second	„	5 to 9	„	„	„	24 „
The third	„	10 to 13	„	„	„	32 „
The fourth	„	14 to 26	„	„	„	16 „

We thus perceive that those forms of Trilobites having a great excess of *free segments* is not large when we consider the whole as a group.

In the higher and more specialised forms of Isopoda of the present day we do not find the number of segments absolutely adhered to without any variation; on the contrary, we constantly meet with individuals in which more or fewer segments are welded together, so as to conceal the normal number of seven thoracic somites between the head and the abdomen.

Such being the case, we cannot be surprised to find considerable variation in a group like the Trilobita, which, if they really are the remote ancestors of the recent Isopoda, must be, according to the views I have suggested above, the prototypes of the larvæ rather than of the adult stage of the living form.

Dr. Dohrn and other writers upon the Arthropoda have pointed out the remarkable similarity between the larval stages discovered by Barrande of certain forms of Trilobites, of which we have reproduced two sets, namely *Trinucleus ornatus*, Sternb., and *Sao hirsuta*, Barr. (See Plate XCI., figs. 1-8, and 9-15), and the larval stages observed in the living *Limulus* (See Plate XCI., figs. 20-24). But the larvæ of the Trilobites pass through these stages after being hatched, whilst those of *Limulus* take place in the egg. Bearing in mind that in the Trilobites we are dealing with animals possessing in many cases a large number of free thoracic segments covered by a firm calcareous crust or shell (at least it is so in



LARVAL DEVELOPMENT OF TRILOBITES AND LIMULUS.



a large number of genera), it is hardly probable that mere branchial feet would serve for their locomotion.

If, however, each free and movable thoracic segment was furnished with a pair of appendages, as among the modern Iso-pods, and as is also indicated in the larva of the *earliest stages* of development within the egg of the modern *Limulus* (See Plate XCI., figs. 17–19), then another point is gained in our investigation, and we see that the earliest embryonal stages are those which naturally foreshadow the earliest and simplest adult forms. In other words, all the immense variety of forms in a group are but the expression of the sum of the stages passed through by the highest individual in arriving at perfection.

Another relation which the Merostomata and Trilobita exhibit, and upon which much stress has been laid by Dr. Dohrn and Prof. Hæckel, is that between these palæozoic types and the Arachnida; particularly between the Eurypterida and the Scorpionidæ.

And it is a most significant fact that the earliest Arachnides occur as far back as the Coal-measures, where the last of the Eurypterida and the Trilobita are also met with. Anyone who has examined a scorpion, or is acquainted with its form and structure from books and drawings, cannot fail to be struck by the remarkable resemblance between it and the Eurypterida, even to the arrangement of the appendages, the position of the eyes, &c., &c. Indeed, we may very fairly infer that from this division of the Crustacea the Scorpionidæ of to-day were derived. Nor is there any insuperable difficulty in accepting this view on sound physiological grounds. The possibility of an animal passing through larval conditions, casting aside, at even a single moult, its branchiæ, and assuming aërial respiration, quitting the water and inhabiting the land, changing its element, its diet, its mode of progression, and its entire life, is no chimerical speculation. Such cases are familiar to the entomologist,* the carcinologist,† and even to the herpetologist.‡

But the acceptance of this proposition does not, as has been assumed by these writers, necessitate the removal of the Eurypterida from the Crustacea; on the contrary, as Fritz Müller well observes, “If all the classes of the Arthropoda (Crustacea, Insecta, Myrapoda, and Arachnida) are indeed all branches of a common stem (and of this there can scarcely be a doubt), it is evident that the water-inhabiting and water-breathing Crustacea must be regarded as the original stem

* The larval and adult *Libellula*, *Ephemera*, &c.

† *Gecarcinus ruricola*, and other land-crabs.

‡ The Batrachia.

from which the other (terrestrial) classes, with their tracheal respiration, have branched off."*

Viewed as a whole, the Crustacea probably present to us the best zoological illustration of a class constructed on a common type retaining its general characteristics, but capable of endless modifications of its parts, so as to suit the extreme requirements of every separate species.

And it is doubtless in great degree due to this plasticity of structure, enabling the species to occupy such diverse positions, and to subsist upon such varied aliment, that the class owes its preservation through the lapse of ages represented by the long series of geological formations, from the Cambrian strata to the present day.

EXPLANATION OF PLATE XC.

- FIG. 1. *Pterygotus anglicus*, Agassiz, ventral aspect restored. From the Devonian of Forfarshire (about one-sixteenth natural size).
- „ 2. *Slimonia acuminata*, H. Woodw., dorsal aspect restored. From the Upper Silurian, Lesmahagow, Lanarkshire (about one-ninth natural size).
- „ 3. *Stylonurus Loganii*, H. Woodw., dorsal aspect restored. From the Upper Silurian, Lesmahagow, Lanarkshire (about one-half natural size).
- „ 4. *Eurypterus Scouleri*, Hibbert, dorsal aspect restored. From the Carboniferous limestone of Kirkton quarry and Bathgate, West Lothian (about one-eighth natural size).
- „ 5. *Hemiaspis limuloides*, H. Woodw., dorsal aspect. From the Lower Ludlow Leintwardine, Shropshire (about two-thirds natural size).
- „ 6. *Prestwichia rotundata*, H. Woodw., Coal-measures, Ironstone, Coalbrook Dale (about two-thirds natural size).
- „ 7. *Bellinurus Königianus*, H. Woodw. sp. nov. Coal-measures, Dudley Coal-field, in clay ironstone (natural size).
- „ 8. *Prestwichia Birtwelli*, H. Wood. sp. nov. Coal-measures, Cornfield Pits, near Padiham, Lancashire (natural size).
- „ 9. *Neolimulus falcatus*, H. Woodw. Upper Silurian Lesmahagow, Lanarkshire (twice natural size).
- „ 10. *Dithyrocaris Scouleri*, McCoy, Carboniferous, Ireland (one-fifth natural size).
- „ 11. Larva or Zöea of the common "Shore-crab," *Carcinus mænas*, Penn. 2nd stage, copied from Mr. C. Spence Bate's paper on the "Development of Decapod Crustacea," Phil. Trans. 1858, p. 589, Pl. XL.

* "Facts and Arguments for Darwin," by Fritz Müller (p. 120). Translated from the German by W. S. Dallas, F.L.S., &c.

[Figs. 1-9, copied and reduced from the plates illustrating Mr. Henry Woodward's Monograph on the Merostomata, published in the volumes of the Palæontographical Society, 1867-72.]

EXPLANATION OF PLATE XCI.

[This plate is reproduced here by permission of the Council of the Geological Society of London from a paper by Mr. H. Woodward, "On the Relationship of the Xiphosura to the Eurypterida, and to the Trilobita and Arachnida." See "Quart. Journ. Geol. Soc.," 1872. Vol. XXVIII. p. 46.]

FIGS. 1-8. *Trinucleus ornatus*, Sternb. sp. (copied from Barrande's "Système Silurien du centre de la Bohême," Prague, 1852, 4to, plate 30). Specimens arranged in series according to their supposed age. (All the stages figured by Barrande are not given here.)

- FIG. 1. Young individual, destitute of thoracic segments, composed of head-shield and pygidium only.
- " 2. Another of the same stage, in which the genal or cheek-spines are developed.
- " 3. Individual with one thoracic segment developed, but without the genal spines.
- " 4. Another of the same stage, with the genal spines.
- " 5. Individual with two thoracic segments, and in which the genal spines are present.
- " 6. Individual with three thoracic segments, and possessing the genal spines.
- " 7. Individual with five thoracic segments, but without genal spines.
- " 8. Adult *Trinucleus*, with six thoracic segments and fully-developed genal spines.

FIGS. 9-15. *Sao hirsuta*, Barrande (copied from plate 7 of Barrande's work above cited). Barrande figures twenty stages of this Trilobite, of which we have only reproduced seven.

- FIG. 9. First stage. A young individual in which the limit of the head-shield is not indicated as separating it from the pygidium.
- " 10. Second stage. Young individual with the head-shield separated, and having inclinations of three soldered segments to the pygidium.
- " 11. Third stage, in which the genal angles of the head and the spiny border of the pygidium are well seen, and four or five soldered segments indicated.
- " 12. Fourth stage, in which two free thoracic segments are developed behind the head, and two or three soldered segments represent the pygidium.
- " 13. Fifth stage, in which the thorax is longer than the head, and is composed of three movable segments and three soldered segments in the pygidium.
- " 14. Sixth stage, in which four free segments succeed the head, and three or four soldered segments form the pygidium.

- FIG. 15. Tenth stage, in which eight free segments succeed the head, and three soldered segments form the pygidium. [In the twentieth stage figured by Barrande the adult has seventeen free thoraco-abdominal segments and two soldered ones (the pygidium).]
- „ 16. Egg of *Limulus polyphemus*: *a*, the chorion; *b*, the exochorion (after Dohrn *).
- „ 17. Third stage in the embryo of *Limulus*: *a*, chorion; *b*, exochorion (after Packard †).
- „ 18. Fourth stage (?) in the embryo of *Limulus* (after Dr Packard's † figure).
- „ 19. Fourth stage (?) in the embryo of *Limulus*: 1, antennules; 2, antenna; 3-6, maxillipeds; 7 and 8, thoracic plates afterwards bearing the branchiæ; *m*, the mouth; *x*, the ovarian apertures (?); *a*, the abdomen (after Dohrn *).
- „ 20. Fifth stage (?) of embryo of *Limulus* (after Dohrn *). At this stage the exochorion is split, and the chorion is expanded by the admission of water by endosmose, in which the embryo is seen to revolve.
- „ 21. Ninth stage (?) of embryo, 'just before hatching' (after Packard †): dorsal aspect.
- „ 22. The same: side view of embryo.
- „ 23. Larva of *Limulus* recently hatched (after Packard †).
- „ 24. Larva of *Limulus* on hatching (the "*Trilobitenstadium*" of Dohrn *).

* "Zur Embryologie und Morphologie des *Limulus polyphemus*." Von Dr. Anton Dohrn. (Jenaische Zeitschrift, Band vi. Heft 4, p. 580, Tafeln xiv. xv.) Received September 30, 1871.

† "On the Embryology of *Limulus polyphemus*." By A. S. Packard, jun., M.D. Read before the American Association for the Advancement of Science, August 1870. ("American Naturalist," vol. iv. No. 8, 1870, October, p. 498.)