Studies on Apus, Limulus and Scorpio / by E. Ray Lankester.

LIMULUS

AN

ARACHNID

Limulus *an* Arachnid. By E. Ray Lankester, M.A., F.R.S., Jodrell Professor of Zoology in University College, London.

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PART I.

A. Introduction and Bibliography.

The prevailing opinion among zoologists at the present day, with regard to the affinities of the King Crab, is that it must be regarded as one of the Crustacea. Even when this view is not fully accepted the King Crab is placed in a special position of isolation and its relationship with Crustacea strongly insisted upon, whilst more remote affinity with the Arachnida is grudgingly admitted.

My friend Edouard Van Beneden, of Liège, is the only zoologist who has definitely taken a divergent line, and has frankly endorsed the instinctive perception of Straus Durkheim in declaring that Limulus is no Crustacean, but simply and unreservedly an Arachnid. Ed. Van Beneden bases his opinion upon embryological data. I have elsewhere expressed my full concurrence in that opinion, but the grounds upon which my conclusion rests are not solely embryological —they have reference to the structure of the adult Limulus and Scorpion. In the following pages I hope to show that Limulus is best understood as an aquatic scorpion, and the Scorpion and its allies as terrestrial modifications of the King Crab.

My views on this subject were formed some eight years ago, and I have to acknowledge the kindness of Mr. Carrington, F.L.S., of the Royal Westminster Aquarium, by which I have been enabled to dissect and make histological study of perfectly fresh specimens of Limulus sent to me in the living state.

It is not desirable at the outset to follow the history of the discussion relative to the zoological position of Limulus. Those who desire to become acquainted with the most important contributions to the subject should consult the memoirs of Anton Dohrn and A. S. Packard, who have given very ample references to the literature of the subject.

I shall here give in alphabetical order a list of the chief works referred to in the following pages, the number attached to an author's name when cited, having reference to the number in the present list. After I have put forward the facts and inferences with reference to the structure and affinities of Limulus which appear to me to be well-established, I shall briefly review the various opinions which have been advanced by recent writers of authority.

Special Memoirs.

1. Dohrn, Anton. "Bau und Entwickelung der Arthropoden," 'Jenaische Zeitschrift,' Bd. vi, 1871.
2. Gegenbaur, Carl. "Anatomische Untersuchung eines Limulus," 'Abhandlungen der naturforschenden Gesellschaft in Halle,' 1858.
3. Grenacher. "Unters. uber das Sehorgan der Arthropoden," 1879.
4. Lankester, E. Ray. "Mobility of the Spermatozoa of Limulus," 'Quart. Journ. of Micr. Science,' 1878.
5. Milne-Edwards, Alphonse. "Recherches sur l'Anatomie des Limules," 'Annales des Sciences Naturelles,' 5th series, Zoologie, vol. xvii, 1873.
6. Newport, George. "Nervous and Circulatory Systems in Myriapoda and Macrourous Arachnida," 'Philos. Transactions of the Royal Society,' part ii, 1843.
7. Owen, Richard. "Anatomy of the King Crab," 'Transactions of the Linnæan Society of London,' 1873.
8. Packard, A. S., Junr. "The Development of Limulus polyphemus," 'Memoirs of the Boston Society of Natural History,' 1872.
9. Packard, A. S., Junr. "The Anatomy, Histology, and Embryology of Limulus polyphemus," 'Anniversary Memoirs of the Boston Society of Natural History, 1880.
10. Van Beneden, Edouard. "De la place qui les Limules doivent occuper dans la classification des Arthropodes," Société Entomologique de Belgique, October, 1871 (translated in the 'Annals and Mag. of Natural History,' 1872).
11. Van der Hoeven. 'Recherches sur l'Histoire Naturelle et l'Anatomie des Limules,' Leyden, 1838.
12. Walcot, C. D. "The Trilobite," 'Bulletin of the Museum of Comparative Zoology at Harvard College,' vol. viii, April, 1881.
13. Woodward, Henry. "A Monograph of the British Fossil Merostomata," 'Palæontographical Society of London,' 1866—1878.

Text-books of Zoology.

14. Claus, Carl. 'Grundzüge der Zoologie,' fourth edition, first volume, third part, p. 638, 1880.
15. Gegenbaur, Carl. 'Elements of Comparative Anatomy,' English translation, 1878, p. 230.
16. Huxley, Thos. H. 'The Anatomy of Invertebrated Animals,' 1877, p. 260 and p. 374.
17. Haeckel, Ernst. 'Generelle Morphologie,' vol. ii, p. xc.
18. Owen, Richard, 'Lectures on Invertebrate Animals,' 1843, p. 181.
19. Straus Durkheim in Appendix to the sixth volume of the French translation of Meckel's 'Comparative Anatomy,' 1829.

Embryology of Arachnida.

20. Balfour, F. M. "Notes on the Development of the Araneina," 'Quart. Journ. of Micr. Science,' vol. xx, 1880.
21. Metschnikoff, Elias. "Embryologie des Scorpions," 'Zeitschrift für Wiss. Zoologie,' Bd. xxi, 1870.

As I am about to endorse the conclusion arrived at by an eminent naturalist of the first half of this century, viz. Straus Durkheim, it will be well to give here at once the grounds upon which he based that conclusion.

Straus Durkheim maintained that Limulus should be classified with the Arachnida, but the publication of his views on the subject appears never to have taken a very definite or satisfactory form. In fact the only record of Straus Durkheim's teaching on this subject which I can find is in the French translation of Meckel's 'General Treatise on Comparative Anatomy.' MM. Riester and Alph. Sanson carried out this translation, and added many notes in the form of appendices to each volume. At the end (p. 497) of the sixth volume, which bears the date 1829-1830, there is a note headed, "Sur l'appareil locomoteur passif des Arachnides," which appears to be an abstract of a memoir 'On the Comparative Anatomy of the Arachnida,' read to the Academy of Sciences, June 1st, 1829, but never, I believe, published. M. Straus Durkheim communicated its contents to MM. Riester and Sanson. From this note I submit a few extracts. The authors commence, "La classe des Arachnides, dans laquelle M. Straus comprend le genre Limule, formant à lui-seul un ordre designé sous le nom de GNATHOPODES, et dont il isole les PYCNOGONIDES qu'il renvoie aux Crustacés, offre dans la disposition de son squelette et des muscles qui en meuvent les diverses pièces, des particularités tellement tranchées qu'on ne peut y méconnaître un type different. C'est de ce squelette que sont tirés les traits principaux propres à characteriser la classe des arachnides en general, et qui consiste dans la *disposition des pattes rayonnant sur un sternum commun, dans la présence d'un sternum cartilagineux intérieur, dans l'absence d'antennes.*"

The Arachnida are then divided into three orders, "les pulmonaires, les branchifères, et les trachéens," but it is not explained whether the term "gnathopodes" is to be regarded as simply a synonym of the order "branchifères."

With regard to the internal sternum, the citation of the views of M. Straus runs as follows:—"Dans l'interieur du thorax de tous les *arachnides*, à l'exception peut-être des *acarides* dont la plupart des espèces sont trop petites pour qu'on puisse les disséquer et connaître leur organisation, on trouve une pièce cartilagineuse diversement configurée suivant les familles, et placée dans le thorax au-dessus du *sternum*. Cette pièce, à laquelle convient le nom de sternum interieur est maintenue librement par le moyen de plusieurs muscles qui se soudent de différents points de sa surface sur le bouclier, ou sur le sternum extérieur auquel ils se fixent. Elle sert en outre de point d'insertion à un certain nombre de muscles des pattes."

Since the time when Straus Durkheim put forward these views a mass of knowledge has accumulated which has tended to throw light on the affinities of Limulus. Of most importance has been the discovery of the complete form of the body of the palæozoic scorpion-like Arthropods known as the Eurypterina, and the quite recent (1873) thorough investigation of the nervous system of Limulus, by Alphonse Milne-Edwards, and further, the investigation of the developmental history of Scorpio, by Metschnikoff, and of Limulus, by Dohrn and by Packard. The gradual growth of the recognition of the Arachnidan affinities of Limulus during the last twenty-five years is obvious enough, and yet all systematic writers, and all who have especially discussed the question, continue to classify Limulus among the Crustacea whilst speculating as to the possible derivation of the Arachnida from that form, or else place Limulus in a distinct group, neither Crustacean nor Arachnidan.

I shall endeavour to show in the following pages that there is a much closer agreement of parts between Limulus and the Arachnida (especially Scorpio) than has been hitherto admitted by any one writer, even by Straus himself. It appears to me that the full extent of the agreement between Limulus and the Arachnida has never yet been stated, for whilst this or that observer has recognised *one* set of facts he has overlooked or misinterpreted another, and thus undervalued the indications of affinity between the two forms which he had admitted to exist. That the King Crab is as closely related to the Scorpion as is the Spider has for years been an open secret, which has escaped notice by something like fatality.

B. Comparison of Limulus and Scorpio.

The Arachnid which comes nearest in structure to Limulus is the Scorpion. In some few points the Spiders and, yet again, the Phrynidæ are more closely similar to Limulus than is that animal. I shall proceed, systematically, through a comparison of the skeletal and chief internal organs of Limulus with those of Scorpio, pointing out where other genera of living Arachnida come into closer agreement with the former than does the Scorpion.

§ *a*. **NERVOUS SYSTEM.**—As the view which may be adopted in regard to the agreement or distinctness of apparently corresponding parts in Limulus and Scorpio depends, to a considerable extent, on the indications afforded by the nervous system, it will be as well to proceed at once to state what is now known with regard to that system in both Limulus and Scorpio.[1]

For a long time our knowledge of the nervous system of Limulus was very defective, owing to the fact that only badly preserved spirit-specimens had been dissected. Hence it has been held by Van der Hoeven (11) and by Owen (7) that the nerves which supply the first two pairs of appendages take their origin from a nervous mass in front of the œsophagus. Dohrn (1) and Huxley (16), on the other hand, have stated that only the nerves to the first pair of appendages are præ-œsophageal in origin. It was reserved for M. Alphonse Milne-Edwards (5) to demonstrate by the dissection of perfectly fresh specimens of Limulus the true arrangement of these parts. I am able, from my own dissection of a fresh specimen of the same animal, to confirm M. Milne-Edward's description, though I must say that such confirmation is a mere formality, since the beautiful memoir in which that author has published his results bears throughout unmistakable evidence of care and accuracy.

With regard to the nervous system of Scorpio, we are not in the same favourable position. No zoologist, so far as I am aware, has studied the nervous system, or, indeed, any of the viscera of Scorpio by the aid of fresh specimens, and I cannot but expect that some very important modifications, in accepted conclusions, may result from a renewed investigation of the anatomy of that animal carried out upon freshly killed individuals. Nor has the nervous system of the adult Scorpion been studied by the aid of the microscope, in regard

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[1] For woodcuts illustrative of the nervous system of Limulus and Scorpio. See Part II.

to which deficiency we are in the same difficulty so far as Limulus is concerned in spite of Packard's recent work in that direction (9); in fact, the comparative anatomy of the nervous system of Arthropoda generally has yet to be placed on a firm histological basis, and until this is done we must not attach a very great importance to the results of simple dissection. With regard to the naked-eye appearance of the nervous system of Scorpion, we have, however, the exceedingly careful work of George Newport (6), which is worthy of all confidence, and what is of more importance we have certain embryological data furnished by the investigations of Metschnikoff (21) and of Balfour (20). The observations of the latter zoologist relate to the Araneina, but may fairly be considered as confirmatory of those of Metschnikoff.

The central nervous system of Limulus consists, according to M. Alph. Milne-Edwards, (A) of a distinctly emarginated brain or cerebral mass which I have elsewhere proposed to call the ARCHI-CEREBRUM,[1] and of two strands of nervous tissue, which embrace the œsophagus and unite behind it, so as to form (B) an oval ŒSOPHAGEAL COLLAR, being continued backward from their point of union along the ventral surface of the animal as (C) the ABDOMINAL CORD to a point some distance in front of the anus. The limbs of the collar are united by from three to eight transverse commissures in front of their point of union with one another and behind the œsophagus. From the archi-cerebrum are given off five nerves only, namely, those to the ocelli, to the compound eyes, and to the frontal integument. From the œsophageal collar a great number of nerves radiate, including those to the first as well as to all the other pediform appendages, and also the nerves to the chilaria (or metathoracic sternites) and to the genital operculum. We find a distinct nerve to each appendage, and a number of large tegumentary nerves also given off from the œsophageal collar. It is important to note that the pair of nerves to the genital operculum is derived from this region and not from the cord-like prolongation of the united strands of the collar. It is also important to observe that at present we have no knowledge of the existence of distinct ganglia or enlarged masses of nerve-cells in the œsophageal collar, so that it is not possible to infer from any such fact of structure how many ganglia corresponding to an equal number of segments are represented by the œsophageal collar. M. Alphonse Milne-Edwards, who holds the "chilaria" to be the equivalents of the Scorpion's "pec-

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[1] This Journal, April, 1881. 'On the Appendages and on the Nervous System of *Apus cancriformis*.'

tiniform organs," considers that eight pairs of ganglia are thus represented, a pair for each of the walking legs, a pair for the chilaria, and a pair for the genital operculum. The "chilaria" appear to me (as explained below) to be simply "sternites," and not related to the Scorpion's "combs;" and and I should therefore consider only seven pairs of segmental ganglia to be represented in the œsophageal collar. The history of development is not yet quite definitely ascertained, but it should decide this point, and should show, supposing the views which I am about to advocate are correct, that there is no ganglionic enlargement of the cord corresponding to the "chilaria," whilst the ganglonic enlargement from which the genital operculum is innervated should at first be more distinctly abdominal in position, and at a later period become fused with the six ganglion-pairs corresponding to the pediform appendages.

The third portion of the central nervous system of Limulus distinguished as the ABDOMINAL CORD, stretches from the œsophageal collar into the abdominal region, and gives off no nerves over a space equalling half its total length; it then enlarges and gives origin to a series of five groups of nerves, of which the first four correspond to and supply the four first pairs of branchial feet, whilst the fifth supplies not only the fifth pair of branchial feet, but also the præanal and perianal regions and the postanal spine. As to the disposition of nerve-cells in this abdominal cord we have no information, that is to say, as to whether it is possible anatomically to define separate ganglia in connection with the five groups of nerves in its hinder part, or in any region in front of them.

A very important relation between the arteries of Limulus and the main nerve trunks was first indicated by Owen (18), but more fully elucidated by Alphonse Milne-Edwards. This consists in the *ensheathing* of the œsophageal collar and of the abdominal cord in an actual arterial trunk; not only this but many of the larger nerves (those to the limbs) are ensheathed also by branches of the same arterial trunk. M. Milne-Edwards has pointed out that this arrangement is most nearly approached in Scorpio, and has recognised the remarkable agreements between the arterial system of the two animals—to which reference will be made further on—though he nevertheless is led by other considerations which are, I think, erroneous, to refuse to Limulus a position among the Arachnida.

When we compare the nervous system of Scorpio, as far as it has been made known by Newport and Metschnikoff, with that of Limulus we find portions precisely corresponding to the three main regions above distinguished in the latter animal. Anteriorly we have (A) a cerebral mass supplying the central and marginal eyes with nerves, (B) a large œsophageal collar, from which radiate the nerves to the appendages and some other parts, and (C) an abdominal cord which terminates in the fourth of the narrow præanal segments of the body.

When we look into details a little more closely we find some very obvious differences between these regions as presented in the Scorpion on the one hand and in Limulus on the other. But it must be remembered, in regard to these differences, that we have no account of the Scorpion's nerve-centres derived from the dissection of fresh specimens, nor of the actual arrangement of nerve-cells and nerve-fibres as revealed by microscopic examination.

In the first place the brain and the œsophageal collar of Scorpio are more intimately fused with one another than are the corresponding parts of Limulus. Moreover, the œsophageal collar is relatively more massive, and exhibits but a small perforation for the passage of the very narrow œsophagus. Instead of being bridged over behind the œsophagus by transverse commissures, as in Limulus, the two halves of the collar appear to be flattened out here and fused with one another. It is possible that a more accurate knowledge of this region in Scorpio might show structure representing the transverse commissures of Limulus.

A long tract of the most anterior portion of the abdominal cord in Scorpio, as in Limulus, gives off no nerves. But in accordance with the elongated form and well-marked segmentation of the hinder region of the body, we find that after this first tract there are, in Scorpio, seven well-marked ganglia placed at intervals on the cord, the most anterior of them sending off nerves to the *third* pair of lung-sacs, but to nothing in front of this.

With regard to the actual origin of nerves, it has always been stated that the first pair of appendages of Scorpio receive each a nerve from the præ-œsophageal ganglion. If this were absolutely the case it would mark a considerable difference between Scorpio and Limulus. But as a matter of fact mere inspection of Newport's drawing is sufficient to show that the nerves to the cheliceræ of the Scorpion have a lateral position embracing the true "archi-cerebrum," which supplies the lateral and central eyes between them, and whatever may be the result to be obtained in the future by microscopic sections or study of fresh specimens, we have the important embryological fact due to Metschnikoff (and confirmed for other Arachnida by Balfour) that the nerve-ganglion mass from which the nerve to the chelicera on each side takes its origin is *quite independent of the archi-cerebrum*, and in the embryo is placed behind the latter, and to the side of the œsophagus right and left. This seems to me sufficient to justify a complete assimilation of the two regions in Scorpio and Limulus, the difference being merely that post-embryonic fusion of the archi-cerebrum and lateral ganglia has proceeded a little further in Scorpio than in Limulus.

From the collar, then, in Scorpio, as in Limulus, the nerves to all six of the pediform appendages take their origin. But the agreement extends even further than this, for the nerves to that region of the Scorpion's body which corresponds with the genital operculum of Limulus also proceed from the œsophageal collar. The *attraction* (if I may use the term) of nerve origins to the œsophageal collar appears to have proceeded further in the Scorpion than in Limulus, for, whereas, in Limulus, the first and remaining four pairs of branchial feet are supplied from the abdominal cord, in Scorpio those parts, which for reasons to be given below, I consider to represent the first, second, and third of the branchial feet of Limulus, all appear to receive their nerves from the œsophageal collar, so that it is not until we come to the representatives of the fourth pair of branchial feet of Limulus (viz. the third pair of lung-books, see below) that we find in the Scorpion a nerve supply from the abdominal cord. This phenomenon of the travelling forward and concentration of nerve origins and their connected ganglia is one sufficiently familiar in various groups of animals. The fact of the dislocation in this way of the nerve supply of the genital operculum of Limulus above remarked on, receives illustration by the still further carrying out of the same process in Scorpio.

The difference in the disposition of the nerve orgins (such as it is) in regard to the *hinder* part of the abdominal cord in the two animals receives its explanation from the difference of general form and segmentation of the hinder region of the body which they respectively exhibit.

It appears, then, that there is when the most recent results of anatomical and of embryological observation are taken into consideration, no important difference between the central nervous system of Limulus and of Scorpio, and more especially it is to be noted for the purpose which we have next in view, viz. that of comparing the skeleton and appendages of the two animals, that there is not a difference of origin in the large nerves supplying the appendages, or the genital or the respiratory region, which can forbid us from unreservedly accepting as exactly representing one another, parts, which on the ground of numerical sequence, appear to reciprocally correspond.

§ *b*. **SKELETON.—I. Tergites, or Dorsal Sclerites.**—It is difficult to separate the description of one part of the skeleton of Limulus and Scorpio from that of another, and in com-

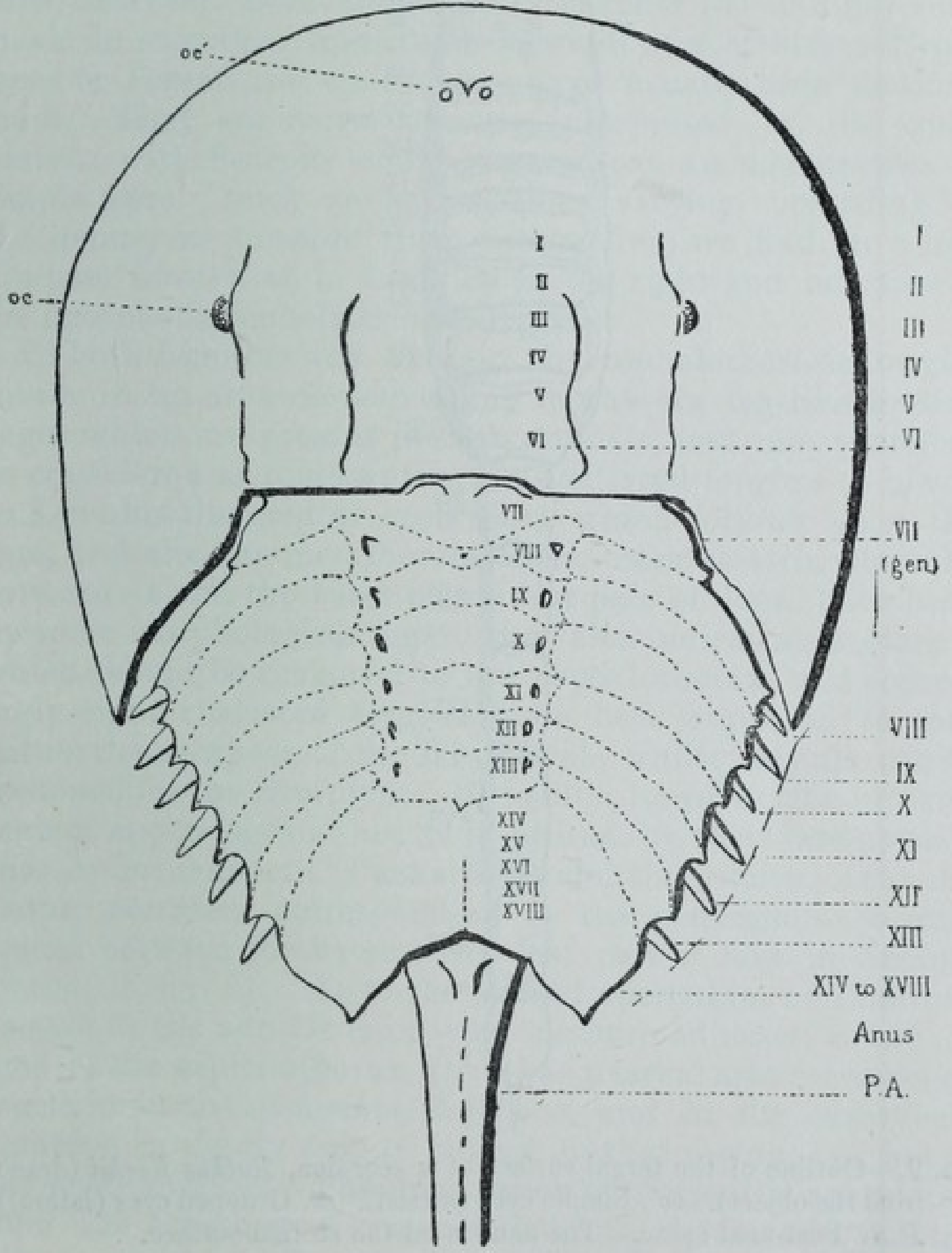

FIG. 1.—Outline of the tergal surface of *Limulus polyphemus* (drawn from the object). The dotted lines correspond to the markings on the abdominal carapace, which in the adult indicate what were separate segments in the embryo. *oc'*. Simple eyes (mesial). *oc*. Compound, or grouped eyes (lateral). *P.A.* Post-anal spine.

mencing with the tergal elements, we must necessarily refer simultaneously to the general disposition of the appendages.

Cephalothoracic tergites.—In Limulus (woodcut, fig. 1),[1] as in Scorpio (woodcut, fig. 2), the anterior region of the body is covered in by a large sclerite, which is known as the cephalothoracic plate or carapace.

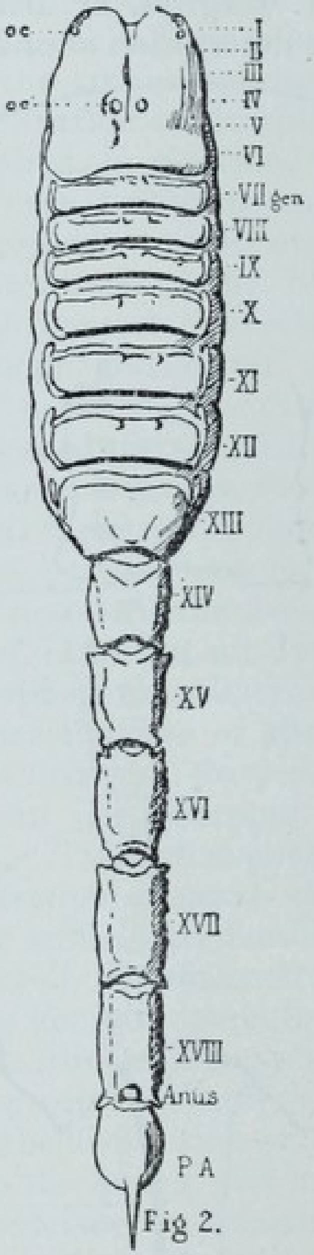

Fig. 2.—Outline of the tergal surface of a scorpion, *Buthus Kochii* (drawn from the object). *oc'*. Simple eyes (mesial). *oc*. Grouped eyes (lateral). *P.A.* Post-anal spine. The anus is on the sternal surface.

In Limulus its margins are produced and its posterior angles extended, so as to produce a form which differs from

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[1] It is necessary to state once for all that where not otherwise expressed I always allude by the term Scorpio, or Scorpion, to the species *Buthus Kochii*, of India, which happens to have been that studied by me. Other species differ in trifling details from this.

that seen in the Scorpion, but in essential points there is remarkable agreement. In both the carapace carries two paired groups of eyes. Nearer the middle line is a single pair of simple eyes (*oc′*), which in Scorpio have an almost central position; more laterally placed (quite laterally in Scorpio) is a group, on either side, of simple eyes (*oc*), which in Limulus *are so closely aggregated* as to form what is often called "a compound eye." The compound eyes of Limulus have, however, been shown by Grenacher (3) to differ very much in structure from the compound eyes of either Crustacea or Insects, to which they have usually been asssimilated. They are more correctly interpreted—as the comparison with Scorpio would suggest—as an aggregation of simple eyes. Such an aggregation (varying, according to the genus, in number from two to five) we find in a less compact form than in Limulus on the right and left side of the Scorpion's cephalothoracic tergite.

In both Limulus and Scorpio the cephalothoracic tergite covers in an area corresponding to the six leg-like appendages which are present in both animals, and may therefore be considered as representing six coalesced tergites (I to VI). In Limulus the genital operculum which follows upon the legs, and also the metathoracic sternites or chilaria which lie between it and the bases of the last pair of legs, have been by some morphologists regarded as also indicating segments which should be reckoned to the cephalothorax, and accordingly eight coalesced tergites have been supposed to constitute the carapace of the King Crab, whilst only six can be reckoned for the Scorpion. In reality, however, the chilaria are not appendages at all, as is proved by their late appearance in development (Packard, 8) and their form; they are simply sternites corresponding to the pentagonal sternite placed between the bases of the last pair of legs in Scorpio (woodcut, fig. 5). As to the genital operculum of Limulus, though in the adult it is in some measure adherent to the region of the cephalothorax, yet it has a tergal area corresponding to it in the *abdominal* carapace, and in the embryonic Limulus is clearly seen to belong to that region, and not to the cephalothorax. The innervation of the genital operculum from the œsophageal nerve-collar has, as already pointed out, no weight as an argument in favour of the association of that coalesced pair of appendages with the cephalothorax, for on the very same grounds it would be necessary to associate a large part of the middle region of the Scorpion's body (as far as and inclusive of the second pair of pulmonary sacs) with the cephalothorax.

Abdominal tergites.—Following upon the cephalothoracic plate we have in the Scorpion seven wide band-like sternites, to which succeed five narrow cylinders, the dorsal part of each of which is tergite, and solidly fused with the ventral half or sternite. In the last of these twelve segments is placed the anus (in fig. 2 its position is marked, though it is not seen on account of its ventral position), and beyond the anus is the postanal spine or sting.

In Limulus (fig. 1), in place of the seven band-like and five half-cylindrical tergites, we find one large chitinous plate, which is known as the "abdominal carapace." In its posterior region is placed the anus, and to it succeeds a postanal spine, sometimes, but erroneously, compared to the cylindrical segments of the Scorpion's body. Clearly enough the postanal spines in the two cases correspond to one another.

If there is correspondence between Limulus and Scorpio of segment for segment and piece for piece throughout (as it is the purpose of this essay to demonstrate), then in the abdominal carapace of Limulus we must find the representatives of the twelve segments, which in the Scorpion exist between cephalothorax and anus. The embryonic Limulus, as has been shown by Dohrn and Packard, exhibits in this region of the body a series of *separated* segments, which fuse together as growth advances, and constitute the one immovable abdominal carapace. In the adult the indications of the former existence of these separate segments is more obvious than has been supposed. In fig. 1 I have indicated by dotted lines the series of ridges, which can be made out in the abdominal carapace of an adult *Limulus polyphemus*, and which clearly mark off a number of the original segments.

With regard to the general form of this region as compared with the body of the Scorpion, it may be pointed out that here, just as in the region of the cephalothorax, there is an excessive development and exaggeration of the margin of the dorsal integument, so that the central area marked out in the figure is the real "body" of the *Limulus*, and the wide spreading lateral areas are only enormous excrescences of a relatively superficial character. It is not difficult to find numerous parallels to these pleural developments in all groups of Arthropoda.

Returning to the examination of the actual number of segments indicated in the abdominal carapace of the adult Limulus, we find areas corresponding to the seven wide tergites of the Scorpion marked in the drawing of *Limulus* by the numbers VII to XIII. Corresponding to these areas are a series of marginal processes, the first corresponding to the first area, is a mere angular process of the integument, but the six which follow are in the form of movable spines.[1]

Corresponding also to the six segments which bear the six spines (that is, to the six hinder segments of the seven in question) are a series of pits in the axial region of the tergum, a pair in each segment.

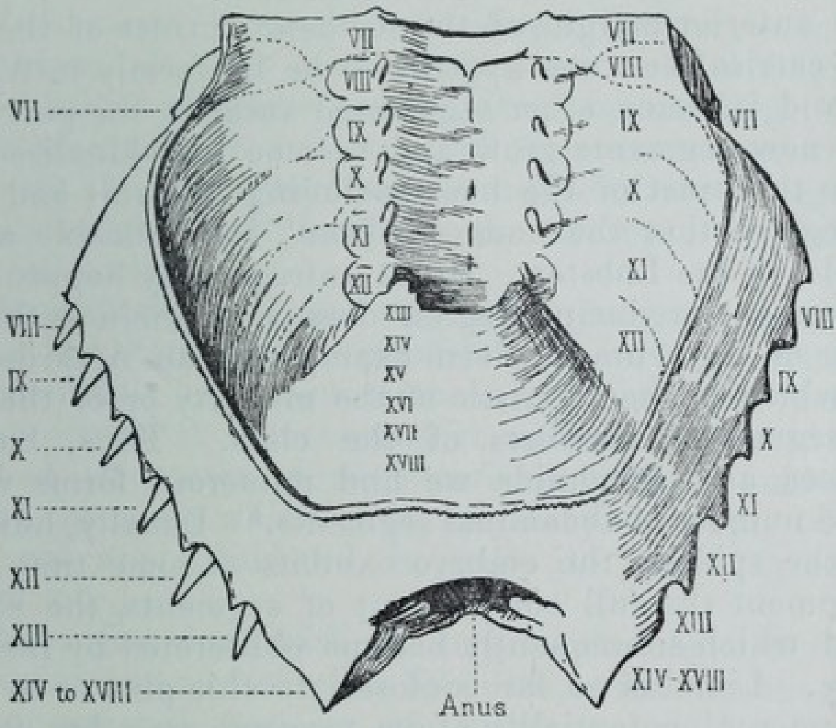

Fig 3.

FIG. 3.—View of the abdominal carapace of *Limulus polyphemus* from below, the soft sternal region and appendages of the anterior six segments and the viscera having been removed.

The figures VII to XII upon the drawing (drawn from the object) are placed by the sides of the tergal entapophyses. The continuation of the same series (XIII to XVIII) is placed upon the chitinized sternal surface of the unsegmented region, which in Limulus represents the seventh abdominal and the five cylindrical præanal segments of the Scorpion.

These are deep invaginations of the integument forming hollow processes, pushed as it were into the body cavity and clothed internally with cartilage, the structure of which has been described by Gegenbaur (2); they give attachment to muscles and are well termed "entapophyses" by Owen (7).

When we look in the abdominal carapace of Limulus for representatives of the five cylindrical præanal segments of the Scorpion, we find nothing but a broad smooth area extending from the marking which indicates the hind

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[1] These spines I have seen slowly moving, independently of one another, in the living King Crab, indicating a separate musculature for each spine.

border of the thirteenth segment (seventh of the abdominal series) to the soft membrane which forms the hinge of the postanal spine.

In the embryo Limulus, however, this area is further segmented. We do not find the five segments of the Scorpion, but we find two of which (as segments) no indication is left in the adult, and the foremost of these carries a movable spine on each side like those in front of it.

The anterior margin of the segment or tract of the body which carries the anus appears to be uniformly in Arthropoda, and in some other segmented animals, the part from which new segments grow and become individualised, and it is to this tract of the body including its præ- and postanal regions that the name " telson " is applicable as, for example, in the Lobster. It not unfrequently happens that this segment-producing region does not produce the full number of segments in given examples of an Arthropodous class, which is characteristic of the majority or of the more fully segmented members of the class. Thus, both in Crustacea and Arachnida we find numerous forms with a reduced number of abdominal segments.[1] Usually, however, as in the spiders, the embryo exhibits at some time of its development the full complement of segments, the hindermost of which subsequently become obliterated by fusion or atrophy. Limulus so far conforms to this plan as to show the segmental potentiality of its præanal area, but fails to exhibit to the observer the full complement of segments even as a temporary arrangement of its living substance.

Accordingly the whole area posterior to the ridge marking the posterior border of the thirteenth segment may be regarded in Limulus as belonging to the "telson," or area of potential segmentation, a certain reservation being observed in respect to the one or two minute segments which appeared and disappeared in this region in the embryo.

We may, when comparing this condition of things with that exhibited by the Scorpion, *either* consider the telsonic area and spine of Limulus as representing the five cylindrical segments and the sting of the Scorpion in an unsegmented state, *or* we may insist rather upon the actuality than the protentiality, and identify the telson or fifth of the cylindrical segments of the Scorpion (viz. that carrying the anus), and the postanal spine with the telsonic area and spine of Limulus, whilst regarding the four anterior cylin-

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[1] Note also the evanescent character of the three last segments of Thelyphonus (fig. 12).

drical segments of the Scorpion as something over and above and not developed in Limulus at all.

It seems, however, probable from the evidence of extinct forms, as well as from the abortive segmentation of the embryo, that Limulus is *not* derived from an ancestor in which the telsonic area was as limited in its production of segments as it is in Limulus itself, but on the contrary, that the ancestor of Limulus had the full complement of segments (and possibly more) which is seen in Scorpio and the Eurypterina. In that case the præanal area and spine of Limulus would not merely be an area representing the five cylindrical segments and sting of Scorpio in *potentiality*, but would be the *actual* representative of those segments gradually reduced and fused in the course of an historic process of change.

II. **Appendages.**—At each stage of the comparison between Limulus and Scorpio, the proofs of the intimate affinity of the two animals become more convincing, since we find that the view which it is necessary to adopt in order to make one set of structures agree closely in the two animals, is precisely the view which it is necessary to adopt, when a second set are considered, in order to make agreement possible.

We have just dealt with the tergites and have found an exact correspondence of piece for piece, with the exception that four præanal segments are suppressed or five fused in Limulus which are discretely present in Scorpio. In order to admit such an agreement of piece for piece as to tergites, we have to reject the view that the chilaria and the genital operculum represent segments belonging to the cephalo thoracic tergite, for in that case the cephalothorax of Scorpio would be a fusion of six, whilst that of Limulus would be a fusion of eight pieces.

When we come to examine the sternites, we shall find that the exclusion of the chilaria from the series of appendages is exactly what is required in order to identify the sternites of Limulus with those of Scorpio, and the removal of the genital operculum of Limulus from the cephalothorax makes its identity with the genital operculum of Scorpio even more obvious than it would otherwise be.

The six pairs of appendages of the cephalothorax of Limulus may be compared one by one with the six pairs of Scorpio.

Cephalothoracic appendage, No. I.—We have already disposed of the obstacle which has been always raised hitherto when the cheliceræ of the Scorpion have been

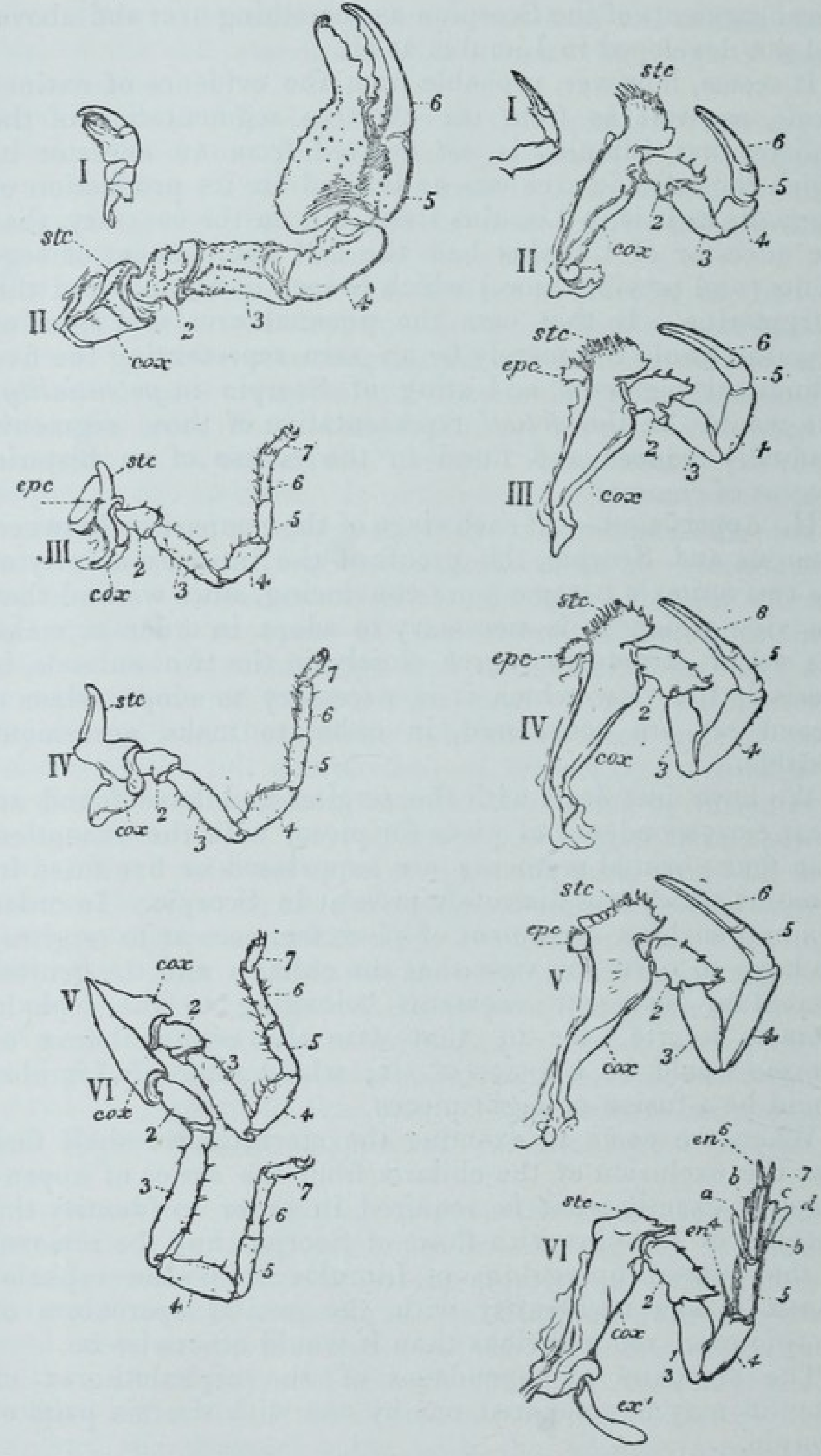

FIG. 4.—Cephalothoracic appendages of Scorpio (left), and of Limulus (right), drawn from the object. *cox*, coxa. *stc*. Sternocoxal process of the coxa. *epc*. Epicoxite. *ex'*. Exite of the coxa of the sixth appendage of Limulus. *en'*. Endite of the fourth segment of the same limb. *a*, *b*, *c*, *d*. Endites and exites of the fifth segment of same. *en*^{6}. Endite of the sixth segment of the same.

assimilated to the cheliceræ or first pair of limbs of Limulus. Instead of there being a difference as to innervation we have seen that there is a real identity.

In Limulus, each of the first pair of appendages is a short pair of nippers (woodcut, fig. 4, I, right) composed of three sclerites; at the base of the two appendages and between them and the mouth is placed an ovate sternite, the camerostome or upper lip. (Plate XXVIII, fig. 4).

In Scorpio (woodcut, fig. 4, I left) a similarly small pair of appendages is found similarly composed of three sclerites, and similarly overhanging an oval "camerostome."

Ceph. thor. app., No. II.—In this and the following leg-like appendages of Limulus six chief sclerites are developed, the basal one or "coxa" being much enlarged, and its interior border produced into a well-marked process provided with tooth-like hairs. The arrangement of the limbs around the mouth and the central sternite which follows it (*pmst* in Pl. XXVIII, fig. 4), is such that the processes of the coxæ of all ten limbs act together as manducatory organs. The process of the coxa may be called "the sterno-coxal process" (*stc.* in the woodcut, fig. 4). The second cephalo-thoracic appendage in the female *Limulus polyphemus* is like the third, fourth, and fifth, a chela—that is to say, the penultimate sclerite is produced so as to form with the last sclerite a pair of nippers. In the male this is not the case, the second pair of appendages being thicker and heavier than in the female, and the penultimate joint not prolonged. The form of appendage seen in the male *L. polyphemus* in this position is similar to appendages seen in other Arachnida than Scorpio, viz. Thelyphonus (woodcut, fig. 12).

The second pair of appendages in the Scorpion is like that of the female Limulus, but relatively larger. It consists of six sclerites as in Limulus, and has a sterno-coxal process on its coxa, which acts with its fellow of the opposite side as a jaw (woodcut, fig 4, II).

Cephalo-thoracic appendage, No. III.—In *Limulus polyphemus* this has, in both sexes, the same form as has the second appendage in the female. It is similarly composed of six sclerites, but in addition to these we find a distinct movable sclerite developed on the median border of the coxa. This sclerite may be termed the "epicoxite" (woodcut, fig. 4, III, *epc.*, right). The epicoxite is a remarkable feature, and is not easily paralleled among Arthropoda. The basal "endite" of the limbs of the Crustacean Apus is similar to it, and perhaps derived from a common ancestral origin.

In Scorpio the third cephalothoracic appendage is in the form of a walking leg, and as such has seven sclerites. It is a remarkable fact that in Limulus the sixth cephalothoracic appendage, which is non-chelate, also presents seven axial sclerites (woodcut, fig. 4, VI, right), so that the Scorpion's ambulatory limbs do not depart from the possibilities of Limulus in developing axial sclerites beyond the number six. It is also important to notice in this connection that the Arachnida exhibit a great variability in the number of joints present in their legs. Thelyphonus develops a four-jointed "tarsus" at the end of the five proximal segments of its ambulatory limbs (woodcut, fig. 12), whilst Galeodes presents a curious increase in the number of segments in the proximal region of its hinder limbs (woodcut, fig. 10).

The most important feature in which the third and subsequent cephalothoracic limbs of Scorpio resemble those of Limulus is in the great development of the coxæ. The sterno-coxal process is present on the third and fourth cephalothoracic appendages, and is even larger relatively than in Limulus. In the third and fourth limbs it is free, overlying a very soft minute sternal region below the mouth, and playing with its fellow of the opposite side the part of an ingestive organ for the mouth. The narrow cleft between the opposed sterno-coxal processes probably acts by capillary attraction in the taking up of such food as the blood of other animals.

The coxæ of the fifth and sixth appendages of Scorpio have, on the other hand, no free sterno-coxal process.

The great enlargement of the coxæ of these four pairs of appendages, and their encroachment upon the median area, is accompanied by, and related to, the suppression of any representative of the sternal sclerite (*pmst.*, fig. 4, Pl. XXVIII) which is present in Limulus. The coxæ of the third pair and of the fourth pair meet one another in the middle ventral line, but are separated by soft membrane. The coxæ of the fifth and sixth pairs do not meet their fellows in the middle line, but are kept apart by the wedge-shaped extremity of a sternite (*met.* in woodcut, fig. 8). They differ from the coxæ of the third and fourth pairs in that the fifth is adherent to the sixth (woodcut, fig. 4, V, VI, left.)

The base of the third appendage in Scorpio exhibits a development internal to the sterno-coxal process, which corresponds to, and probably represents, the "epicoxite" of Limulus. This is in the form of a movable plate (woodcut, fig. 4, III, *epc.*, left), which presents parallel ridges on its surface.

Cephalothoracic appendage, No. IV.—Appendage No. IV in Limulus closely resembles No. III. As in No. III, an epicoxite is present.

The corresponding appendage of Scorpio has been already mentioned. It has seven joints and a large sterno-coxal process, but no epicoxite, such as occurs in the limb next in front of it.

Cephalothoracic appendage, No. V.—In Limulus this resembles Nos. III and IV, like them having an epicoxite.

In Scorpio, No. V, is a seven-jointed ambulatory limb, with large coxa fused to the coxa of the next following appendage, but devoid of sterno-coxal process.

Cephalothoracic appendage, No. VI.—In Limulus this is the characteristic digging limb, unlike in the special modification of its parts and their remarkable function (for which see the citations of Lockwood and of Lloyd in 'Owen's Memoir,' No. 7) any other arthropod appendage.

In structure it is remarkable for exhibiting the feature of secondary movable arthrites diverging from the axis of the limb, unusual in Arthropoda other than the Crustacea. Seven axial sclerites or segments can be distinguished, the coxa being large, as in the other limbs, but devoid of an epicoxite. On the other hand, whilst the "endite" is thus absent, an "exite" is developed in the form of a flattened elongated piece articulated to the external border of the coxa (woodcut fig. 4, VI *ex′* right).

The second and third segments of the axis are devoid of apophyses, but the fourth bears a large spine-like articulated endite. The fifth joint of the axis carries four flattened apophyses (endites and exites), which are articulated and capable of active movement. The sixth joint bears one articulated endite, and, further, the short terminal seventh or ultimate segment of the axis, which is relatively much longer in newly hatched individuals than in the adult.

The sixth cephalothoracic appendage in Scorpio is quite similar to the three preceding walking legs. Its large coxa is fused to that of the fifth appendage of the same side. The spinous outgrowths on the sixth and seventh segments of this and the other legs are in character somewhat similar to the more highly developed apophyses of the digging limb of Limulus.

The seventh pair of appendages or genital operculum.—In Limulus lying between the bases of the sixth pair of cephalothoracic appendages is a pair of sclerites, the chilaria of Owen, actually the metathoracic division of the sternum (woodcut fig. 5, *st.* right), which belongs to the segment carrying the sixth pair of appendages. Precisely similar in position in Scorpio is a pentagonal[1] sclerite divided into a right and a left half by a median groove (woodcut fig. 5, *st* left upper figure). This is, in like manner, the metathoracic sternite, of which more will be said below.

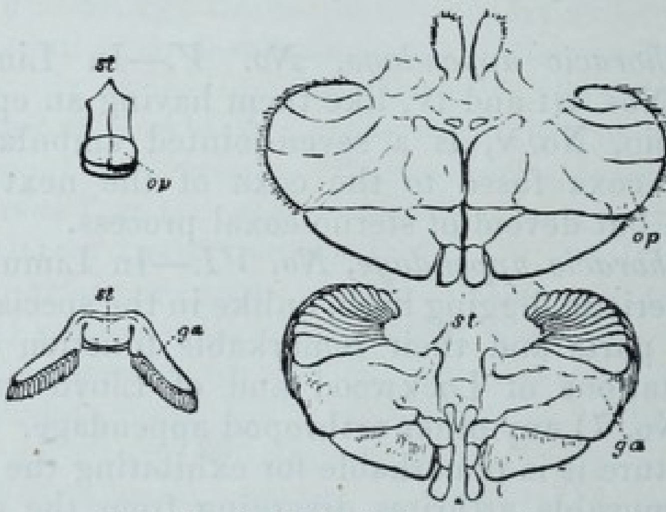

Fig. 5.—The seventh (*op*) and eighth (*ga*) pairs of appendages of Scorpio (left) and Limulus (right), together with the thoracic metasternites (*st* of the upper figures), and sternites of the eighth segment (*st* of the lower figures). The anterior face of the appendages is shown Drawn from the object.

Following in Limulus as in Scorpio upon the metathoracic sternite, is a lid-like plate, the hinge of which is transverse to the long axis of the body, and on the inner face of which are placed, both in Scorpio and in Limulus, the genital apertures, male or female, as the case may be (woodcut fig. 6, VII, right Limulus, left Scorpio).

The history of development in Limulus shows that this genital operculum starts as two independent processes of the body, which are to be regarded as the appendages of the seventh segment. The operculum retains throughout life evidence of its double origin, and closely resembles in form the five succeeding pairs of appendages which carry the respiratory lamellæ.

In Scorpio, on the other hand, the genital operculum is relatively of very small size, as seen in figs. 5 and 8 *go*; in fig. 6, it and the following appendages are drawn on an enlarged scale for the purpose of comparison with the corresponding parts in Limulus. Very little trace of having been formed by the union of two lateral appendages is exhibited by the genital operculum of Scorpio. At the same time its

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[1] Pentagonal in the subgenus Buthus, from which my drawings and notes are taken, but more triangular and reduced in size in the subgenus Androctonus.

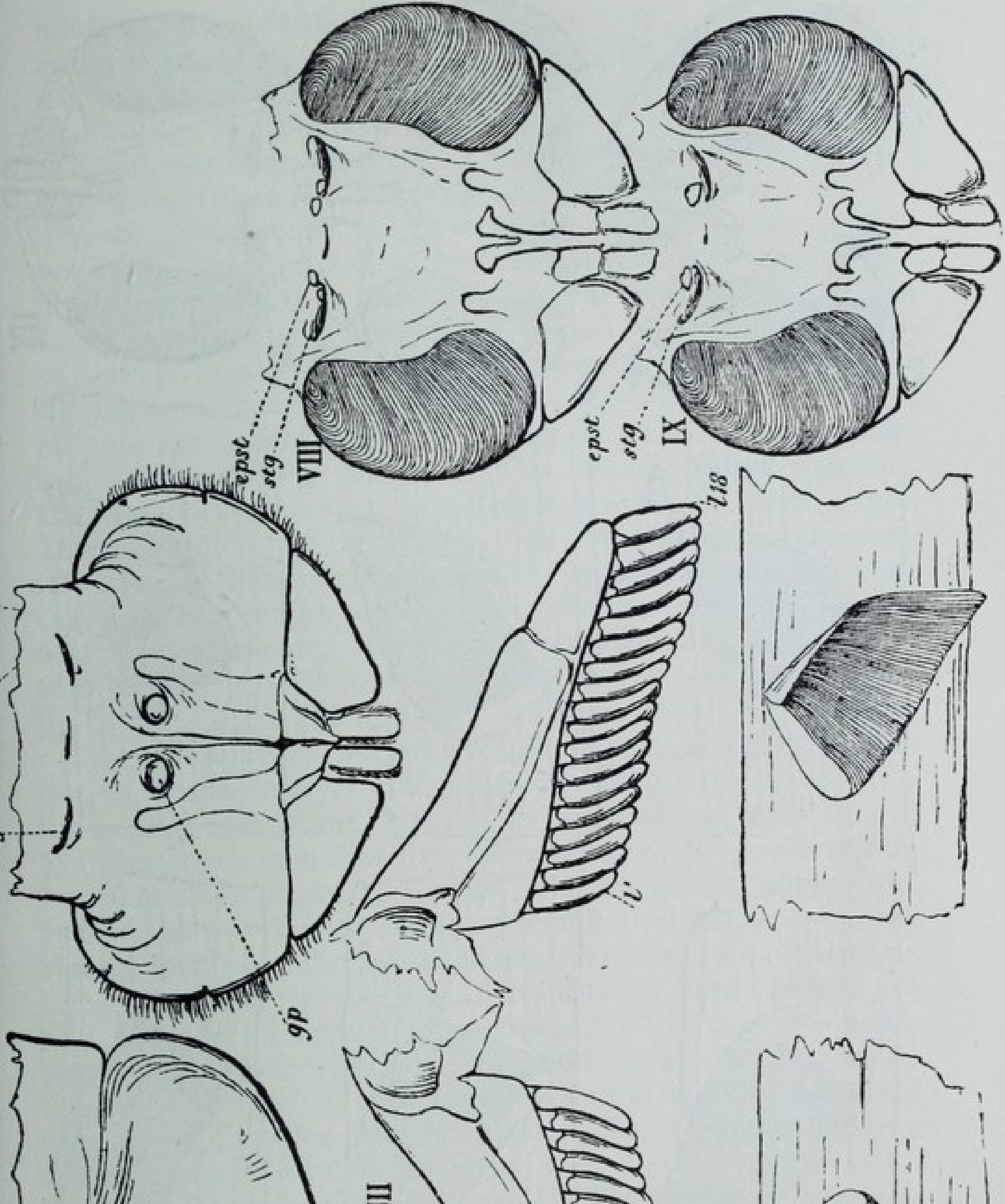

Fig. 6.—The seventh, eighth, and ninth pairs of appendages of Scorpio (left) and Limulus (right). The posterior face of the appendages is shown. *gp.* Genital pore. *stg.* Parabranchial muscular stigmata (tendons of the thoraco-branchial muscles) of Limulus. *epst.* Epistigmatic sclerites of same. Drawn from specimens.

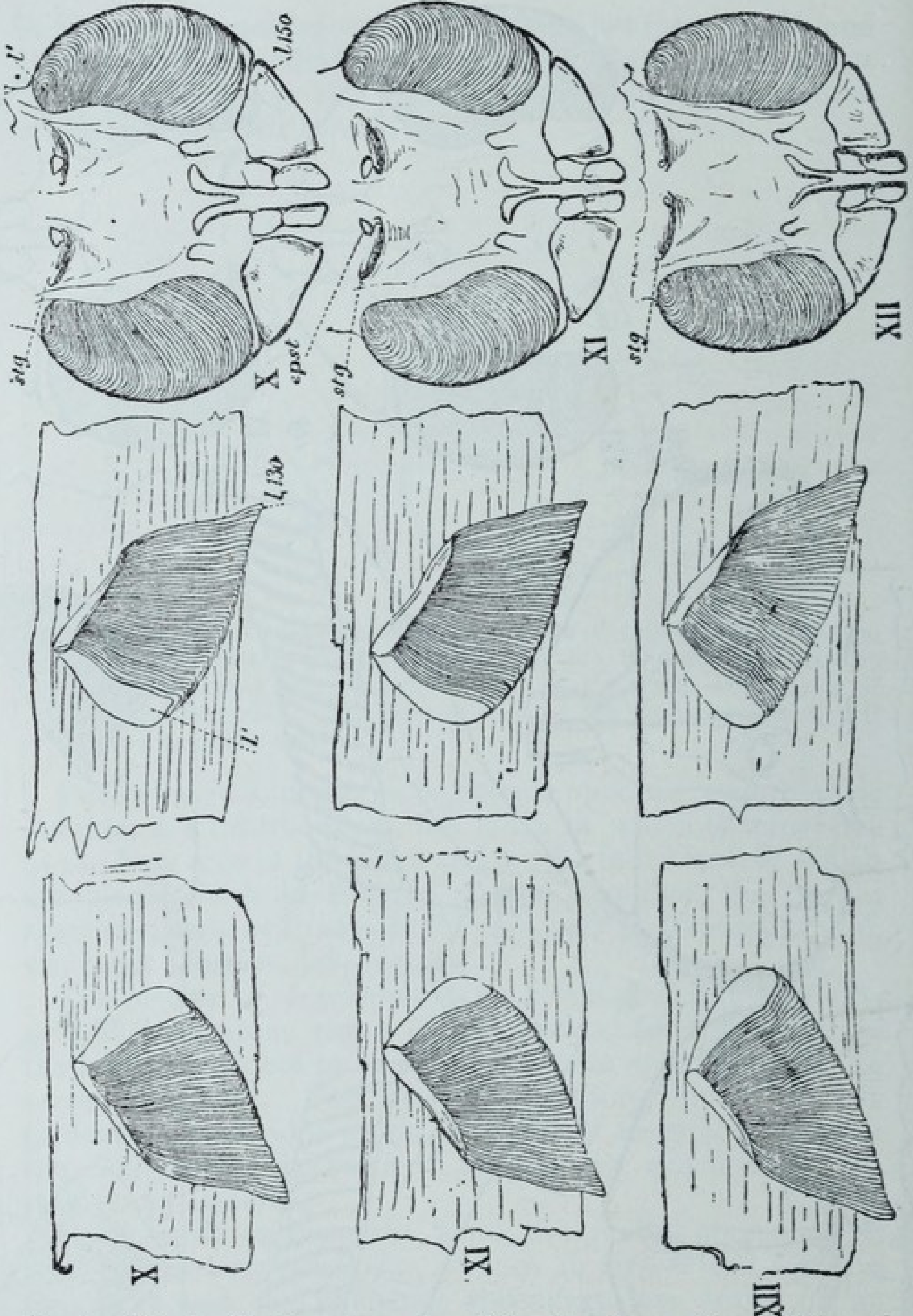

Fig. 7.—The tenth, eleventh, and twelfth pairs of appendages of Scorpio (left), and of Limulus (right). The posterior face of the appendages is shown. *stg*. Parabranchial stigmata of Limulus. *epst*. Epistigmatic sclerites. *l'*. Mediad, or first lamella of the lamelligerous appendages. *l*130. External, or one hundred and thirtieth lamella of the same in Scorpio. *l*150. External, or one hundred and fiftieth lamella of the same in Limulus. Draw from specimens. It is important to note that in these and other figures the lung-books of the Scorpion are represented as *entirely freed from the delicate pulmonary sac which invests them.*

bifid margin speaks of such an origin, and, as a matter of fact, such appears to be its embryological history.

I shall here quote a passage from 'Balfour's Embryology,' recounting Metschnikoff's observations upon the existence of rudiments of appendages in the segments of the Scorpion's body following upon the cephalothorax with its six pairs of limbs. The observations have great importance, not only in reference to the genital operculum but also in regard to the pulmonary sacs and their "branchial books" which are found in succeeding segments.

Balfour says, "Rudimentary appendages appear on the six segments behind the ambulatory legs. . . . They persist only on the second segment, where they appear to form the comb-like organs or pectines. The last abdominal segment, *i.e.* that next the tail, is without provisional appendages. The embryonic tail is divided into six segments, including the telson. The lungs are formed by paired invaginations, the walls of which subsequently become plicated, on the four last segments, which bear rudimentary limbs, and simultaneously with the disappearance of the rudimentary limbs" ('Comp. Embryology,' vol. i, p. 359).

Hence it appears that, in Scorpio, in front of the comb-like organs, that is to say, in the position subsequently occupied by the genital operculum, there is in the embryo, as in that of Limulus, a pair of rudimentary appendages. We know that in Limulus these grow together to form the genital operculum. It is in the very highest degree probable that the same history obtains for the similarly related genital operculum of Scorpio.

In discussing the tergites, it has already been pointed out that the genital operculum corresponds to a separate band-like tergite in Scorpio (VII, in woodcut, fig. 2), and to an emarginated area on the anterior border of the abdominal carapace of Limulus (VII, in woodcut, fig. 1), which is more distinctly marked in the embryo.

The eighth pair of appendages.—In Scorpio we find, on the ventral surface corresponding with the eighth tergite (six tergites being reckoned to the cephalothorax) a pair of appendages carrying fine lamellæ set like the teeth of a comb along the inferior margin (woodcuts fig. 5 *ga*, left, and fig. 6 VIII, left; see also Plate XXVIII). They are developed from the second pair of rudimentary abdominal appendages of the embryo.

In Limulus, in the corresponding position, we find a pair of appendages, the first of a series of five pairs (woodcuts fig. 5 *ga*, right, and fig. 6 VIII, right). The appendages of the two sides, as in the case of the genital operculum, do not diverge from one another but are directed towards one another and united across the middle line by a soft plate-like fold of the sternal integument; the result being that a plate-like body is formed from two originally distinct right and left appendages. On the under surface of each of the combined appendages a series of very delicate lamellæ is found *corresponding to the lamelliform teeth of the Scorpion's comb-like organs.*

Ninth, tenth, eleventh, and twelfth appendages.—In Limulus, corresponding to the tergal areas marked IX, X, XI, XII, we find a series of pairs of appendages precisely similar to that belonging to the eighth segment.

In Scorpio it will be remembered that in the embryo rudimentary appendages appear corresponding to the first six abdominal segments, or the seventh, eighth, ninth, tenth, eleventh, and twelfth of the whole body. Of these the first pair we have seen, become in all probability the genital operculum; the second pair are known to become the "pectines;" the pairs on the ninth, tenth, eleventh, and twelfth segments *disappear*, as the lung sacs on those segments develop by a process of invagination.

They disappear, but only from view. It has not been shown by actual observation, but it cannot well be doubted, that these rudimentary appendages sink within the lung-invaginations, and become the lamelligerous appendages which are found in them in the adult Scorpion.

The four pairs of stigmata on the ventral surface of the ninth, tenth, eleventh, and twelfth segments of the Scorpion's body (woodcut, fig. 8) lead into sacs, each of whch contains, concealed within it, an appendage consisting of an axis bearing a series of delicate lamellæ (woodcuts, figs. 6 and 7, IX, X, XI, XII, left).

Each of these concealed appendages is strictly comparable in structure to one of the comb-like organs of the eighth segment, the axis corresponding to the axis, and the delicate lamellæ to the teeth of the comb.

Thus, then, we find five pairs of lamelligerous appendages on the five segments of the Scorpion's body numbered 8, 9, 10, 11, 12, of which the first pair is external, and accordingly modified, whilst the next four are sunk below the surface, and accordingly modified. In Limulus, on the exactly corresponding segments, namely, those numbered 8, 9, 10, 11, 12, we find five pairs of lamelligerous appendages, but these are all external, and all alike modified for the purposes of aquatic respiration.[1]

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[1] Latreille, though holding the Limuli to be Crustacea, and not Arachnida, was the first to insist on the branchia-like character of the Scorpion's lung-books

Furthermore, it is important to notice that in Scorpio neither in the embryo nor at any other time does the seventh abdominal segment (thirteenth of the whole series) carry a pair of appendages, nor do any of the subsequent cylindrical segments. Similarly in Limulus no appendages or rudiments of appendages are to be detected after the last pair of lamelligerous organs—the twelfth of the whole series.

The segmented region, devoid of appendages in the Scorpion, is represented by an unsegmented region devoid of appendages in the King Crab.

Before entering into a more minute comparison of the lamelligerous appendages of the Scorpion with those of Limulus, with the object of establishing the identity of origin of the two series by the detection of agreement between them in details of structure, it will be most convenient to examine another series of skeletal elements, namely, the sternites.

III. **Sternites.**—In Limulus, in the cephalo-thoracic region, we find that the integument of the sternal area, though to a large extent soft and devoid of hard chitinous plates, yet presents here and there well-marked sclerites. On the sub-frontal area, a small discoidal piece, the sub-frontal sclerite is found (Pl. XXVIII, fig. 4, *sf*). Between the mouth and the bases of the first pair of appendages a much more important sclerite occurs, to which the term used by Latreille for the similarly placed sclerite in Arachnida, viz. (camerostome), may be used.

In the Scorpion (fig. 8, in front of the mouth to which the line M points) a similar tubercular sclerite is found. There is advantage in not merely designating this piece "labrum," since there is but little ground for holding it to be equivalent either to the labrum of Insecta or to that of Crustacea.

In the Spider Mygale (fig. 9) and in Galeodes (figs. 10 and 11, *cam*), this same piece is observed, attaining a remarkable development in the latter.

When we come to the region behind the mouth, we find in Limulus a large median sclerite extending from the pharynx backward. It lies between the bases of the third, fourth, fifth, and sixth pairs of cephalothoracic appendages. On account of its position, it may be termed the thoracic promeso-sternite (Pl. XXVIII, fig. 4, *pmst*), since it appears to represent elements which, in other Arachnida, are marked off as distinct prosternite and mesosternite.

In Scorpio we find nothing corresponding to this piece. By the enlargement and mesiad production of the coxæ of the four hinder cephalothoracic appendages it has been as it were

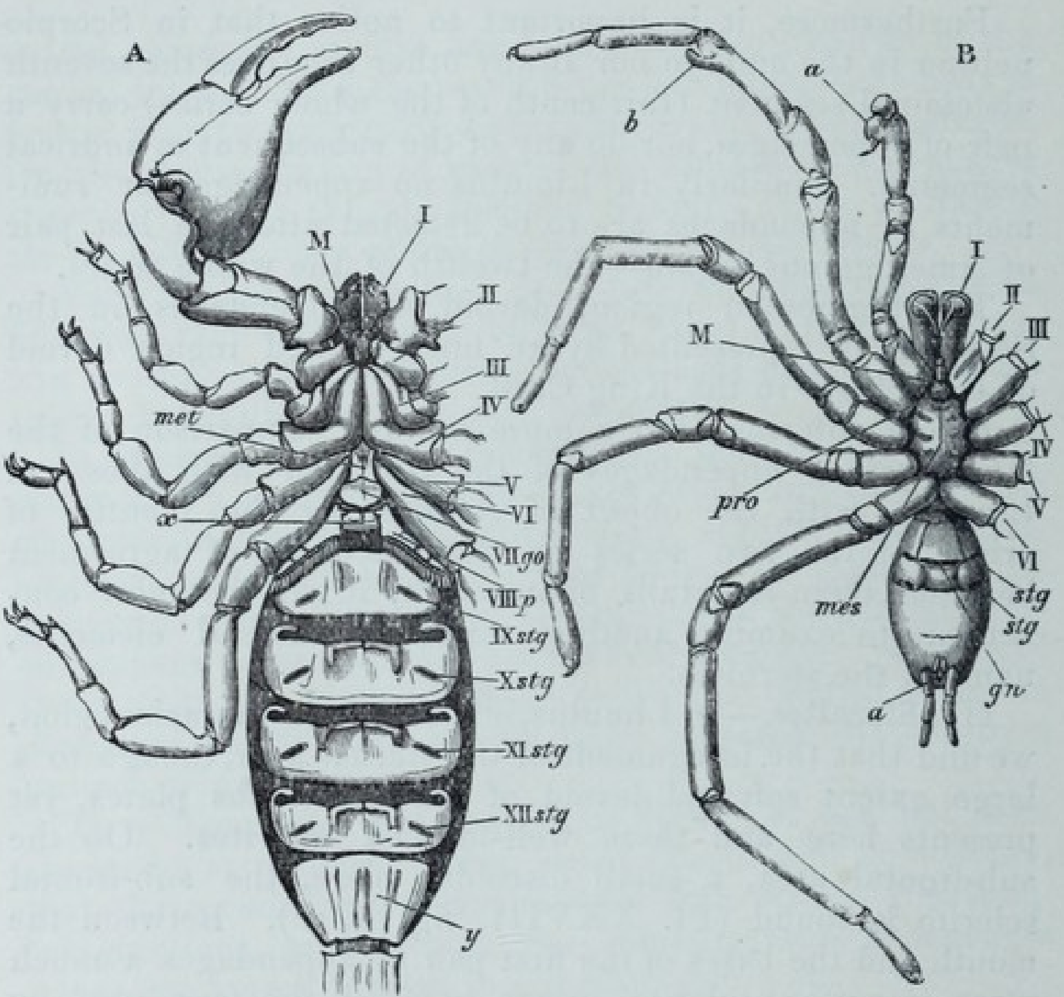

FIG. 8 (A).—Ventral aspect of a scorpion (*Buthus Kochii*), with the terminal segments omitted. Drawn from the object. I to VI. The cephalothoracic appendages. II. Points to the sterno-coxal process of the great chelæ. III. To the sterno-coxal process of the first walking leg. IV. To the sterno-coxal process of the second walking leg. *met.* Thoracic metasternite. VII *go.* The genital operculum. VIII *p.* The pectines, or eighth pair of appendages. *x.* Sternite of the eighth segment. IX *stg,* X *stg,* XI *stg,* XII *stg.* Stigmata leading into the pulmonary sacs, containing the appendages of the ninth, tenth, eleventh, and twelfth segments. *y.* Sternite of the thirteenth segment devoid of appendages. M. Mouth, in front of which is seen the camerostome.

FIG. 9 (B).—Ventral aspect of a bird's nest spider (Mygale sp), the hairs removed. Drawn from the object. I to VI. Cephalothoracic appendages. M. Mouth, in front of which is seen the camerostome. *pro.* Thoracic prosternite. *mes.* Thoracic mesosternite. *stg.* The apertures of the two pulmonary sacs of the left side. *gn.* Genital aperture. *an.* Anus.

obliterated. A similar obliteration has taken place in Galeodes (fig. 10), but in Thelyphonus (fig. 12), a triangular sternite (*st′*) is found (though erroneously omitted in the figure given in the last edition of Cuvier's 'Regne Animal') in front of the coxæ of the fourth pair of cephalothoracic appendages.

The Arachnids, which come nearest to Limulus in the

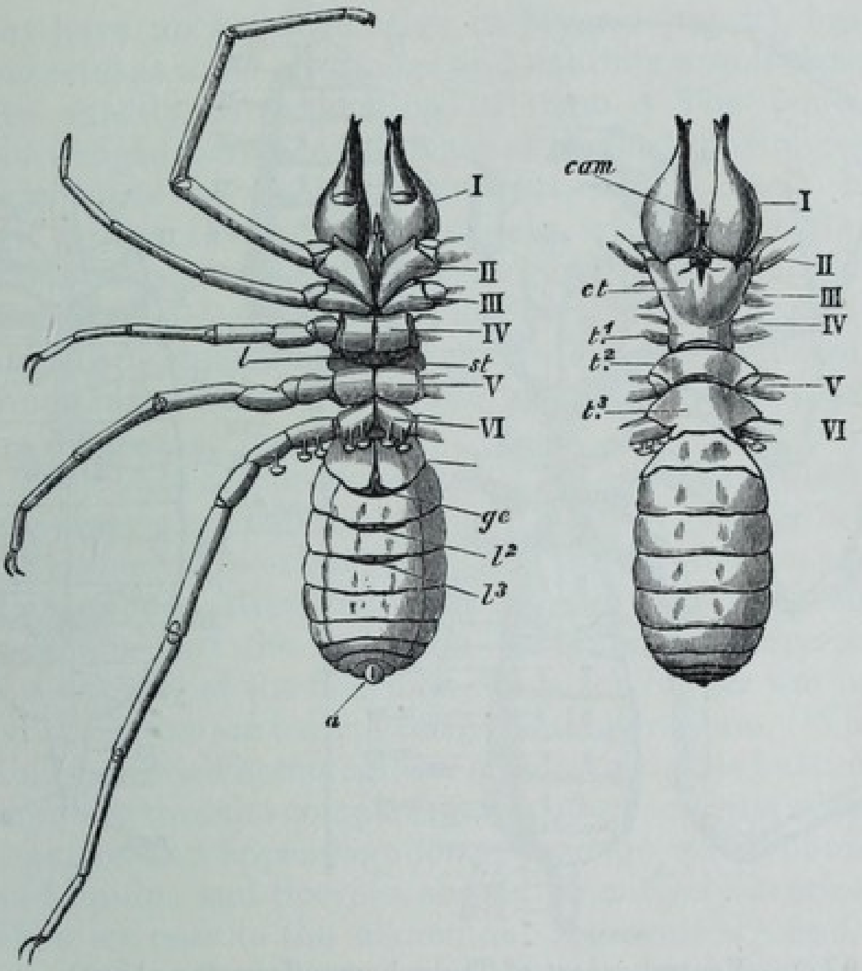

FIG. 10 and 11.—Ventral and dorsal aspect of Galeodes sp. (from the object). I to VI. The cephalothoracic appendages. *l.* Thoracic right tracheal aperture. l^2, l^3. Abdominal tracheal apertures. *ge.* Genital aperture. *st.* Sternal surface. *a.* Anus. *cam.* Camerostome. *ct.* Cephalothoracic tergite. t'. Prothoracic portion of the cephalothoracic tergite. t^2. Separate mesothoracic tergite. t^3. Separate metathoracic tergite.

character of this portion of the sternal area, are the Spiders. In Mygale (*M. avicularia*) the coxæ of the five hinder cephalothoracic pairs of appendages are arranged around a large oval sternite (fig. 9), which is divided into two portions, an anterior small prosternite (*pro*) and a larger mesosternite (*mes*). This double piece appears to correspond to the sternite of Limulus, marked *pmst* in fig. 4, Pl. XXVIII.

It is not a little remarkable that, in a structural feature observed in Limulus and *not* repeated in Scorpio nor in any Crustacean or Insect, the closest parallel should be found in another Arachnid; it is remarkable because it tends still further to determine the association of Limulus with the Arachnida in classification rather than with any other group.

Behind the thoracic promesosternite of Limulus, separated from it by soft integument and posterior to the coxæ of the

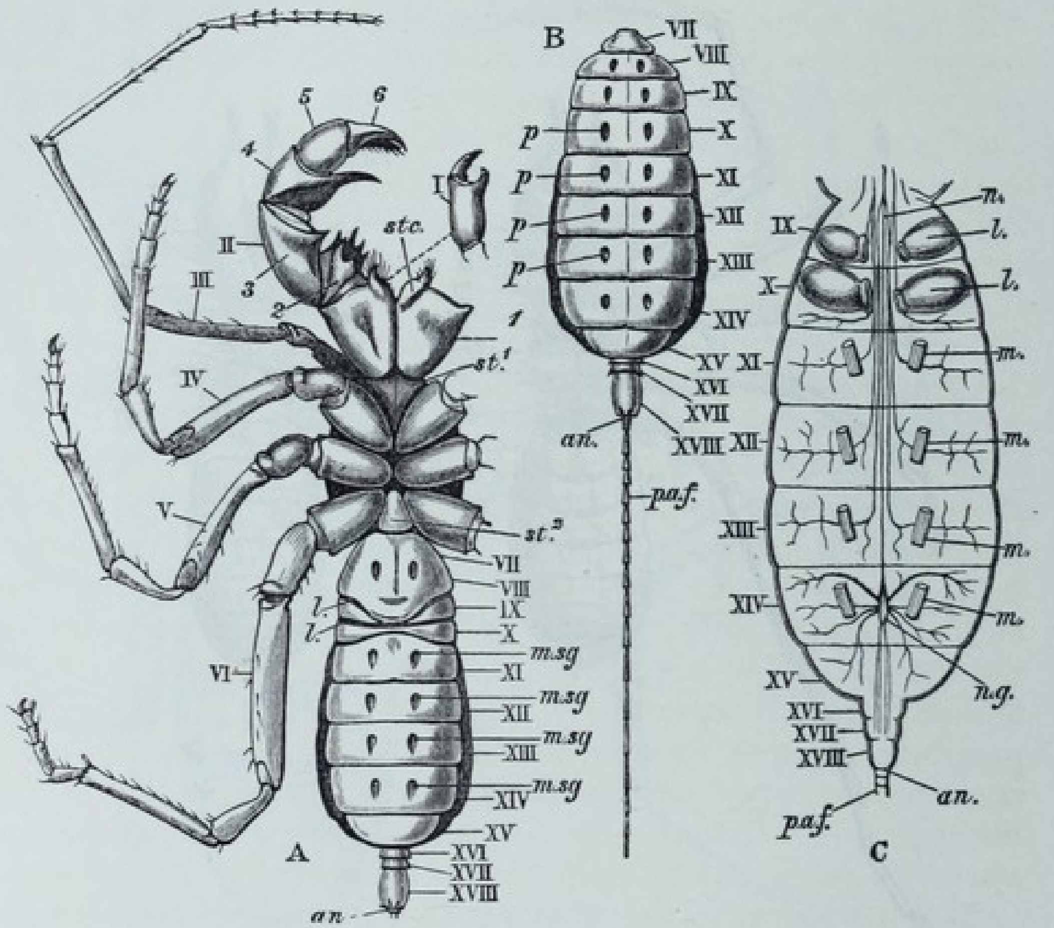

FIG. 12 (A).—Ventral aspect of Thelyphonus (from the object). I to VI. Cephalothoracic appendages; the first, which is concealed by the coxa of the second, is represented as removed from its attachment. *stc.* Sterno-coxal process of the coxa of the left second appendage. *st*^{1}. Thoracic prosternite. *st*^{2}. Thoracic metasternite. VII to XVIII. Segments of the abdomen. *l*, *l*. Apertures of the right lung sacs in the ninth and tenth segments. *msg.* Muscular stigmata on the sternites of the tenth, eleventh, twelfth, thirteenth, and fourteenth segments. *an.* Anus.

FIG. 13 (B).—Dorsal aspect of the abdominal segments of the same. *p.* Muscular pits corresponding to the entapophyses of Limulus. *paf.* The jointed postanal filament.

FIG. 14 (C).—Abdominal segments of the same, with the terga and viscera dissected away (after Blanchard). *n.* Nerve cord. *ng.* Abdominal nerve ganglion. *l*, *l*. Pulmonary sacs in the ninth and tenth segments. *m*, *m*, *m*, *m*. Muscles attached to muscular stigmata of the four following segments. *an.* Anus. *paf.* Postanal filament.

sixth pair of cephalothoracic limbs, we find a pair of closely opposed upstanding sclerites, the chilaria of Owen (*metst* Pl. XXVIII, fig. 4, and woodcut, fig. 4). The late development of these pieces, as determined by Packard, as well as their position, leaves no doubt that they are not to be regarded, as is supposed by some, as rudimentary appendages. They are a paired development of the metathoracic sternal area and may be designated metasternites.

They have no representative in Mygale (fig. 9), but here Scorpio returns to its allegiance and exhibits a well-developed sclerite exactly corresponding to them. The pentagonal sclerite wedged between the coxæ of the last pair of cephalothoracic limbs in Scorpio (woodcut, fig. 8, *met*) clearly enough agrees in position precisely with the chilaria of Limulus (see also woodcut, fig. 5). It is true that the form of the pentagonal metasternite of Scorpio differs from that of the two little tubercles of Limulus, but the exclusion from the functions of the mouth of the former sufficiently accounts for the difference.

In Thelyphonus (woodcut, fig. 12, *st.*^{2}) a triangular metasternite corresponding in position to that of Scorpio is found.

It is exceedingly astonishing that so careful an observer as M. Alphonse Milne-Edwards should have suggested, as he has done, that the "chilaria" of Limulus correspond to the "pectines" of the Scorpion, since the former are in front of and the latter are behind the genital operculum. When the possibility of such homologies is entertained, it is but a natural consequence that the complete series of agreements of segment for segment and appendage for appendage which obtains between Limulus and Scorpio, should be entirely overlooked.

When we pass to the abdominal segments we find a very considerable difference between Limulus and Scorpio in the development of sternites.

The sternal integument of the region at the base of the genital operculum and the gill-bearing appendages, is almost entirely soft and free from sclerites in Limulus. In Scorpio, on the other hand, whilst the sternal region around the genital operculum is soft, a well-developed sternite (woodcut, fig. 8 x) is found supporting the pectiniform appendages; and for each of the five following segments a broad band-like sternal sclerite is developed. The four anterior of these are perforated, each by a pair of slit-like apertures leading into four pairs of recesses, in each of which a lamelligerous appendage is sunk. The fifth is imperforate, and bears no appendage. The segments of the so-called "tail" which follow present a complete chitinisation of the integument, so that the sternites of each segment is confluent with the tergite.

When we examine the sternal area of the segments of Limulus which carry lamelligerous appendages, we find that although the integument is mostly soft and flexible, yet there are small sclerites present, *and, in fact, stigmata or apertures leading into pits corresponding to the stigmata of the pulmonary sacs of Scorpio.*

These parabranchial stigmata of Limulus have hitherto escaped observation.[1] They are found on the posterior face of the median sternal elevation or lobe which unites the two lateral elements or appendages which go to form one of the double lamelligerous organs of that animal (Plate XXVIII, fig. 10 *stg*, and woodcuts, figs. 6 and 7 *stg*). The lips of the stigma are chitinised, and the opening leads into a funnel-like cavity with chitinised walls. The sternal integument further shows one or two small sclerites, the "epistigmatic sclerites" (*epst*), by the side of the stigma. These stigmata occur in the position mentioned, not only at the bases of the appendages of the four segments corresponding to those which carry the pulmonary stigmata in the Scorpion, namely, the ninth, tenth, eleventh, and twelfth, but also at the base of the appendages of the eighth segment, which represent the pectines of the Scorpion, and at the base of the genital operculum. They are connected with the attachment of a series of powerful muscles, the thoraco-branchials, which, taking their origin in the thorax, are inserted into the integument right and left at the base of each of the six pairs of abdominal appendages. The function of these muscles is clearly enough to agitate this series of plate-like organs, either for the purpose of respiration or for that of locomotion, probably for both simultaneously.

The fact that the insertion of a muscle into the integument of Limulus is connected with a "cupping" of the area of attachment is remarkable but not without parallel. The series of dorsal entapophyses have a precisely similar significance, and in other Arachnida, *e.g.* Thelyphonus (fig. 12 *msg* fig. 13 *p*, and fig. 14 *m*), we find an identical arrangement on both ventral and dorsal surface, the stigmata being, however, much shallower than in Limulus.

I am not aware of the occurrence of such "muscular stigmata" in any other Arthropoda than the Arachnida, at any rate, of stigmata comparable to those of Limulus. Usually the tendons of muscles are in Arthropoda formed by solid fibrous extensions of the subepidermic layers of the integument.

The tendons or processes connected with the parabranchial stigmata, and with the dorsal entapophyses of Limulus, are by no means entirely formed by the invaginated epidermis and its chitinous product. The tissue below the epidermis is developed in a very special manner, and forms part of an endoskeleton which in the thoracic region gives rise to a very remarkable internal sternum or entosternite. The struc-

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[1] I communicated an account of their occurrence and probable significance to the Royal Society on May 26th, 1881.

ture of this deep skeletal tissue has been investigated by Gegenbaur, who has shown that it may have the form either of a fibrous or of a more distinctly cartilaginous modification of the connective tissue into which it gradually passes, and from which, on the other hand, is developed in other regions a series of vascular channels constituting the capillaries, veins, and arteries. On the present occasion I do not propose to enter into histological details with regard to Limulus, but I may just mention that whilst the hollow entapophyses are invested on their visceral surface by a richly developed cartilaginous modification of the connective substance, with a well developed capsular arrangement of the intercellular substance, the funnel-like invaginations connected with the parabranchial stigmata are clothed and continued by a fibrous tissue not unlike the tendon of Vertebrata. The same tendon-like tissue also forms the entosternite.

In Plate XXVIII, fig. 11, the internal connection of the pair of parabranchial stigmata of a lamelligerous appendage-pair of Limulus is drawn. The integument has been dissected away from the whole of the anterior face of the appendages and their uniting sternal bridge, so as to show the inner aspect of the integument of the posterior face. The pouch-like character of the invaginations into which the stigmata lead and the attachment of the thoraco-branchial muscle is thus exhibited. In fig. 13, Pl. XXVIII, one of the funnel-like tendons, consisting internally of chitin borne on epidermis, and externally of fibrous tissue, is shown in an isolated condition. It is possible to introduce a probe into the funnel to the depth of an inch, the axial cavity of invagination extending to that distance. The funnel-like pouch of Limulus thus constituted, I consider to be the homologue (that is, the genetic representative or homogen) of the pulmonary sac of Scorpion.

It will now be convenient to give, in a tabular form, a summary of the view which has been set forth in the preceding pages. Having thus exposed what I conceive to be the legitimate conception of the morphological relations of Limulus and Scorpio, I shall endeavour to justify, by a closer examination, the identification (which forms an essential part of it) of the pectines of the Scorpion and its four pairs of book-like organs sunk in recesses of the integument with the five pairs of lamelligerous appendages of Limulus.

(The tabular statement is given on the next page.)

Segments.	LIMULUS.			
	Tergites.		*Sternites.*	*Appendages.*
1	Cephalothoracic carapace with central and peripheral eyes.		Camerostome (small tubercular sclerite) in front of the mouth	Small chelæ.
2			The fused pro- and mesothoracic sternites (a narrow elongate sclerite stretching from the mouth to the chilaria).	Chelæ.
3				Chelæ.
4				Chelæ.
5				Chelæ.
6			The chilaria or paired metastoma, or metathoracic sternites.	Digging legs.
7	Narrow emarginate area at the anterior border of the abdominal carapace. No dorsal pits.	Abdominal carapace.	Soft integument and stigmatic pits (muscular), posterior to base of operculum.	Genital operculum.
8	1st pair of lateral spines. 1st pair of dorsal pits and entapophyses.		Epistigmatic pair of sclerites and stigmatic pits.	1st gill-book pair projecting.
9	2nd pair of lateral spines. 2nd pair of dorsal pits and entapophyses.		Epistigmatic pair of sclerites and stigmatic pits.	2nd gill-book pair projecting.

Segments.	SCORPIO.		
	Appendages.	*Sternites.*	*Tergites.*
1	Cheliceræ.	Camerostome (of Latreille), or upper lip.	Cephalothoracic carapace with central and peripheral eyes.
2	Chelæ.	Obliterated by the mesiad extension of the coxæ of the four walking legs; the two anterior movable, the two posterior fixed. (In Mygale a distinctly marked small prothoracic sternite is followed by a large oval mesothoracic sternite.)	
3	Walking legs.		
4	Walking legs.		
5	Walking legs.		
6	Walking legs.	Pentagonal elongate sclerite or metathoracic sternite.	
7	Genital operculum.	Soft integument.	A separate narrow band-like sclerite.
8	Pectinæ, or pair of comb-like organs; modified gill-book projecting.	Separate small rectangular sclerite.	A separate narrow band-like sclerite.
9	1st gill-book pair sunk in pulmonary sacs.	A separate broad transverse sclerite with stigmata leading to pulmonary sacs.	A separate band-like sclerite.

Segments.	LIMULUS.			
	Tergites.		*Sternites.*	*Appendages.*
10	3rd pair of lateral spines. 3rd pair of dorsal pits and entapophyses.	Abdominal carapace.	Epistigmatic pair of sclerites and stigmatic pits.	3rd gill-book pair projecting.
11	4th pair of lateral spines. 4th pair of dorsal pits and entapophyses.		Epistigmatic pair of sclerites and stigmatic pits.	4th gill-book pair projecting.
12	5th pair of lateral spines. 5th pair of dorsal pits and entapophyses.		Epistigmatic pair of sclerites and stigmatic pits.	5th gill-book pair projecting.
13	6th pair of lateral spines. 6th pair of dorsal pits and entapophyses.		Large and solid sclerite forming the sternum of the "Telson," *i.e.* of the præ-anal region of potential segmentation, which includes a soft invaginate area on which opens the ANUS.	None.
14	Only in the embryo this segment is separate, and has a 7th pair of lateral spines.			None.
15	Only in the embryo this segment is indicated.			None.
16	These three segments are never expressed and are represented by the præanal region of the telson.			None.
17				None.
18				None.
	Post-anal spine.			

Segments.	SCORPIO.		
	Appendages.	*Sternites.*	*Tergites.*
10	2nd gill-book pair sunk in pulmonary sacs.	A separate broad transverse sclerite with stigmata leading to pulmonary sacs.	A separate band-like sclerite.
11	3rd gill-book pair sunk in pulmonary sacs.	A separate broad transverse sclerite with stigmata leading to pulmonary sacs.	A separate band-like sclerite.
12	4th gill-book pair sunk in pulmonary sacs.	A separate broad transverse sclerite with stigmata leading to pulmonary sacs.	A separate band-like sclerite.
13	None.	A separate broad transverse sclerite devoid of stigmata.	A separate broad band-like sclerite.
14	None.	Ventral half of a distinct cylindrical sclerite.	Dorsal half of a distinct cylindrical sclerite.
15	None.	Ventral half of a distinct cylindrical sclerite.	Dorsal half of a distinct cylindrical sclerite.
16	None.	Ventral half of a distinct cylindrical sclerite.	Dorsal half of a distinct cylindrical sclerite.
17	None.	Ventral half of a distinct cylindrical sclerite.	Dorsal half of a distinct cylindrical sclerite.
18	None.	Ventral half of a distinct cylindrical sclerite, in which is placed the ANUS.	Dorsal half of a distinct cylindrical sclerite.
			Post-anal spine or sting (a jointed filament in Thelyphonus).

IV. The common characters of the lamelligerous appendages of Scorpio and Limulus.—When we have once, on the ground of a certain general agreement in structure and of a definite identity in relation to other parts which correspond one to another, started the hypothesis that the lamelligerous appendages of the Scorpion agree each to each in their order with the lamelligerous appendages of the King Crab, two further proceedings are naturally the consequence. We inquire first of all whether there are any less obvious agreements in the structure of the organs compared which may be brought out and made to give their testimony in favour of our hypothesis, and, secondly, we inquire how can we form a plausible conception of the origin of the two sets of structures from one set of organs present in a common ancestor of Limulus and Scorpio? this last inquiry having especial value, in that it may lead us to give due value to structures present either in Scorpio or Limulus which had appeared previously to have no special significance in the matter.

A close comparison[1] of the lamelligerous appendages of Scorpio and Limulus—including under this head the pectines and the pulmonary books of the former, and the branchial books of the latter—reveals the important fact that they agree closely with one another in the mode in which the lamellæ are set upon the supporting axis.

In all, we find an axis springing from the body wall, transverse to which, on its posterior face, are set a series of lamellæ. In order to compare one of these appendages with another, it is necessary that all should be placed in one and the same position. We must be careful not to compare the anterior aspect of one with the posterior aspect of the other. In the woodcuts, figs. 6 and 7, the posterior face of

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[1] The account which I give in the text of the lung-books of Scorpio differs a good deal from that which is current, due to Joh. Müller as long ago as 1828. I have not had specimens sufficiently well preserved to enable me to determine the relation and possible adhesions of the proper wall of the pulmonary sac (the invaginated sternal surface) to the lamellæ, but have freed the appendage from the investing membrane. I hope to be able by the examination of fresh specimens to give on a future occasion a more thorough account of the pulmonary sacs and lamelligerous appendages of the Scorpion.

[Since the preceding remarks were published I have been able to examine a better preserved specimen of Buthus than that which I had previously used, which was, in fact, a good deal macerated. This has led to a confirmation of J. Müller's statements in reference to several important points. I have accordingly added some further remarks on the relation of the respiratory appendages of the Scorpion to those of the common ancestor of Limulus and the Arachnida at the commencement of Part II, to which the reader is requested to refer at once.]

the appendage as it hangs from its sternal attachment has been represented.

There is no difficulty about determining this face for the pectines of the Scorpion or for the branchial appendages of Limulus, but the pulmonary books of the Scorpion require some consideration. Supposing them to have once been external, we must suppose that, with the gradual invagination of their surface of attachment, they have become more and more deflected into the cavity of invagination, moving on their fixed base at first backwards, then upwards, and finally forwards. As we now find them (in a spirit specimen !), on viewing the inner surface of the ventral sclerites by removing the terga and viscera, they can be rotated on their hinge line so that they may be made to lie prone forwards, exposing the stigma or opening of the pulmonary recess posteriorly, as in Pl. XXVIII, fig. 1 *a*, or they may be made to lie prone in the reverse direction, hiding from view the stigma, as shown in Pl. XXVIII, fig. 2 *a*, and in the woodcuts, figs. 6 and 7. The position which corresponds with that of the external appendages the pectines and the branchial organs of Limulus, when viewed from the posterior face, so as to show (in the case of Limulus) the lamellæ, is that in which the lung-book is directed backward so as to hide the stigmatic aperture and is looked at from within the Scorpion's body, that is, by dissecting off the terga, viscera, and muscles.

When the pectines, lung-books, and branchial books are thus placed we find that the lamellæ are not set precisely at right angles upon the axes, but obliquely, so that there is an imbrication of the successive lamellæ. In all three it is the proximal lamella which is uppermost (see Pl. XVIII, fig. 2 and 2 *a l′* and fig. 10 *l′*). *The imbrication is identical in all.*

As to *number* of lamellæ, we find in the pecten of *Buthus Kochii* eighteen (in other scorpions there are more or less); in the lung-books of some scorpions[1] as many as 130, and in the Limulus gill-book as many as 150. These numbers vary slightly, increasing with growth in all probability.

As to *structure* of lamellæ, those of the pecten are more solid and strongly chitinised than those of the other two organs, but are, nevertheless, true lamellæ flattened transversely.

Those of the lung-books are exceedingly delicate plates composed of two closely approximated membranes, between which the blood circulates; they are, in fact, flattened bags.

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[1] I believe the form in which I counted these to be a species of Androctonus.

They carry on their free margins a few chitinous spinules (Pl. XXVIII, fig. 8). The lamellæ of the gill-books of Limulus are similarly delicate flattened bags with a setose free border. I am not able to institute any comparison of the histological structure of the lamellæ of the Scorpion's lung-book with that of the King Crab's gill-book, for although I have been able to work out that of the latter on fresh material, no such opportunity has yet presented itself of investigating the Scorpion.

As to the *shape* of the lamellæ, those of the pecten are narrower and relatively thicker than those of the lung-books or gill-books; the whole eighteen are also more nearly equal to one another in size and shape. In the lung-books the shape differs at the two extremities of the series a little, and in size the proximal laminæ are much larger than the distal. The average shape may be described as that of a broad scythe-blade (Pl. XXVIII, fig. 8) with a narrow base support (*a b*). The lamellæ of the gill-books of Limulus, on the other hand, are approximately semicircular in shape, with a wide base of origin (*a b* in fig. 9, Pl. XXVIII). Moreover an important difference, which is explained by the convergence in place of divergence of the axis of the limb relatively to the mid line of the body, is seen when the lamellæ of the gill-book and of the lung-book are compared, in the fact that in the gill-book the proximal laminæ are the smallest (Pl. XXVIII, fig. 10 *l′*), whilst in the lung-book they are the largest.

Further comparison of the grouping and form of the lamellæ is facilitated by the figures on Pl. XXVIII, where fig. 1 and fig. 1 *a*, fig. 2 and figs. 2 *a* and 10, fig. 3 and figs. 3 *a* and 3 *b*, give representations of the three varieties of lamelligerous appendages in a series of identical positions. Fig. 1 should, for comparison with fig. 1 *a*, be looked at by inverting the plate.

The axes which support the lamellæ in the three varieties of lamelligerous limb differ much from one another, but in a manner directly corresponding with obvious functions.

The pecten has a large free axis firmly chitinised, imperfectly divided into two joints. It is flattened by antero-posterior pressure. The function of the pecten is not actually known, but it appears to be tactile. It is not respiratory, and the Scorpion is of terrestrial habit; hence its comparatively solid character and protective development of chitin.

The gill-book of Limulus is supported on an axis, which is flattened by dorso-ventral pressure, protection being thus afforded to the otherwise naked and very delicate lamellæ. It is not free except at its extremity, where it exhibits a jointing of separate chitinous plates. Its base is very wide, and is attached, not to a flat sternal surface, but to an outstanding sternal lobe, which extends between the bases of fellow-appendages, and gives rise to a teat-like soft process in the median line (Pl. XXVIII, *m d*, fig. 10). The character of this axis is obviously an adaptation to the branchial function of the lamellæ combined with a locomotor function.

The lung-book of Scorpio has no locomotor function, and it is protected by the recess of the sternum, in which it lies. It is not tactile, nor is it exposed to desiccation and rough usage, as are the pectines. It is specialised for respiratory purposes. The axis is exceedingly small and simple, for the greater part of its length adherent to the invaginated sternal wall, leaving, however, a small free distal portion (see Pl. XXVIII, fig. 2 *a*). Its walls are quite free from chitinisation, and of great delicacy. It is little else than a horizontal vascular tube[1] supporting the lamelliform bags into which its cavity leads (Pl. XXVIII, 2 *a*, *b*).

Though the axis is here reduced to its simplest expression, it is not possible to overlook in it the representative of the vertically compressed chitinised axis of the pecten, and of the horizontally compressed chitinised axis of the gill-book.

V. Hypothesis as to the mode of origin of the three varieties of lamelligerous appendages in Scorpio and Limulus.—The view which I have advanced in this memoir as to the practical identity of the gill-books of Limulus and the lung-books of Scorpio implicitly contains the affirmation that either the structures of Limulus have been derived from those of Scorpio, or those of Scorpio from those of Limulus, or that a third (now extinct) form has given rise to both Limulus and Scorpio. Further, it is to be observed that such extinct form might be more like to Limulus than to Scorpio, or *vice versâ*, in respect of any particular element of structure.

To make a long story as short as possible I may say that, without prejudicing the recognition of the (as I think) well-established morphological identities above pointed out, we may best explain their existence by assuming that an aquatic

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[1] Once filled with blood in ancestral forms, but in the Scorpion filled with air instead, which enters by the slit-like stigma. The slit within the stigma does not communicate with the pulmonary sac or "investing" sac, but with the cavity of the appendage itself. See Part II (commencement).

form breathing the dissolved oxygen of the water inhabited by it, by means of book-like gills, was the common ancestor of Limulus and of Scorpio. From the book-like gills of this ancestral form the broad series of Limulus and the narrower lung-books, *as well as the pectines or combs* of the Scorpion, have been derived. The form of the book-like gills of this Arachnidan ancestor was probably something intermediate between the three existent modifications of it, and best conceived of, perhaps, by imagining the teeth of the Scorpion's "pectinate organs" to become soft and flattened and increased in number (see Pl. XXIX, fig. 1).

To obtain from these the Limulus gill we have but to suppose certain definite changes of dimension, the imbrication and character of the lamellæ, and their external position remaining unaltered (Pl. XXIX, figs. 2 *a* and 3 *a*).

To arrive at the book-lungs of the Scorpion, we have to imagine the ventral surface on each side in close proximity to the short appendages carrying the gill-books—to have become deeply cupped or depressed, so that two series of cup-like pits should be formed, a right and a left, a pair being placed in each segment, corresponding to each pair of gill-books. Each cup must have become so large in area and so deep as to embrace within its limits the relatively small adjacent gill-book (XXIX, fig. 2 *b*). Further, when once the gill-book had been involved in this cup-like depression, the walls of the cup must have tended to grow together so as to form a pulmonary chamber with only a narrow slit-like opening to the exterior (Pl. XXIX, fig. 3 *b*), and *pari passu* with this closing in of the cupped area, and the protection of the respiratory lamellæ, the Arachnid must have acquired the power of leaving the water and of breathing the atmospheric oxygen admitted to the damp chamber formed by the cave-like areas of depression.

Whilst framing such a hypothetical account of the way in which the transition from naked "gill-book" to in-sunken "lung-book" could have taken place, one naturally asks—"Is it not somewhat gratuitous to assume that cupped areæ should form conveniently by the side of the gill-books of the aquatic ancestor, so as to be ready to increase in size, and ultimately draw into themselves, as it were, the gill-books?" "Is there," we are led on further to ask, "any known instance in Arachnida of the formation of cupped areæ on the chitinous surface of the body? If so, can we show in what mechanical relation they are formed? And, lastly, can it be demonstrated that such mechanical relation probably existed in connection with the gill-books of the assumed common ancestor of Limulus and Scorpio?" If all these questions can be affirmatively answered, then our hypothesis as to the transition of the aquatic Arachnid to the pulmonate condition acquires great plausibility.

The answer to these questions appears to me to have more than ordinary interest, since the formation of cupped areæ on the chitinous surface of the body and the mechanical relations connected with their formation have, as pointed out a few pages back, come to light as demanded by the hypothesis. They exist in Limulus itself and in Thelyphonus. In Limulus there are two great muscles, a right and a left, inserted into the soft ventral integument near the base of each double gill-plate. These muscles serve (together with others that enter the appendage itself) by their contractions to move the gill-plates in the water and so aid in aquatic respiration. The position of the insertion of each muscular mass is marked by a deep funnel-like depression of the integument. From the external surface this depression appears as a "stigma," which we have already described as the parabranchial stigma. The funnel-like depression has a narrow mouth which is often as much as half an inch in length. Internally the invaginated cuticle stands up as a flexible tendon clothed with fibrous tissue and giving attachment to the muscle already mentioned.

In Limulus we find a pair of these "muscle-stigmata," right and left behind the genital operculum, and a pair (right and left) behind each of the lamelliform fused appendages which carry the gill-books.

We have only to suppose the appendages carrying the gill-books *not* to have fused as yet in the middle line, and the muscular stigmata to have become greatly developed (perhaps by increased development of the muscle aiding in aquatic respiration when the appendage itself grew small and therefore less efficient) and we have at once the gill-book sinking within the area of the stigmatic pit, Pl. XXIX, fig. 2 *b*.

A very important feature in the supposed further development is the correspondence of the atrophy of the muscle (which atrophy is required to fit in with our hypothesis, and to convert the muscle-pit into a pulmonary sac) with the changes in the structures which would necessarily result were the physiological conditions gradually to become such as to favour aërial in place of aquatic respiration. The violent agitation of the gills by the muscle attached to the stigmatic pit would become useless, supposing an exposure of the gill-lamellæ to the atmosphere became by degrees habitual with the ancestral Arachnidan. In proportion as these hypothetical creatures acquired the habit of aërial repiration—the deepening and arching in of the stigmatic pit would be favoured, and the atrophy and final disappearance of the muscle which was attached to its inner surface, and mechanically brought it into existence, would also be directly promoted.

A further confirmation of the view now advanced is found in the remarkable East Indian Arachnid Thelyphonus. This Arachnid has not four pairs of lung-sacs like Scorpio, but only two pairs, corresponding to the two foremost lungs of Scorpio, and to the second and third gill-book-pairs of Limulus (woodcut, figs. 12, 13, 14). Nevertheless, as we have seen in a previous section of this Essay, the *four* segments of the abdomen posterior to these are *each marked by a pair of shallow stigmata placed in line with the orifices of the pulmonarg sacs of the two anterior segments, msg.* When the internal structure corresponding to these parts is examined, it is found that a large muscle (similar to the similarly placed muscle of Limulus) is inserted into each of the four right and four left stigmata in the segments posterior to the pulmonary sacs (woodcut fig. 14, *m.*) The two segments into which the two pairs of pulmonary sacs are sunk, have *no such muscles*. The pulmonary sacs are, therefore, to all appearance, enlarged muscular stigmata, from which their former muscles have disappeared by disuse and atrophy.

VI. **The Entosternite.**—Leaving now the comparison of segments and appendages, which is undoubtedly the most important element in determining our judgment as to the affinity of Limulus with Scorpio, we come to the consideration of a number of other structures, which we shall find some more and some less favorable to the hypothesis of a close relationship between the two animals.

Connected with the exoskeleton and locomotor system is that remarkable development of an endoskeleton in the Arachnida, which Straus Durkheim put forward in the passage cited at the commencement of this article, as one of the leading characteristics of the class and one of the obvious features in which Limulus shows itself to be a true Arachnid.

As already remarked, in speaking of the entapophyses and parabranchial stigmata, Limulus shows a marked tendency to the development of cartilage and fibro-cartilage by the modification of its connective substance at certain points and in certain areas.

The most striking result of this tendency, is the formation of a large fibro-cartilaginous plate which lies in the cephalothoracic region between the alimentary canal above and the nerve collar below, and unconnected by hard parts with any portion of the exoskeleton. It is represented of the natural size as seen from the ventral (sternal) aspect in fig. 7, Pl. XXVIII. It has been previously figured by Van der Hoeven (12), whose figure is not very accurate, and is copied by Owen (7).

This body is the base of origin of a large number of muscles, and may be regarded as an enlargement and interlacing of their respective tendons. In the figure, nothing but the skeletal structure, cleaned of its muscles, is represented.

In Scorpio, a similarly shaped loose skeletal piece is found, which gives attachment to muscles in the same way and has a similar relation to the ventral nerve-mass and artery, by which in Scorpio it is perforated (Pl. XXVIII, figs. 6 and 6 *a*). The corresponding body in Mygale is (Pl. XXVIII, figs. 5, 5 *a*) more closely similar in form to that of Limulus than is that of Scorpio.

In order to make a close comparison of these Entosternites, it will be necessary to determine exactly the insertions of the muscles to which they give origin; and further, to ascertain how far the histological structure of those of Scorpio and Mygale agrees with that of Limulus. The results of this investigation I hope to make the subject of a future publication. In the meantime the close correspondence in general character of the three Entosternites figured on Pl. XXVIII cannot escape notice, and fully justifies the importance which Straus Durkheim attached to them. The two pairs of tendinous outgrowths right and left of the central plate in Limulus correspond with the three pairs seen in Mygale, whilst the deep anterior notch in the latter corresponds with the shallower excavation in Limulus, in which the number 7 is placed in the drawing, and in which in the animal itself the bend of the alimentary canal is placed, the mouth being actually below the central region of the plate, so that the alimentary canal passes first forwards beneath the plate and is then reflected so as to pass backwards whilst resting on the upper surface of the plate.

Whilst of this as of so many other structures of the Arachnida (such as the lung-books, &c.) which have been compared in the present memoir with structures in Limulus, a renewed and critical examination is absolutely needed, yet we have sufficient ground, even in our present incomplete knowledge, for concluding that the agreement as to them presented by the two animals is a very close one.

In no Crustacean is a free entosternite at all similar to the organ under discussion known. The apodemes of the sternal surface of Decapodous Crustacea do not resemble it in form though of a similar function. The nearest approach to it is seen in the rod-like skeletal organ found in the abdomen of Lepidoptera, and described by Leydig ('Bau des Thierischen Körpers,' Atlas, pl. vi, fig. 1). Its shape and position are very different, however, from the entosternites of Limulus and other Arachnida. It agrees with these only so far as that it is a free internal skeletal piece.

In the abdominal region of Limulus small loose fibro-cartilages, similar in nature to the Entosternite, are found, connected with the tendons of muscles. I have isolated four such pieces. They are mentioned by Straus Durkheim.

PART II.

Further remarks on the pulmonary sacs and lung books of Scorpio.—In the comparison of the lung books of Scorpio and the gill books of Limulus, given in a preceding portion of this memoir, and in the attempt to derive the two modifications of lamelligerous appendage from a common ancestral form, I have carried the supposed history only so far as to reach a hypothetical Scorpion-like form in which the lamelligerous appendage is supposed to be filled with blood, the "pulmonary sac," or "investing sac," or "cave of invagination" (the homologue of the funnel-like cavity of the tendon of the thoraco-branchials of Limulus), being still filled with air and communicating persistently with the atmosphere by means of a stigma, which in this case is the original orifice of invagination of the investing sac.

Such *was* probably the condition of an ancestral Scorpion. *In living Scorpions a further development has taken place.* The original stigma has become entirely closed up; the investing sac—that which I have spoken of as pulmonary sac—contains no longer air but blood. A *new* opening (the stigmatic slit) has formed within the area formed by the closure of the *primitive* opening of the cave of invagination in the form of a slit-like fissure in the delicate membranous wall of the axis of the in-sunken pulmonary appendage (see woodcut, fig. 15). By this aperture air now enters where, in Limulus and the

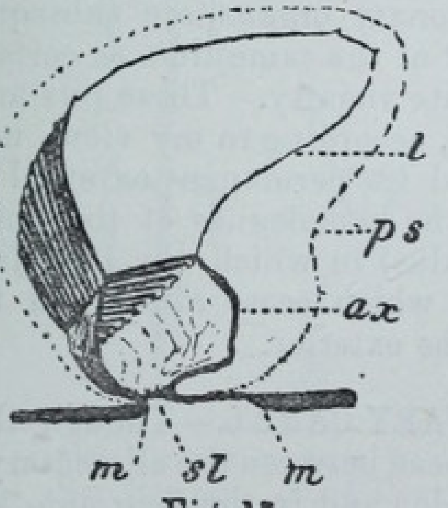

Fig.15

FIG. 15.—Diagram of a Scorpion's lung-book, enclosed in the pulmonary sac and divided by a cut at right angles to the lamelligerous axis. *ax*, axis; *l*, lamella; *ps*, pulmonary sac or cave of invagination; *m*, raised margin of the stigma; *sl*, slit leading from the exterior into the axis of the lamelligerous appendage.

early Scorpion ancestors, there was blood. A blood space has become converted into an air space just as an air space (that of the investing sac) has become converted into a blood space.

That a blood space should have become converted into an air space is not exceptional. All tracheæ in Arthropoda are potential blood-vessels, and their blood-vessels are potential tracheæ. The air-carrying spaces of Arthropoda have been in fact in many cases probably produced by a direct conversion of blood-vessels.

The changed contents of the Scorpion's as compared with the King Crab's respiratory appendage does not affect the morphological significance of its parts nor the importance to be attached to the evidences of its having once projected on a free surface, although now sunk within a sac formed by a recess of the body surface.

The minute embryological history of the Scorpion's lung book is the evidence which we now want in order to actually demonstrate that the *primitive* stigma is the orifice of invagination of the investing sac into which the lamelligerous appendage sinks, and that the opening into the axis of the appendage from the surface is a secondary formation, produced after the primitive stigma had been occluded and completely closed by the adhesion to the lips of that orifice of the axis of the in-sunken lamelligerous appendage.

So much as is already known of the embryological history of the Scorpion's lamelligerous lung sacs is not opposed to the view here advocated. Rudimentary appendages, which in the embryo project from the surface of the segments in which the pulmonary organs are subsequently found, disappear from view at the same time as certain pits are formed in their immediate vicinity. These pits and their orifices of invagination are, according to my view, not the air-containing chamber and its permanent external opening, but the investing sacs (the homologues of the hollow parabranchial tendons of Limulus) in which the lamelligerous appendage is enclosed, and which cease after their formation to communicate with the exterior.

§ *c*. **ALIMENTARY CANAL.**—Though there are very considerable differences between the alimentary canal and its offgrowths in Limulus and in the Scorpion, yet there are some remarkable agreements of a fundamental character. The differences, such as they are, can be viewed as the results of special adaptation. There is the same difficulty with regard to the facts relative to the Scorpion's alimentary system as in regard to all its viscera. I shall rely upon Newport, but I

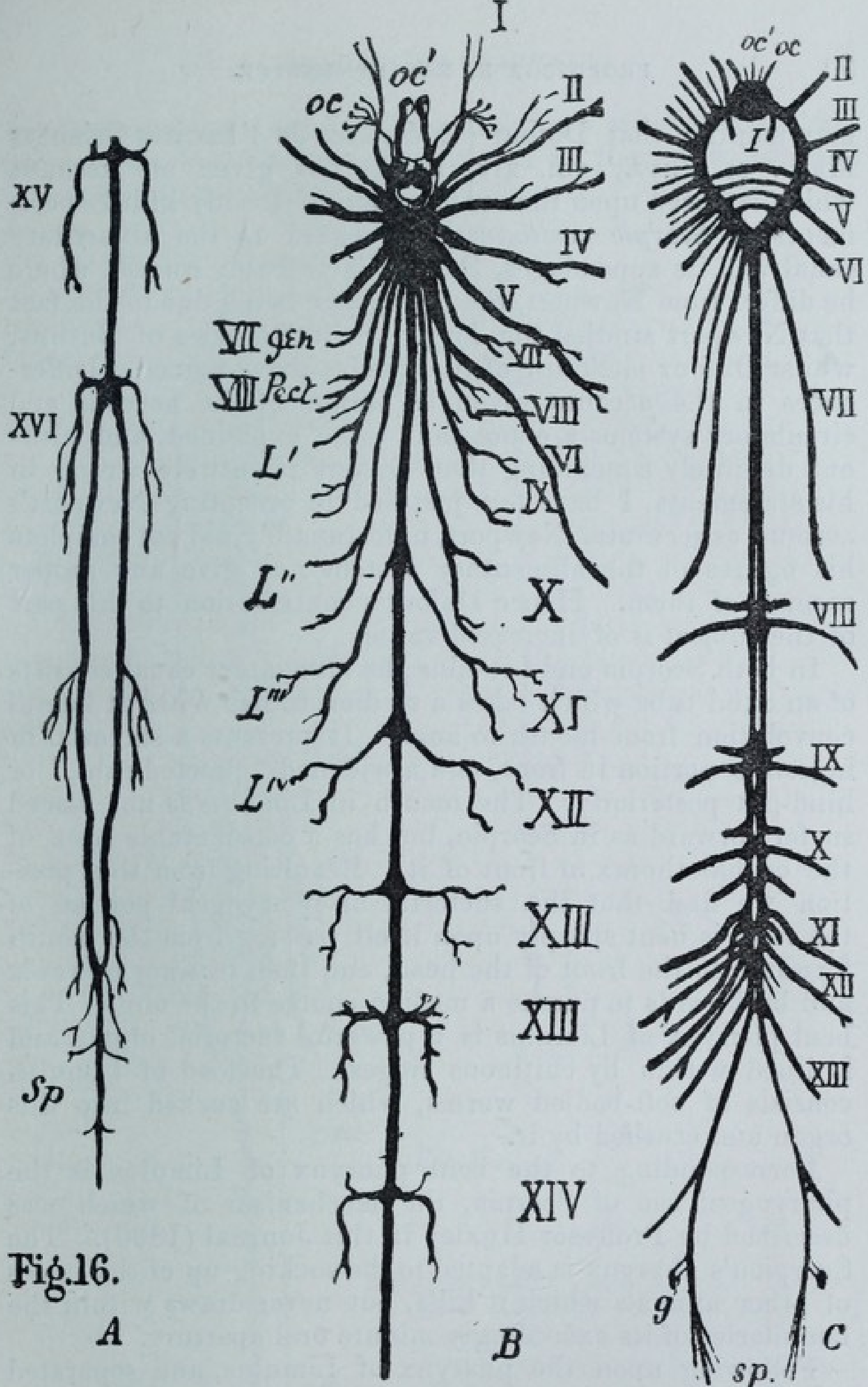

Fig. 16.

Fig. 16.—Diagrams of the nervous system (see page 6); *A B*, of Buthus (Scorpion), after Newport. *C*, of Limulus, constructed from Milne-Edwards. I to VI, nerves to the cephalo-thoracic limbs; VII, nerve to the genital operculum; VIII to XII, nerves to the lamelligerous appendages, of which all arise from the ventral cord in Limulus whilst VIII, IX, and X are, as it were, drawn up to the œsophageal collar in Buthus. *oc*, nerve to the compound or grouped eyes; *oc'*, nerve to the simple eyes; L^{i} to L^{iv}, position of the four respiratory appendages of the left side of the Scorpion; *g*, rectal ganglia of Limulus; *sp*, nerves to the post-anal spine.

may mention that Dufour ('Mémoires de l'Institut Sciences Math. et Phys.,' vol. xiv, 1856,) has given an account which is based upon the examination of freshly killed specimens of *Scorpio occitanus*. In regard to the alimentary canal and its appendages, Dufour is probably correct where he differs from Newport, the divergence being due to the fact that Newport studied the large oriental species of Buthus, whilst Dufour made use of the species above-named. Differences in the account given by Dufour of the nervous and circulatory systems are not thus to be explained, and without definitely concluding that Dufour is entirely wrong in his statements, I have felt justified in accepting Newport's account as accurate. Newport, unfortunately, did not complete his figures of the alimentary system nor give any proper account of them. Hence Dufour's contribution to this part of the subject is of increased value.

In both Scorpio and Limulus the alimentary canal consists of an axial tube which takes a median course without lateral convolution from mouth to anus. It presents a suctorial or ingestive portion in front, and a widened "proctodæum," or hind-gut posteriorly. The mouth in Limulus is not placed so far forward as in Scorpio, but has a considerable area of the cephalothorax in front of it. Resulting from this position we find that the suctorial or pharyngeal portion of the tract is bent sharply upon itself, passing from the mouth forwards to the front of the head, and then turning upwards and backwards to pursue a median course to the anus. This bent pharynx of Limulus is a powerful suctorial organ, and is lined within by chitinous ridges. The food of Limulus consists of soft-bodied worms, which are sucked into this organ and crushed by it.

Corresponding to the bent pharynx of Limulus is the pharyngeal sac of Scorpio, the mechanism of which was described by Professor Huxley in this Journal (1860). The Scorpion's pharynx is adapted to the sucking up of the juices of other animals which it kills, but never draws within the boundaries of its exceedingly minute oral aperture.

Following upon the pharynx of Limulus, and separated from it internally by a valvular arrangement, is the digestive portion of the alimentary tract. It is remarkable for presenting two pairs of tubular outgrowths, which are the stalks of the huge saffron-coloured gland which fills up the space offered by the horseshoe-shaped carapace, and even extends into the region of the abdomen. The digestive section of the alimentary tract runs through the whole series of appendage-bearing segments, and in the telsonic region joins the proctodæum or anal invagination, from which it is very sharply marked off by a groove and by the expansion and plication of the walls of the proctodæum.

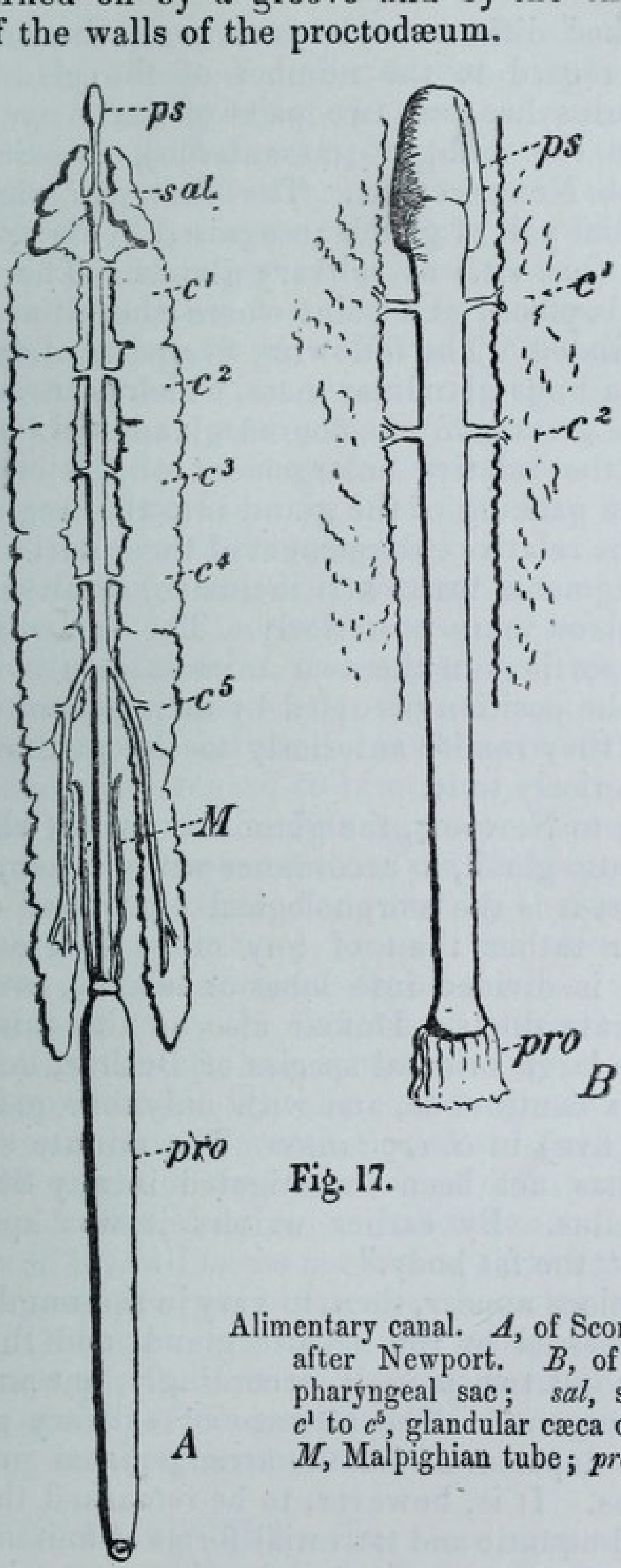

Fig. 17.

Alimentary canal. *A*, of Scorpion (Buthus); after Newport. *B*, of Limulus. *ps*, pharyngeal sac; *sal*, salivary gland; c^1 to c^5, glandular cæca of the mid-gut, *M*, Malpighian tube; *pro*, proctodæum.

The corresponding section of the Scorpion's alimentary tract *also* carries *more than one pair* of glandular cæca, and ends in a voluminous proctodæum, which commences, precisely as in Limulus, in that region of the body which succeeds the thirteenth segment, as indicated by the superficial sclerites.

Very marked differences, however, exist between the two animals in regard to the number of the glandular cæca. Whilst Limulus has but two pairs of ducts opening at an interval into the mid-gut (mesenteron), the Scorpion has (according to Newport) six. The first pair are connected with a peculiar pair of glands recognised by Newport, Dufour and Huxley (loc. cit.) as salivary glands. The opening of these ducts is placed at a point where the alimentary canal is slightly dilated. The following five pairs of ducts are the conduits of a huge glandular mass, which corresponds undeniably to the great saffron-coloured gland of Limulus. But in Limulus the relative enlargement of the cephalothorax results in the packing of the gland into that region, whereas in Scorpio the relative enlargement of the anterior part of the abdomen (segments VII to XIII inclusive) results in the packing of the gland more posteriorly. The same difference of external proportions in the two animals results in a similar contrast in the position occupied by their generative glands; in Limulus they ramify anteriorly to the genital orifice, in Scorpio posteriorly to it.

According to Newport, the glandular mass (which I shall call the hepatic gland, in accordance with custom, and not as implying that it is the morphological equivalent of the vertebrate liver rather than of any other outgrowth of the mesenteron) is divided into lobes or lappets, corresponding to the separate ducts. Dufour also admits this to be the case for the large oriental species of Buthus, but describes the organ as continuous, and with only four pairs of ducts (in place of five) in *S. occitanus*. The minute structure of this gland has not been investigated in any Scorpion nor yet in Limulus. By earlier writers it was spoken of in Scorpion as "the fat body."

The Scorpions appear, then, to vary in the number of pairs of ducts possessed by the hepatic gland, and the fact that Limulus has but two pairs is, accordingly, not an important point of divergence. The absence of salivary glands is a more serious departure from the arrangements prevailing in the Scorpions. It is, however, to be remarked that on comparing allied aquatic and terrestial forms of animals, salivary glands are not unfrequently found to be present in the latter whilst absent from the former.

When we come to compare the proctodæum of the two animals we find, perhaps, the most important difference which can be pointed to as obtaining between

Limulus and Scorpio. The exceeding shortness of the proctodæum of Limulus is only a part of that general reduction of its hinder segments which is paralleled in many other groups of Arthropoda. But in Scorpio there are given off from the anterior border of the proctodæum two delicate tubes. According to Dufour, in *Sc. occitanus* there are four of these tubes, of which one pair is branched. Newport, however, figures only one pair in Buthus. These delicate tubes are the Malpighian glands, found alike in Myriapoda, Hexapoda, and Arachnida, but never in Crustacea. They have been shown in Spiders by Mr. Balfour (20) to develop from the proctodæum, or anal invagination of the epiblast; they have a renal function, and *possibly* represent morphologically 'nephridia,' such as those of Gephyræa and Rotifera.

Their absence from Limulus is a difficulty in the way of associating Limulus and Scorpio, but it is also a difficulty in the way of associating the Crustacea with the other Arthropoda. Leydig has pointed out, in the proctodæum of Copepoda, structural evidence of the existence of a region which may functionally represent the Malpighian tubes of the tracheate Arthropoda, and careful histological study may give similar evidence with regard to Limulus. As to the development of actual cæcal tubes in this region, two views are admissible: either the common ancestor of the Arthropoda possessed these tubes and they have been lost by Crustacea and by Limulus (and some others) among the Arachnida, but retained by the various tracheate classes, *or* the common ancestor possessed only the functional "renal region" of the proctodæum, which has remained undifferentiated in form in Crustacea and in Limulus, but has taken on the form of cæcal tubes in the air-breathing forms, perhaps independently, in the course of the evolution of different groups. If we are to hold that Malpighian tubes can only once have originated, and that all forms possessing them have a common ancestor, we must suppose either that Limulus has lost them or that all Tracheata are descended from the Arachnida. Amongst these possibilities we have no decisive indications. The whole question of the genealogy of the various classes of Arthropoda is involved in the issue.

§ *d.* **VASCULAR SYSTEM.**—The close agreement between the vascular system of Limulus and Scorpio has been ably insisted upon by M. Alphonse Milne-Edwards, who, eight years since, gave the results in his beautiful memoir, already cited, of a series of injections carried out upon perfectly fresh specimens of Limulus. It is not possible to say, in the absence of any adequate investigation of fresh specimens of Scorpio, how far the resemblance may go; but, depending upon the careful dissectious by Newport of spirit specimens (and discarding those of Dufour which are very incomplete), we are able to point to very close agreements.

In Limulus a more complete vascular system has been demonstrated than in any other Arthropod, and Scorpio comes nearest to it in this respect of all members of the group. The arterial channels do not end in wide spaces bounded by the connective (vasifactive) tissue which clothes muscles and viscera, but the connective tissue here, as in other animals in which fine vessels are developed for the passage of the blood, forms in most regions of the body a series of canals, which constitute a capillary system and lead into definitely constituted veins.

It is worthy of remark by the way that canalisation of the connective tissue is the same phenomenon and due to the same processes of growth in all Arthropoda, whether the canals so formed are connected with the atmospheric air by stigmata or are filled by the blood fluid of the primitive cœlomic cavity.

It does not fall within the scope of this memoir to give a detailed account of the vascular system of Limulus; for that the reader is referred to the memoir of M. Milne-Edwards. I shall content myself with drawing attention to the agreement between Scorpio and Limulus in respect of—(1) the existence of capillaries and veins; (2) of the well-developed vessels conveying blood to the limbs and viscera, and more especially in respect of the great spinal artery and its mode of origin; (3) of the intimate association of the arteries and nerves; (4) of the details of the structure of the heart.

The memoir by George Newport, in the 'Philosophical Transactions' for 1843, and that by M. Alphonse Milne-Edwards, in the 'Annales des Sciences Naturelles' of 1873, contain the exposition of the facts in detail relatively respectively to the Scorpion and the King Crab. Of the latter animal, M. Milne-Edwards says: "The venous blood, in place of being distributed in interorganic lacunæ, as in the Crustacea, is in a considerable portion of its course enclosed in special vessels whose walls are perfectly distinct from the adjacent organs; they often take their origin in ramifications of a remarkable delicacy and lead into reservoirs which are for the most part definitely circumscribed. The nutrient liquid passes from these reservoirs into the branchiæ, and after having traversed these respiratory organs, passes by a system of branchio-cardiac canals into a pericardial chamber, and then penetrates the heart. From the heart, the dimensions of which are considerable, it is forced into the tubular arteries with resisting walls, the distribution of which is exceedingly complex, with frequent anastomoses, whilst their terminal ramifications, which are of marvellous tenuity and abundance, can be followed into the substance of the most delicate membranes." These capillaries are figured by M. Milne-Edwards, but we have not of them, any more than of the tissues of Scorpio, a satisfactory histological account. Gegenbaur (2), whose observations were made on spirit specimens, did not observe these finer ramifications of the vessels, but supposed the arteries to lead into intercommunicating lacunæ without definite walls.

As to Scorpio, it may be justly said that it was the main purport of Newport's memoir to make known just such an extended vascular system in the Myriapoda and Arachnida as above indicated for Limulus, though M. Alphonse Milne-Edwards does not cite Newport's work, but unjustly appeals to the second-hand authority of M. Blanchard, for the few facts which he mentions relative to the Scorpion. And further, the general description of the circulation above given as to Limulus is strictly applicable as a summary of Newport's observations upon the course of the blood and distribution of the vessels in the Scorpion.

Newport's description and figures of the heart and its main arteries in Scorpio show a close agreement with these parts in Limulus, as described by Milne-Edwards. A revision of these structures in the Scorpion, in the light of what is now known as to Limulus, would probably show a still closer agreement in some details, especially were injection practised upon freshly killed specimens.

The diagrams here given will enable the reader to judge of the general features of the arterial system in the two animals.

The heart of both Limulus and Scorpion is an elongated organ, constricted so as to form eight successive chambers, which are imperfectly marked in the Limulus, but more obvious in the Scorpion, since in that animal imperfect transverse septa occur within it, less complete, according to Newport, than in other Arthropod hearts. In front of the eight chambers the heart is continued in both animals as a truncus arteriosus towards the head. Posteriorly it is continued as a posterior aorta in Scorpio into the cylindrical tail; but in Limulus, in accordance with the reduction of that region of the body, it ends blindly. The eight chambers of the Scorpion's heart appear to be the exact equivalents of the less strongly marked divisions of the King Crab's heart, *being originally placed in corresponding segments of the body.* At the anterior margin of each division there is a pair of valvular apertures, and there are accordingly eight pairs in each

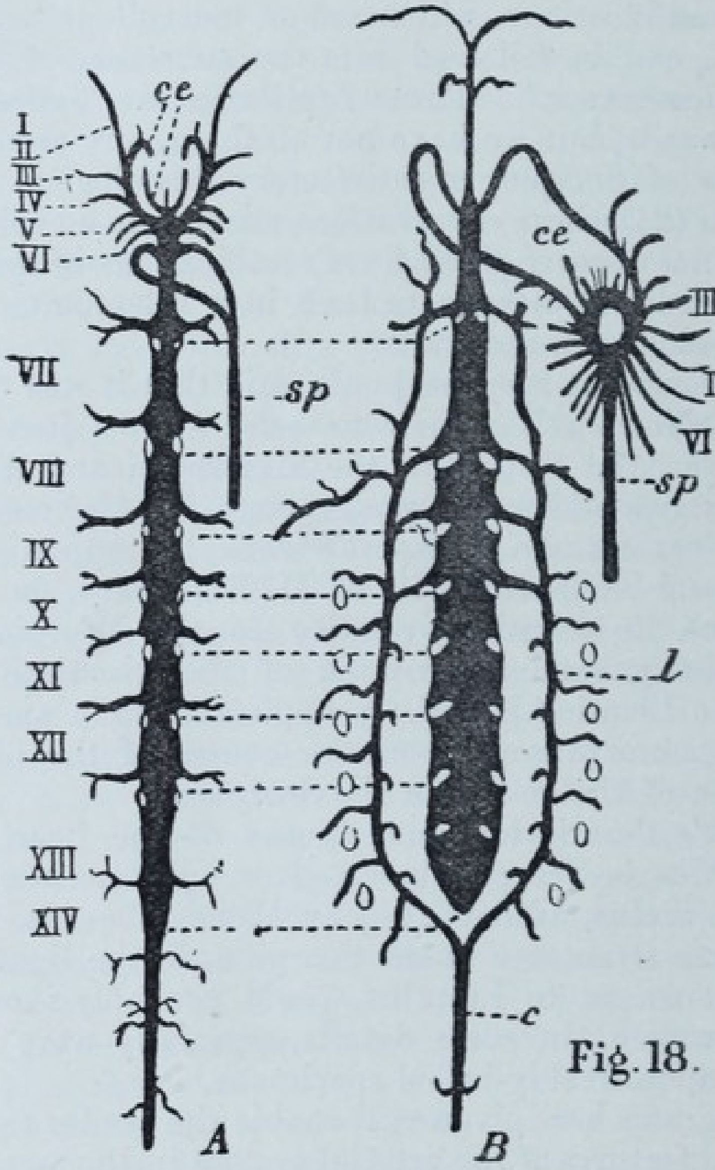

Fig. 18.—Heart and origin of the supra-spinal artery. *A*, of the Scorpion (Buthus), after Newport; *B*, of Limulus, after Milne-Edwards. I to VI, arteries to the six pediform limbs; VII to XIV, the eight chambers of the heart; *sp*, supra-spinal artery; *ce*, cerebral arteries; *c*, caudal artery; *l*, lateral anastomatic artery of Limulus.

heart. At the hinder margin of each division in the Scorpion a pair of lateral arteries is given off (eight pairs in all); such lateral arteries exist only in connection with the first *three* divisions of the King Crab's heart, their place being taken by secondary longitudinal trunks (woodcut, fig. 19, *l*). From the base of the truncus arteriosus, that is, just in front of the most anterior pair of valvular apertures, a pair of lateral arteries is also given off in both hearts.

The eight chambers of the Scorpion's heart are placed in the seven anterior abdominal segments, the first corresponding to the segment which bears the genital operculum, the last two being placed in one segment (thirteenth of the whole series), the broad triangular segment which precedes the first cylindrical caudal segment.

The eight chambers of the King Crab's heart have a similar relation, though not so obvious. The anterior portion of the heart is somewhat drawn forward, so that the segments indicated by the valvular apertures are (like the corresponding nerve ganglion of the genital operculum) a good deal shifted to the front of the appendicular portions of the skeleton to which they are segmentally related.

In place of the five hinder pairs of lateral arteries present in Scorpio, we find in Limulus large lateral arteries (fig. 18 *l*), which take origin by an anastomosis from the three pairs of anterior lateral arteries of the heart, and from the pair of lateral arteries of the base of the truncus arteriosus.

The truncus arteriosus (or anterior portion of the heart, as M. Milne-Edwards prefers to call it) presents a remarkable agreement in the two cases in regard to the distribution and character of the vessels given off from it, although upon the basis of a fundamental agreement very wide differences in detail are to be noted. At the base of the truncus, just in front of the most anterior pair of valvular apertures of the heart, we have the pair of lateral arteries similar to those given off from the heart. Then the trunk is continued forwards (through the cephalothoracic region in Scorpio), and gives off two branches, which form a small vascular collar around the œsophagus in the Scorpion, but a wide pair of arterial commissures in the King Crab, which meet upon the postœsophageal portion of the nerve collar. *In front* of the vascular collar in Scorpio the trunk divides into a median and two lateral stems, and from these, arteries are given to the cephalothoracic appendages, to the brain and to the eyes, as shown in the woodcut. Its main continuation, however, is in the vascular collar, the arches of which form a large vessel which, as the *supra-spinal artery*, takes a course backwards along the upper surface of the ventral nerve-cord (see woodcut, *s p.*). The association of this part of the arterial system with the nerve-cord and its branches is very intimate, so as to have excited special remark on the part of Newport.

A parallel but more intimate association of the corresponding part of the vascular system in Limulus, with its nerve-ganglion collar, cord, and main nerves, was first observed by

Owen ('Lectures,' 1855), but has been fully demonstrated and described in detail by Milne-Edwards. The supra-spinal artery of Scorpio is represented by a complete arterial investment of the nerve-ganglion collar, including the brain, and of the chief nerves, as well as of the ventral nerve-cord arising from it, so that the nerves actually lie *inside* arteries and the brain, nerve-collar and nerve-cord are placed in the interior of a great arterial trunk corresponding to the supra-spinal artery of the Scorpion.

The agreement of these parts in Limulus and the Scorpion has been insisted upon by M. Milne-Edwards at page 19 of his memoir (5).

No Crustacean presents so complete a vascular system as Limulus, nor can we find anywhere but in Scorpio an artery originating by arterial arches embracing the œsophagus and passing through the body in close association with the nerve-cord as a main channel for the distribution of the blood.[1]

The chief difference (by no means a small one) between this part of the arterial system in Limulus and Scorpio is that the arteries to the cephalothoracic limbs and brain are in the former given off from the œsophageal vascular collar, or from its united factors, whilst in Scorpio they originate from a distinct trifurcate anterior continuation of the dorsally placed truncus arteriosus (see woodcut, fig. 19).

§ *e*. **GENERATIVE GLANDS.**—The position of the external openings of the generative organs has already been shown to correspond exactly in Limulus and Scorpio, being placed in both in the segment next following that to which the sixth pair of leg-like appendages are attached, and being covered in by an opercular plate with a bifid margin, the plate being formed by the coalescence of the two appendages proper to this segment.

Limulus and Scorpio agree in having the sexes distinct. They also agree in the general form and character of the ovaries and testes respectively, and in the fact that the ovary and the testis are in fundamental form like to one another.

Though it might be possible to find an ovary or a testis similar in form to those of Limulus and Scorpio among Crustacea (I do not know of one), yet it is an important fact, as part of our cumulative evidence of affinity between the two, that in both these animals the ovaries and the testes present

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[1] This statement requires modification, since Dr. Delage, of Paris, has, whilst this article is in the press, described in a very valuable memoir a periœsophageal vascular collar and a præ-neural spinal artery in the Isopodous crustacea.

the same characteristic form, and that that form is an unusual one. The tubular genital gland is not disposed as a simple central body with two ducts, nor as right and left lobes united by a central isthmus, nor as a single or double bunch of simple or arborescent cæca, but it is distinctly *retiform*. There are two genital ducts, which pass from the two genital pores right and left, and are continued into a widely diffused meshwork. The meshwork may be regarded as a continuation of the two genital ducts which give rise to branches, which anastomose and also join their fellows of the opposite side; it has a tubular structure, and its walls present follicles in which the generative cells are produced. In Scorpio the ovarian follicles are less numerous and more highly developed individually than in Limulus, and also in the former animal the meshwork formed by the gland is more symmetrical and its meshes larger than in the latter, but the reticular arrangement of the genital gland is the same in both.

The main differences in the genital glands of Limulus, as compared with those of Scorpion, are related to two modifying causes: firstly, the greater relative size of the cephalothorax in Limulus; and, secondly, the terrestrial mode of life of Scorpion which replaces the aquatic mode of life of Limulus.

Owing to the first of these causes we find that, whereas in Limulus the retiform generative gland extends *both* in front of and behind the genital pore, that is to say, into the cephalothorax (segments 1 to 6) and into the abdominal segments (segments 7 to 13), in Scorpio we find its meshworks spread entirely in the region posterior to the genital pore, that is, in the wide and thick abdominal segments (7 to 13).

The second cause has brought about a very important difference in the secondary arrangements of the generative system. Limulus does not copulate, but the male discharges the spermatozoa into the water on to the surface of the eggs which have just been laid by the female. Such a method of fertilisation is impossible in any animal of strictly terrestrial habits. Copulation is a necessity in such animals. It is only those terrestrial animals which pass into the water during the breeding season which can dispense with intromission. Accordingly we find the efferent ducts, both in male and female Scorpions, modified to subserve copulation. The ejaculatory apparatus in the male is complicated; the distal portion of each of the efferent ducts is modified so as to form an intrommittent organ, and accessory glands are developed from its sides. The two oviducts in the female are enlarged to form vaginæ. There are thus two penes and two vaginæ in the male and female Scorpion respectively.

In copulation the female appears to lie upon her back and, it has been suggested, with much plausibility, that the pectens (the lamelliferous appendages of the eighth segment) serve as tactile organs, guiding and stimulating the movements which result in the coitus.

The female Scorpion is even further specialised in reference to its genitalia as compared with Limulus. Whilst it retains the reticulate gland and the *two* ducts, each with its external aperture as in Limulus, it develops no special spermatheca or receptacle for the spermatozoa received in copulation, but the semen passes along the tubular oviduct and into its net-like branches. Here the semen fertilises the ova, which are placed in follicles set upon the sides of the mesh-forming ovarian tube. The development of the egg proceeds actually within the follicle and the Scorpion produces her young in the living condition.

Connected with this viviparous character is the specialisation of the egg-bearing follicles carried by the ovarian meshwork. In Limulus more numerous eggs are produced, and there is no specialisation of follicles, but from all parts of the ovarian reticulum egg-cells appear to develop and to become free in the lumen of the tubular structure of which the reticulum consists.

The best account extant of the generative organs of the Scorpions appears to be that of Dufour (loc. cit.), who studied fresh specimens, but his account leaves everything to be done in respect of the histology, and one may even hesitate to feel confidence in his description of large features.

There is, also, no complete account of the generative glands of Limulus. We may hope that the American naturalists, who have abundant Limuli on the sea-shore, will soon give us a precise account of the form of the fully developed ovary and testis, as well as an account of their histology. At present our knowledge is confined to the figure given by Owen of a *portion* only of the ovary, and to his description, which is very definite as far as it goes, and sufficient for the purpose of a general comparison with Scorpio. The testis was immature in a male specimen recently dissected by me, and in an earlier dissection I was unable to clear out this organ fully on account of the special objects which I had in view.

I was, however, able on that occasion to determine an important point of agreement between Limulus and Scorpio, namely, in regard to the character of the spermatozoa. It is a familiar fact that the spermatozoa of the Arthropoda exhibit the greatest diversity of form, and also great want of uniformity, as to the presence or absence of a motile flagelliform tail. In Crustacea generally they are immobile and of very various shapes; but in Cirrhipedia, and possibly some others, they are filamentous, with a motile tail. In chilopod Myriapods they have a vibratile tail. In Chilognaths they are motionless. In hexapod Insects they have a vibratile tail. In some Arachnida (*e.g.* Spiders) they are devoid of such a process. We owe to Kölliker the observation that in the *Scorpio europæus* the spermatozoa are filamentous in form, with a vibratile tail. Accordingly, it is compatible with Arachnidan affinities for the spermatozoa to be either motile or immobile; at the same time, as an element in the cumulative evidence of affinity between the King Crab and Scorpion, which it has been my object in this essay to bring together, the presence of vibratile spermatozoa in Limulus is a fact of value. The spermatozoa of Limulus are, as I observed four years ago (4), provided with a long vibratile tail; they agree, therefore, with those of the Scorpion.

C. The Eurypterina as a Connecting Link between Limulus and Scorpio.

The intimate affinity of the extinct Eurypterina with Limulus is no longer doubted. The researches of Hall, Huxley, and Woodward, have thoroughly established the fact that Pterygotus, Eurypterus, Slimonia, and Stylonurus, are to be regarded as Limuli, in which one pair of leg-like organs (probably the most anterior) has been suppressed, and in which the telsonic region, instead of exhibiting but an imperfect development of segments posterior to the twelfth, and that only in the embryo, gives rise to a series of segments forming a large tail-like region of the body. The result of this development of segments between the anus and the last appendage-bearing segment (the twelfth of Limulus) is that the so-called "macrourous" form of body is produced, and consequently a general similarity in appearance is observed between the Eurypterina and Scorpio.

The two woodcuts (figs. 19 and 20) sufficiently exhibit this general resemblance. In other respects, allowing for the suppression of an anterior pair of appendages in the Eurypterina, we find obvious agreements with Limulus. The actual fifth pair of limbs—theoretically the sixth—present constantly in all the genera that enlarged form and specialisation of their terminal joints which are noticed in the corresponding limbs of the King Crab. The coxæ of these and of the three pairs of limbs in front are brought up to the mouth, and denticulated so as to serve as jaw-organs.

A genital operculum of the same proportions as that of Limulus is present, and traces of appendages (sternal plates), corresponding to the five pairs of branchial plates of that animal, have been detected on the following segments. The cephalothoracic tergum is, in some Eurypterina, horseshoe shaped as in Limulus, though relatively smaller in size, and the eyes appear to have been similar to those of Limulus in character and position, though the compound eyes are close to the margin of the carapace instead of at some distance from it. Though in many Eurypterina the cephalothoracic appendages are simple tactile or ambulatory organs, yet in others we find (as in Pterygotus) the chelate form appearing, as with the majority of these limbs in Limulus.

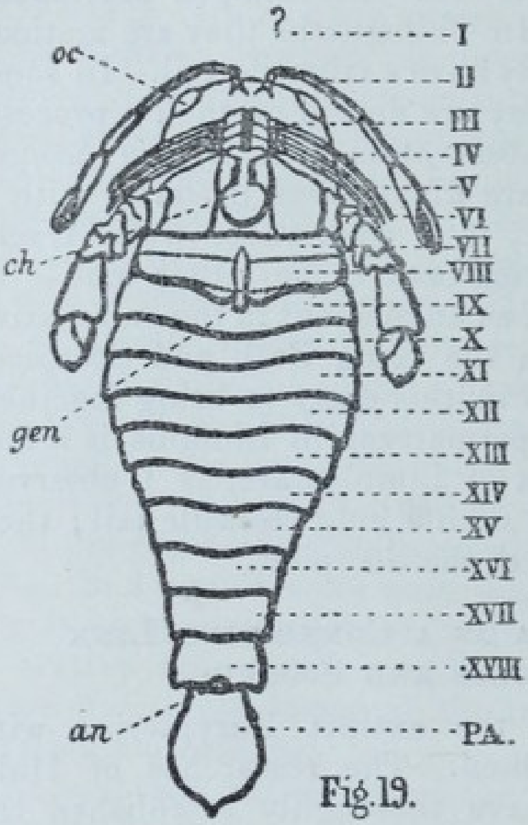

Fig.19.

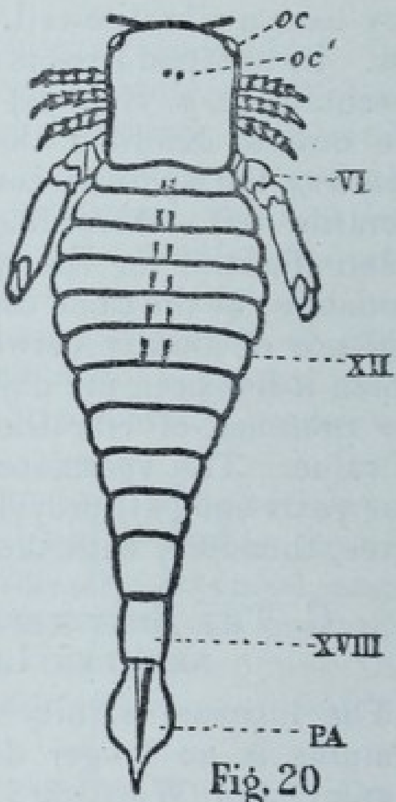

Fig. 20

FIG. 19.—*Pterygotus Anglicus.* The segments are numbered to show their agreement with those of the Scorpion (see Fig. 2). *oc*, compound eye; *ch*, chilarium; *gen*, genital operculum; *an*, anus; PA, post-anal spine or plate.

FIG. 20.—*Slimonia acuminata.* *oc*, compound eye, lateral; *oc'*, simple eye, central; PA, post-anal spine.

I am anxious here to point out that there is not only a general resemblance of the Eurypterine body to that of the Scorpion, but that in many of the most important points in which they differ from those of Limulus the Eurypterine body and appendages agree precisely with those of the Scorpion, and not in a merely general way. The Eurypterina in fact serve in a most important manner to directly confirm the assimilation of segments and appendages in the two animals which I have already insisted upon.

In the first place, it is to be admitted once for all that Limulus and Scorpio agree with one another, and differ from the Eurypterina in possessing six pairs of cephalothoracic appendages. An anterior pair has disappeared in the Eurypterina, and this reduction is the distinctive character of the order. That such a loss of an anterior pair of limbs has occurred is rendered probable by the fact that there is evidence of a tendency for this abortion of anterior appendages to go on further still. The actual anterior pair corresponding to the second pair of Limulus and Scorpio is very small in some Eurypterina (see fig. 20), and suggests the existence of causes tending to the suppression of appendages in the anterior region. Such a suppression of anterior appendages is not without parallel among the Arthropoda (*e.g.* certain Crustacea), and for the Arachnida it has always been regarded as characteristic whenever the attempt has been made to compare the appendages of those forms with those of either the hexapod Insects or of the Crustacea. It is not, therefore, assuming too much when we admit that just as possibly (though I do not at the moment assert the fact) one pair of appendages is suppressed in all Arachnida as compared with other Arthropoda, so a second pair has been suppressed in the Eurypterine order of Arachnida.

Counting the segments of the Eurypterina upon this assumption, we find that they exactly agree with those of the Scorpion. The segments succeeding the cephalothorax and anterior to the anus are twelve in number, gradually towards the anus, though not *suddenly*, diminishing in size after the seventh, as in Scorpio. Posteriorly to the anus is the postanal spine, broad and flat in most Eurypterina for swimming, and neither rod-like, as in Limulus, nor globose, as in Scorpio. Any difficulty which the unsegmented telsonic region of Limulus may have presented in the comparison with Scorpio is removed by the simple inspection of the abdomen of the fossil Limuloid (woodcut, fig. 20).

Secondly, a difference between Scorpio and Limulus of some importance is seen when the form of the cephalothoracic limbs is compared, since in Scorpio certain of those which are chelate, in Limulus are simple ambulatory organs. Here, too, the admittedly Limuloid Eurypterina remove all difficulty; for among them all the cephalothoracic appendages are in some genera non-chelate (fig. 20) and exhibit a considerable range of character, being (as in other Arachnida) either ambulatory or tactile organs. The chelate limbs are thus seen to be a special feature of Limulus, and not essentially characteristic of the Limuloid Arachnida. Accordingly there is no difficulty in deriving the Scorpion's ambulatory limbs from those of such Limuloids.

Thirdly, certain features are presented by the cephalothorax of the Eurypterina, in which they agree very closely with the Scorpions, and in which Limulus differs from them.

A great difference between Limulus and Scorpio, leading to differences in the form and size of internal organs, is that presented by the much greater size of the cephalothorax in Limulus. Among the Eurypterine Limuloids we find, however, genera, in which the cephalothoracic carapace has precisely the quadrangular shape and small relative size, as compared with the abdomen, which is noticed in Scorpion (fig. 20). It cannot be doubted that the packing of the viscera was correspondingly affected, and there is great probability that the liver was connected by more numerous ducts with the intestine in these forms (as in Scorpion) than it is in Limulus. It is also probable in the very highest degree that the generative glands were developed in these Eurypterina posteriorly to the genital pores, and not anteriorly, as in Limulus.

Further, the disposition of the eyes on such a quadrangular carapace as that of Slimonia (fig. 20) is singularly like that seen in the Scorpion. Centrally are two small simple eyes, *oc′*, and precisely in the position which they occupy in Scorpion, viz. at the anterior lateral margin of the carapace, right and left, are groups of eyes, *oc*. In the Eurypterina, as in Limulus, these groups are close set in composition, so as to form what is called a compound eye, whereas in Scorpio the individual members of the group are separate.

The individual factors of the compound eye of Limulus are more archaic in their histological structure than are the simple eyes of spiders, but at present we do not know the minute structure of the grouped eyes of Scorpio. It is possible that they may show closer agreement with the Limulus eye than do those of Spiders; or, again, it is not difficult to suppose that from a loose aggregation of very simple marginal eyes, which existed in the common ancestor of Limulus, Eurypterines, and Scorpio, there has been developed, on the one hand, by coalescence, the compound eye of the former; and on the other hand, by individual elaboration, the separate eyes of the modern Arachnid.

Lastly, in regard to that element of the sternum which in *Buthus* is the pentagonal "thoracic metasternite," and in Limulus forms the "chilaria" or paired metastoma, the Eurypterines serve to tie Limulus more tightly to the Scorpion. The duplicate character of the chilaria of Limulus renders it at first difficult to admit that they are represented by a single median plate in Scorpio. This right-and-left character even led M. Alphonse Milne-Edwards to ignore the position of the genital apertures and to identify the chilaria of Limulus with the pectens of Scorpio. The Eurypterines show clearly enough (even in the absence of embryological evidence) the sternal nature of the King Crab's chilaria, for they possess, just where the chilaria of Limulus are found, a single broad oval plate, which rises up from the surface in such a way as partly to cover in and work as lower lip to the four pairs of coxal jaws in front of it (see woodcut, fig. 19 *ch*). This single metastoma, or chilarium, is readily understood also as the equivalent of the single pentagonal sternite of Scorpio, which is dwindled in size and pushed away in that animal from the functional jaws by the large ankylosed coxæ of the fifth and sixth pairs of cephalothoracic appendages.

D. REVIEW OF OPINIONS OF MODERN AUTHORITIES AS TO THE AFFINITIES OF LIMULUS.

So far in preceding pages my object has been to point out definite points of special resemblance between Limulus and Arachnids, especially the Scorpion. I have not paused to insist upon the absence of any such special agreements between Limulus and the Crustacea. I propose briefly to do this now by examining the statements of those who have asserted that any such special agreements exist.

Clearly between Limulus and any other Arthropod there must exist agreements which are the common characters, more or less, of all Arthropods. It may also be possible to find structural features which are exhibited only by Limulus and by Crustaceans, one feature finding its parallel in one Crustacean and one in another. But I think it must be definitely conceded (1st) that there is no one Arthropod in which anything like so large a number of the structural features found in Limulus are paralleled as the Scorpion, and (2nd) that there are several structural features exhibited by Limulus which have no parallel in the Crustacea at all, but are common to Limulus and the higher Arachnida.

Putting together Limulus and the Eurypterines we may briefly summarise their agreements with Arachnida and disagreements with Crustacea as follows:

1. Limulus and the Eurypterines (the one supplementing the other) agree precisely with the Scorpion in the existence of eighteen segments expressed in the structure of their bodies, and in the distribution of these segments into three groups of six each, viz.: a leg-bearing cephalothoracic region, an anterior abdominal region, in which each segment carries lamellate appendages, and a posterior abdominal region devoid of appendages, ending with the anus and a postanal spine. No Crustacean presents this number and grouping of its constituent somites.

2. Limulus and the Eurypterines agree with the Scorpion precisely in the position of the genital aperture beneath an opercular plate formed by the coalescence of the seventh pair (in Eurypterines the actual sixth pair of appendages). No Crustacean has the generative orifice so far forward, and in none is there a genital operculum of the kind having such relations of position to the genital apertures.

3. They agree with the Scorpion in the character and position of the mouth and upper lip.

4. They agree with the Scorpion in possessing a metathoracic sternite, in the possession of a fibro-cartilaginous entosternite, and in the precise form and relations of that organ. No Crustacean possesses an entosternite or any structure resembling it.

5. They agree with the Scorpion in the disposition of central (single) and lateral (grouped) eyes on the cephalothorax. No Crustacean has an identical arrangement of single and grouped eyes.

6. Limulus agrees with the Scorpion in the form of the alimentary canal and its lateral outgrowths (liver), which are more than one pair. In Crustacea it is very exceptional to find more than one pair of such diverticula, though a single pair may carry numerous secondary branches.

7. It agrees with the Scorpion in possessing a supra- or circum-medullary (spinal) artery, which arises from the dorsal aorta by two arches embracing the œsophagus. No Crustacean has such a supra-spinal artery so originating.[1]

8. It agrees with the Scorpion in the form of the generative glands. No Crustacean has its generative glands in the form of an anastomosing network.

9. It agrees with Scorpio in possessing vibratile spermatozoa. No Crustacea except Cirrhipedia are known to have vibratile spermatozoa.

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[1] But see note on p. 58.

10. It agrees with Scorpio and Spiders in having a brain which (like that of the embryo Scorpion and Spider) supplies only eyes and integument with nerves, and not any appendage. In all Crustacea, except some Phyllopoda, such an archicerebrum does not exist; but even in young stages the brain is found to supply at least one pair of appendages as well as the eyes.

11. It agrees with Scorpio in the concentration of the origins of nerves supplying the anterior part of the abdomen, in the cephalothorax in the form of a nervous collar, perforated by the pharynx. Such a nerve-collar has its parallel in Crustacea among the brachyurous Decapoda, which, however, are in other respects the Crustaceans which least resemble Limulus.

The points in which Limulus agrees with the Crustacea and differs from Arachnida are three only. They are as follows:

1. Limulus agrees with many Crustacea, and differs from Arachnida, in that its respiratory organs are adapted to an aquatic in place of an aërial medium.

2. Limulus agrees with Crustacea, and differs from Arachnida, in that it possesses a pair of groups of eyes, in which the association of the individual eyes of each group is so close as to constitute a compound eye.

3. Limulus agrees with Crustacea (excepting some Isopoda?), and differs from Arachnida, in *not* possessing glandular cæca (the Malpighian tubules) growing out from the proctodæum.

The first of these agreements is purely one of functional adaptation. The lamelligerous organs of Scorpio and the Spiders act upon atmospheric oxygen, as might be expected in animals living on dry land. The fact that the corresponding organs of Limulus respire the oxygen dissolved in sea water, as do the gills of Crustacea, does not even remotely tend to establish a morphological agreement between Limulus and Crustaceans. All attempts to associate organisms in one genealogical group on account of an agreement in the ultimate mode of performing such functions as respiration and locomotion, without reference to the exact nature of the organs by which those functions are performed, are liable to serious error. We cannot, as a principle, associate in genealogical classification all animals that breathe air, or all animals that breathe water, or all animals that fly, or all animals that swim, or all animals that walk. On the contrary, we must hold the actual structure and anatomical relations of organs to be the only guide to the genetic affinities of the animals which possess them, quite irrespective of the special adaptations of those organs to an aquatic or aërial mode of life.

The second agreement, viz. that as to the existence of compound eyes, is more apparent than real; for it is quite obvious that a coming together of simple eyes might at any stage in the evolution of Arthropods produce a compound eye, whilst further in the actual details of structure of its compound eye, Limulus is altogether unlike the Crustacea. The resemblance of the compound eyes in the two cases is a superficial one, due to homoplasy.[1]

The third agreement is of a purely negative character. Limulus and the Crustacea may have independently lost the Malpighian tubules which were perhaps possessed by the earliest ancestral Arthropods; or, on the other hand, these organs may have developed for the first time in the terrestrial Arachnida, and have been derived from them by the other Arthropoda which possess them (Hexapoda, Myriapoda); or, again, the latter may have also developed such organs *de novo*. In any case their absence from Limulus is no evidence of affinity to Crustacea. It is to be noted that the smaller terrestrial Arachnida are also devoid of these organs.

It will now be convenient briefly to point out and criticise some of the views which have recently been expressed as to the affinities of Limulus.

Dohrn (1), in 1871, whilst pointing out at some length the affinities of Limulus and the Eurypterina, originally suggested by MacCoy and placed on a firm basis by Hall, and also whilst demonstrating some of the relationships of the larvæ of Limulus to Trilobites, proposes to unite these forms in one group—Gigantostraka (a name originally proposed by Haeckel for the Eurypterina alone), and to place this group near the Crustacea, not absolutely within that class.

Although Dohrn cites the views of Straus Durkheim, he does not support them, and definitely states that we are not in a position to say what may be the relationships of Gigantostraka to Arachnida.

Dohrn holds that the first pair of appendages of Limulus, though not the second, is innervated from the cerebral ganglion, but he is free from the erroneous conception of the post-anal spine of Limulus as representing a series of segments. At the same time he failed to be struck with the exact identity in the number and disposition of the segments which is revealed when Limulus and the Eurypterina taken

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[1] See 'Annals and Mag. of Nat. Hist.,' July, 1870, on the use of the term "Homology."

together, on the one hand, are compared with Scorpio, on the other.

Claus (14), as late as 1881, adopts exactly Dohrn's view of the systematic position of Limulus. He accepts the group Gigantostraka (including Merostomata and Xiphosura), and places it as a division of the class Crustacea, in opposition to the Eucrustacea, consisting of the great subclasses Entomostraca and Malacostraca. Of the relationships of the Gigantostraka to Arachnida, Claus says nothing.

Owen (7), in his monograph on the King Crab, discusses Dohrn's views and brings to the question a large mass of anatomical and palæontological fact. His conclusion that Limulus exemplifies "that lower condition of the Crustacea which has been expressed by the term Entomostraca," is vitiated by the fact that although one of the first to recognise that the "chilaria" are sternal elements and not appendages, he yet seeks for the representatives of missing body segments in the postanal spine, and, above all, it is falsified by his adhesion to the opinion of Van der Hoeven, that two pairs of appendages are innervated from the cerebral ganglion. That no appendages are so innervated is now demonstrated by the dissections of A. Milne-Edwards which I have confirmed Accordingly, Professor Owen would now probably be amongst the first to admit the affinities of Limulus with the Arachnida, since he observes: "If it were a fact that in Limulus only the foremost pair of limbs was innervated from the superœsophageal ganglion, the rest deriving their nerves from the abdominal ganglionic chain, the advocate for its elimination from the Crustaceous class would have an argument of weight for the affinity of Limulus and its extinct allies with the Scorpion and the Spider."

Huxley (16), who has at various times approached the question of the affinities of Limulus, holds that it has relationships, on the one hand, through the Eurypterina to the Copepod Crustaceans, and on the other hand, to the Phyllopoda through the Trilobites, and again independently to the Scorpion. At the same time he definitely places it in the class Crustacea in the order Merostomata, together with Eurypterina and the Trilobites. Presumably this implies that Limulus is a nearly related representative of an ancestral form which gave rise to the Copepods as one branch, to the Trilobites and Phyllopoda as another, and to the Arachnida as a third.

Without discussing for the moment the possibility of any close connection between the Phyllopoda and Trilobites, I may remark that the connection of Limulus and the Eurypterina with the Copepoda appears to me to have only the support of a certain resemblance of general form in its favour, such resemblance of general form being one which frequently recurs in the Arthropod series, and has the significance merely of a homoplastic agreement, *i.e.* is a like moulding of readily modifiable parts brought about quite independently in the cases compared by the operation of like adaptive causes. Other examples in relation to the Eurypterina have been previously cited by Professor Huxley ('Lectures on Nat. Hist.,' 1857), *e.g.* the Cumacea and the Zoea of some Decapods. I cannot find, on comparing a Copepod, on the one hand, with the full organisation, on the other, expressed by a combination of the characters of Limulus and the Eurypterina, any points which appear to me indicative of close affinity; the agreements are such as either are common to the majority of Arthropods or are agreements of general form, of a nature similar to those which exist between the macrurous Arachnida and the macrurous Decapod Crustacea. Such agreements as exact coincidence in the position of the genital apertures, in the number, form, and grouping of the appendages, in the disposition of the eyes, in the development of sternal plates, and over and above the individual agreements such intimate connection as is implied by the multiplied significance of the combined occurrence of two, three, or more of these agreements, cannot be established as between the Copepoda and Limulus.

Between Eurypterina and such Copepoda as Cyclops, there is a general resemblance of the form of body. We find a broad carapace covering segments bearing five pairs of limbs, followed by a tapering series of segments, of which the anterior carry limbs, and may be distinguished as a separate region from those which follow. But whilst the Copepod body terminates in a characteristic furcal postanal process, the Eurypterina present, like the Scorpion and King Crab, a single spine or plate. The number of segments succeeding the carapace in the Copepoda is at most ten; in the Eurypterina it is, as in the Scorpion, twelve. Most significant is the position of the genital apertures, which in Limulus (and presumably in the Eurypterina) are placed on the first segment succeeding the six-segmented carapace, whilst in the Copepods the whole series of five segments, bearing swimming feet (which would be compared to the lamelligerous feet of Limulus), intervene between the carapace and the genital segment. In structure and position the eyes on the carapace of Copepods have no resemblance to the central and lateral eyes of Limulus, the Eurypterina, and the Scorpions.

When we examine the appendages, one striking resemblance is seen between the males of some free-living Copepods, on the one hand, and Limulus and Pterygotus, on the other. The first pair of appendages is in these forms prehensile. No other Arthropods except Arachnida have such a form of the first appendage. But many Eurypterina have non-chelate anterior appendages (see fig. 20), and the comparison of appendages in various Crustacea shows clearly that such a modification is readily acquired and readily suppressed. In one other respect some appendages of some Copepoda appear to resemble those of Limulus, viz. in the union of the basal portions of the swimming feet. In Limulus, however, this union is effected rather by the upgrowth of a median sternal process than by the coalescence of the bases of the appendages themselves.

In other respects the appendages of Copepoda are quite unlike those of Limulus and the Eurypterina in form, and they do not agree with them in number. Those near the mouth have jaw-like coxæ, as in all Crustacea, but they, have the usual Crustacean elements of endopodite, exopodite and epipodite more or less clearly developed, and are not simple rami, as are those of the Eurypterina. What may have been precisely the character of the limbs on the segments following the carapace in Eurypterina we do not know, but there is reason to suppose them to have been lamelligerous, and that is their distinguishing feature in Limulus. No such lamelligerous appendages are known in Copepoda, but in the region which might be compared to that carrying the genital operculum and the five lamelligerous appendages of Limulus —were it not for the fatal difference indicated by the reversed position of the generative orifices—we find four or five pairs of simple biramose swimming feet.

In internal organisation there is nothing in the characters of the nervous, digestive, reproductive, or circulatory organs (such as are present) of the Copepoda to suggest an alliance with Limulus, whilst the presence in the former of the characteristic Entomostracous shell-gland marks a special divergence between them. It is true that Packard has assimilated a brick-red coloured structure occurring at the base of the cephalothoracic limbs of Limulus to a shell-gland, or to a renal organ. In this I cannot agree with him. It is not even apparent, at present, that this brick-red organ, which I have examined, is of a glandular nature at all.

In his 'Manual of the Anatomy of Invertebrate Animals' Professor Huxley has recognised the possibility of the relationship of Limulus to Scorpio as well as to Copepoda, and has also instituted a comparison between the appendages of Limulus and those of the Podophthalmous Crustacea.

He considers only one pair of appendages of Limulus to be innervated from the cerebral ganglion, and regards the chilaria as the seventh pair of appendages, whilst he associates the genital operculum (his eighth pair of appendages) with the cephalothoracic carapace instead of with the abdominal carapace. In these respects recent investigations have necessitated a change of view (as I have explained at some length above), and accordingly the comparisons based upon the earlier view of the facts are erroneous. Thus, Huxley identifies the first pair of appendages of Limulus with the antennules of Astacus, and regards it as absent in Scorpio. The second pair he identifies with the antennæ of Astacus and with the cheliceræ of Scorpio, the third pair with the mandibles of Astacus and with the great chelæ of Scorpio, the fourth and fifth with the two pairs of maxillæ of Astacus and with the two first walking legs of Scorpio, the sixth (the digging leg) of Limulus with the first maxillipede of Astacus and the third walking leg of Scorpio. The chilaria or metathoracic sternites, which are considered by Huxley as the seventh pair of appendages, he identifies with the second maxillipedes of Astacus and with the fourth walking leg of the Scorpion, whilst the genital operculum is identified with the third pair of maxillipedes of Astacus and with the genital operculum of Scorpio.

The comparison of Limulus with the Podophthalmous Crustacean appears to me one which, in reality, it is not possible to carry out so as to establish any identities, or plausible points of contact. Even when we reckon the "chilaria" as appendages we find divergence and difference as the result of the comparison; but when these are removed from the series there is an absolute want of any relation in the grouping of the appendages compared. Not so with the Scorpion. Professor Huxley, in consequence of his view as to the nature of the chilaria, is obliged to assume that the cheliceræ of the King Crab are something over and above what is present in the Scorpion, and thus, eventually, in counting down the segments, he brings the genital operculum of the one into coincidence with that of the other. But when the chilaria are removed from the series offered by Limulus there is no need to assume an existence of extra appendages in front in that animal; the whole series in the two animals compared, viz. Limulus and Scorpio, are found, on inspection, to be identical in general form and relation from one end of the body to the other.

It is not possible, it should be observed, to maintain both positions. If the identification with the parts of the Scorpion is maintained, then all assimilation of the appendages and regions of the body of Limulus to those of a Podophthalmous or of a Copepodous Crustacean must be abandoned. There is no contact whatever between Limulus and Astacus until a common ancestral form is reached which exhibited in the most generalised condition the segmentation and appendages which are the common inheritance of all Arthropoda.

It appears to me quite impossible to assume that this ancestral form had the characters of the Podophthalmous Crustacea. Such differentiation and numerical grouping of appendages as are seen in that highly developed Crustacean order are of late appearance, and accordingly such forms as Astacus and Homarus should not be made use of as standards of comparison representative of the Crustacea, but less differentiated examples must be sought. On the other hand, when we find it possible to establish a series of agreements between a form of doubtful affinities, such as Limulus, and a highly differentiated Arthropod, such as the Scorpion, the closeness of the genealogical connection thereby proved is greater in proportion as the differentiation of the forms compared is high, and as the number of points of agreement are numerous.

The two authors who have had the facts in reference to Limulus and Scorpio most fully before them (since some of the more important were established by their own researches), and yet have not drawn the conclusion from those facts to which it seems to me that they necessarily lead, are MM. Alphonse Edwards and Dr. A. S. Packard. M. Alphonse Milne-Edwards, although he showed that the cerebral ganglion of Limulus was unlike that of the Crustacea, could not admit of its assimilation to that of the Scorpion, not being acquainted, apparently, with Metschnikoff's observations on the development of the latter animal; and although he recognises the similarity of the perineural arterial system of Limulus to the supraneural or "spinal" arterial system of Scorpio, yet he is led away from the assimilation of the two animals by holding to the strange notion that the chilaria of the King Crab placed *just in front* of its genital operculum are the homological equivalents of the pectiniform appendages of the Scorpion placed *just behind* its genital operculum. M. Milne-Edwards places the

Limuli neither with the Arachnida nor with the Crustacea, but in a group apart. The fact that this investigator did not attempt a complete study of the skeleton of Limulus, and a comparison of that and other organs with the corresponding parts of the Arachnida, Eurypterina, and Crustacea, sufficiently explains the conclusion at which he arrived. He confessedly made use of but few data, and those such as he himself brought to light in the case of Limulus. The value of his contributions to our knowledge of the anatomical structure of the King Crab are not in any way diminished by the vulnerability of the conclusion which he based upon them.

With regard to the conclusions of Dr. A. S. Packard, it is difficult to avoid an expression of surprise. We owe to Dr. Packard the important observation of the late appearance of the chilaria, and other observations as to the segmentation of the telsonic region in the young Limulus, and the primitive connection of the genital operculum with the so-called abdomen rather than with the cephalothorax. He has probably seen more of young and old King Crabs than any other naturalist, and yet, writing in 1880 (No. 9), with all the literature before him, with all the facts under his hands, he still maintains that the Limuli are Crustacea, examines the aphoristic statements of Van Beneden to the effect that they are Arachnida and rejects them. Dr. Packard simply adopts from Dohrn the group of Gigantostraca as Claus has done, and as Gegenbaur has done; but whilst Gegenbaur uses for it the old term Pœcilopoda, Packard thinks it necessary to bestow upon it the new name Palæocarida.

An examination of Dr. Packard's latest memoir on Limulus will, I think, show that he clings to the notion that Limulus is a Crustacean, and is unable to perceive that its true place is among Arachnida, because he entertains certain erroneous preconceptions as to the value of the various parts of an arthropod body as indicative of genetic affinity. A respiratory appendage, however, unlike in structure to anything seen in Crustacea, is, if it acts as a branchia, to be considered as "of the Crustacean type" according to Dr. Packard. This is a simple confusion in logic. It is true that many Crustacea have branchial appendages, but it does not follow as a consequence that all branchial appendages are borne by Crustaceans, or that such appendages are of "the Crustacean type." So too Dr. Packard speaks of "true antennæ" and a "true mandible," "a thorax," and "an abdomen," as though these were recognised and definable elements of arthropod structure, instead of being as they are descriptive terms devoid of homological significance. Really what Dr. Packard has to deal with is a series of segments and a series of appendages, and he can only compare those of one animal with those of another by taking them in numerical sequence. When an author allows himself to set up such intangible criteria as are involved in Dr. Packard's distinction between "true" and "false" antennæ, he clearly opens the way to any conclusion he may fancy, and may colour a picture as he may choose by the use of these epithets.

Dr. Packard's estimate of the significance and import of parts in the attempt to determine the affinities one with another of various Arthropods, is, it seems to me, fallacious, owing to the fact that it is based upon an old-fashioned morphology. Though he makes use of the phraseology of the doctrine of evolution, and constructs genealogical trees, he has "the doctrine of types" at heart, and meets a matter of fact question in morphology by the use of such phrases as the "crustacean type," the "tracheate type," and the "hexapodous type." With such phrases no critic can possibly deal, for no one can say what Dr. Packard means by these "types." We are told by him that the Arachnida have their mandibles and maxillæ "on hexapodous type," whilst the Merostomata (Limulus) have "only their morphological equivalents (Guathopods)." This is meant to appear as though a wide divergence between the Scorpion and King Crab were being in so many words established, and to Dr. Packard so it may really appear. To me it seems that in the statement quoted, phrases of doubtful meaning are being used in such a way as to vaguely assert the opposite of one of the most obvious facts, namely, that the first and second pairs of appendages of a King Crab are far more like the first and second pairs of appendages of a Scorpion than those of either are like the mandibles and the maxillæ of hexapod insects.

Dr. Packard summarises his views as to Limulus and the Crustacea thus: "The facts that seem to us to point to the Crustacean nature of Limulus and its allies are: (1) the nature of the branchiæ, those of Limulus being developed in numerous plates overlapping each other on the second abdominal limbs; those of the Eurypterida being, according to H. Woodward, attached side by side, like the teeth of a rake; while the mode of respiration is truly Crustacean; (2) the resemblance of the cephalothorax of Limulus to that of Apus; (3) the general resemblance of the gnathopods to the feet of the Nauplius or larva of Cirripedia and Copepoda; (4) the digestive tract is homologous throughout with that of Crustacea, particularly the Decapoda, there being no urinary tubes, as in Tracheata; (5) the heart is on the Crustacean type as much as on the Tracheate type, and the internal reproductive organs (ovaries and testes) open externally, at the base of and in the limbs, much as in Crustacea."

To this series of statements I would reply categorically—(1) the "nature of the branchiæ" is *not* such as is found in any Crustacean, but is only paralleled in the lamelligerous appendages of Arachnida. Other animals have branchiæ besides Crustacea. The mode of respiration is neither truly nor falsely Crustacean, but is simply 'branchial.'

(2) The cephalothorax of Limulus does *not* resemble that of Apus, but differs from it as much as it does from any Arthropodous cephalothorax, as, for example, in the overlapping of posterior segments by the free posterior margin of the carapace of Apus; in the excavation of the carapace in Apus by the shell-glands; in the widely different position of the first and second pair of appendages in relation to the cephalothoracic margin; in the total difference of the eyes; and, above all, in the totally different form, number, and arrangement of the gnathites.

(3) The gnathopods have *no* "general resemblance to the feet of the Nauplius" which calls for remark. They have a *general* resemblance to the feet of any Arthropod, but *less* to the feet of the Nauplius than to many other varieties of Arthropod feet, owing to the fact that the former are biramose, non-chelate, natatory, and feebly chitinized, which those of Limulus are not.

(4) The digestive tract is homologous throughout, not only with that of Crustacea, but with that of all other Arthropods. How Dr. Packard can suppose that it is homologous, particularly with that of Decapoda, I am unable to comprehend, unless he proposed to himself, when writing this passage, to associate Limulus genealogically in a special branch with the Decapoda. Unless this is the case Dr. Packard makes use of the word 'homologous' with a meaning which is unusual and unknown to me.

(5) That "the heart is on the Crustacean type as much as on the Tracheate type" I will not dispute, for I do not feel sure that I know what Dr. Packard means, and he appears to take up a neutral attitude, in regard to the heart at any rate. I will, however, remark that, putting types aside, there is no heart of a Crustacean which so closely resembles the King Crab's as does that of the Arachnid

Scorpion, and there is no heart which so closely resembles the Scorpion's as does that of the King Crab.

That the internal reproductive organs should open externally in the neighbourhood of limbs is certainly not a peculiarity of Crustacea. The relation of the openings to limbs is *not* 'much as in Crustacea,' but quite unlike anything seen in Crustacea. In no Crustacean does a pair of limbs in front of the genital apertures unite to form with a median lobe carrying those apertures—a broad plate, as in the King Crab. A genital operculum of this nature is found only in the King Crab, the Eurypterina, and the Scorpion.

The extreme anterior position of the generative apertures has no parallel among Crustacea nor among Arthropods, excepting the Arachnida, where it is identical in position. Even the chilognathous Myriapods do not exhibit so forward a position of the genital orifices.

E. CONCLUSION; LIMULUS AND THE ANCESTRY OF TRACHEATE ARTHROPODA.

The nature and degree of intimacy of the relationship between Limulus and the Scorpion—which is indicated by the facts and arguments set forth in the preceding essay—have yet to be considered. It is one thing to establish the fact that a closer relationship obtains between Limulus and Scorpio than between Limulus and any Crustacean, and another thing to estimate more precisely the affinity between the two animals.

A brief consideration of the facts is sufficient to show that the points in which Limulus agrees with Scorpio and Mygale include those structural features on which we have to rely in attempting to characterise the class Arachnida. At the same time it must be admitted that all attempts at limiting classificatory groups by simple definition are hopeless, provided that the groups are intended to express degrees of genealogical affinity, and not merely arbitrary categories, held together by more or less obvious class marks. The real question which we have to attempt to answer, in assigning Limulus and the Arachnida their place in a genealogical classification of the Arthropoda is not, "How may groups be defined which shall give due expression to the structural likenesses and unlikenesses of these forms?" but, "How may groups be arranged so as to exhibit the probable history of ancestral development in relation to these forms?" Owing to the occurrence of degeneration, and to the suppression in some forms of structural features which were the distinguishing characteristics of their immediate ancestry, we find that frequently genealogical groups do not admit of strict definition in terms of structure. And, further, we find that, even in order to arrive at a clear notion with regard to the relationships of a limited portion of a large group—such a portion as are Arachnida in regard to the Arthropoda—it is necessary to consider the genealogy of the whole series included in the larger group.

The Arthropoda form a very large branch of a great phylum to which I have applied the name 'Appendiculata'—cœlomate animals with more or less distinct metameric segmentation of the body and possessed of lateral lobes or processes of the body itself which serve primarily as locomotor organs. Besides the Arthropoda the phylum Appendiculata includes the Rotifera and the Chætopoda. Each of these three great branches of the Appendiculata has its special developments, but it seems to be probable that they all started from a common ancestry which had characters intermediate to those of such a Rotifer as Pedalion and of such a Chætopod as Syllis. Probably the Arthropoda were developed from an ancestry resembling the Chætopoda, but devoid of the chætæ carried by the appendages of the latter.

The distinguishing motive of the development of the Arthropod branch of the Appendiculata is the adaptation of one or more pairs of the appendages proper to the segments succeeding the mouth, to the purposes of the prehension and mastication of food. Hence it would be well to substitute the term Gnathopoda for Arthropoda. All Arthropoda are not arthropodous, that is to say, do not exhibit a jointing of the exo-skeleton of the appendages. Peripatus though truly a Gnathopod is not an Arthropod or Condylopod. The disappearance of such jointing in connection with a softening of the integument and a scavenger mode of life amongst rotten wood, is one of those changes which it is probable might occur as an adaptation, and accordingly it is very doubtful whether we should regard the non-arthropodous condition of Peripatus as a retention by it of the soft-bodied character proper to the Chætopod-like ancestry of the Arthropoda.

The structure of its eye, the presence of two lateral nerve-cords in place of a double ventral cord, the limitation of the jaw-feet to a single pair, the existence of paired nephridia in each segment of the body, the peculiar histological structure of the muscular tissue, seem to me to be conclusive evidence in favour of the view that Peripatus is a representative of an exceedingly primitive grade of Arthropod development, corresponding to a period when the Arthropod branch had advanced but little on its special lines of differentiation.

At the same time Peripatus is specialised and adapted to a terrestrial mode of life. It possesses no remnants of branchial organs but a peculiar tracheal system, air being admitted to the fine vessels formed by its vasifactive tissue through irregularly scattered gland-like pits of the integument.

Its specialisation as a terrestical organism has, it is impossible to doubt, affected in Peripatus the locomotor appendages also, so that much important information is wanting to us, which, on the contrary, an aquatic form belonging to the phase of development indicated by the eyes, nerve-cords, nephridia, and gnathites of Peripatus, could have furnished.

It appears to me that we have no such aquatic representative form, and that Peripatus stands as a specialised terrestrial off-shoot at a much lower point in the Arthropod family-tree than that at which we find outgrowths of existing branchiate Arthropoda.

The antennæ of Peripatus probably are identical with the similar organs of Chætopoda (cf. Spio and Phyllochætopterus), and are *not* originally post-oral appendages which have become præoral by adaptational shifting of the oral aperture, but are actual lobes or processes of the primitive prostomium, like the tentacles on the head of a snail, and innervated by the archicerebrum or original prostomial ganglion.

In the interval between the giving off of Peripatus and the production of the Phyllopod-like ancestors of the Crustacea from the aquatic Pro-Arthropoda, a vast change had to be effected in regard to appendages as well as in the fusing of the nerve-cords, abolition of nephridia, production of a compound eye, striation of muscular tissue, &c. The prostomial antennæ disappeared and their place was taken first by one, then by two pairs of post-oral appendages, which gradually acquired a præ-oral position as actually occurs in their individual growth in the embryo at the present day; eventually the simple prostomial ganglion (archicerebrum) became complicated by the fusion with it of ganglionic material proper to the two shifting appendages, though in the existing Phyllopod Apus it still retains its original purity and independence.

The other appendages probably all acquired at one stage a development of their basal portion which served as an accessory organ for the purpose of bringing food to the mouth and in some degree in crushing such food (as seen in Apus), but this development was specially carried out and localised in two pairs of appendages posterior to the one already so differentiated in Peripatus.

The segments, each with its pair of appendages, were indefinite in number and frequently exceeded one hundred. The definite Crustacean character was attained when two pairs of appendages had become præ-oral, at least three pairs specialised as jaws and no longer locomotor, whilst the remaining appendages retained locomotor, manducatory, and respiratory functions to be subsequently specialised in the further development of the Crustacean stem.

It appears to me probable that the Merostomata, including under this head the Xiphosura (Limulus), the Trilobita, and the Eurypterina, diverged from the main stem[1] of the Arthropod pedigree at a point between that indicated by the grade of organisation of Peripatus and that occupied by the Pro-Phyllopoda or earliest Crustaceans.

Probably none of the known Merostomata suffice to give us a true picture of the structure of the ancestral Merostomata from which they are all derived. Probably these ancestral Merostomata were devoid of the prostomial antennæ—the non-appendicular antennæ. At the same time none of their post-oral appendages had become definitely prœ-oral in position and nerve supply, though not less and probably not more than six pairs of pediform appendages were closely set round the mouth, their bases acting as powerful manducatory organs. To this group of appendages, of which the corresponding segments were more or less completely fused with the prostomium (forming the *prosoma*), succeeded a mid-region of the body (the *mesosoma*), consisting of numerous segments carrying biramose, probably pediform appendages, the bases of which were beset with respiratory lamellæ.

The generative apertures were situate in the first or one of the anterior segments of this mid-region of the body. A third region of the body (the *metasoma*), also consisting of numerous segments, was probably distiuguished by the form and smaller size of its appendages and by a tendency of the segments to fusion. Posteriorly to the anus was a median plate or spine. Probably the eyes placed on the dorsal sur-

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[1] I have treated the line of descent leading to the Crustacea as the main stem of the Arthropod family-tree; it is obviously a matter which may be determined by convenience as to whether one or other of the branches of a genealogical tree shall be treated as the main line of the family.

face of the anterior region of the body were simple eyes, but arranged in two lateral groups and a central group.

From such a form the Xiphosura were derived by retention of the full number of the appendages of the prosoma, the limitation of the segments of the mesosoma to six, and their specialisation as plate-like organs serving as genital operculum, branchiæ and swimmerets, further by the limitation of the segments of the metasoma, first of all to six, and their subsequent fusion and partial disappearance even from embryonic expression, and the atrophy of the appendages proper to them. At the same time the lateral groups of simple eyes were replaced by a peculiar form of compound eye.

The Eurypterina diverged from the Xiphosura after most of these features had been elaborated, but so as to retain the six free segments of the metasoma, whilst at the same time they lost one pair (probably the most anterior) of the appendages of the prosoma, and possibly the three hindermost of the appendages of the mesosoma.

The Trilobita diverged from the common ancestry of the Xiphosura and Eurypterina probably at a time when the number of six segments to the mesosoma and six to the metasoma had not become a definite limitation, and when appendages were carried by both those regions of the body, differing only from the leg-like gnathites of the prosoma in possessing a second ramus and lamelliform branchial processes. Possibly the compound eye of the Trilobite was inherited from an ancestor common to it and the Eurypterina. According to Walcot (12), a very distinctive feature in the differentiation of the Trilobita was the reduction of the number of appendages of the prosoma from six pairs to four. In all these forms it is important to note that the appendages of the prosoma, whether six pairs in number or less, whether chelate, tactile, ambulatory, or natatory, so far as the 'palp' or chief ramus is concerned, yet all, with the exception of the most anterior pair, continue by means of their enlarged basal joint to act as manducatory organs. As a set-off to the loss of the manducatory functions of their coxæ, the first pair possess, with rare exceptions, nipping or stabbing palps.

The relationship of the Scorpion and other living Arachnida to the Merostomata appears to be this. From an ancestral form, which was nearly related to the common progenitor of the Xiphosura and Eurypterina, which possessed six pairs of appendages to its prosoma, the terga united to form a carapace, six free segments to its mesosoma and six free segments to its metasoma—the metasoma devoid of appendages as in Xiphosura and Eurypterina, the mesosoma provided with a genital operculum (united appendages) on its anterior segment and with five pairs of lamelligerous respiratory appendages on the five succeeding segments—from such a form by a very slight process of change, consisting in adaptation to terrestrial in place of aquatic conditions, the primitive Scorpions were developed. It is probable that the particular form antecedent to the differentiation of Xiphosura and Eurypterina, from which the Scorpions took origin had not developed lateral compound eyes, but still exhibited a primitive condition, which is retained by the Scorpions and other Arachnida, viz. a lateral grouping of simple eyes.

The structural changes necessary to produce a Scorpion from such an ancestral Merostom as has been just sketched are so small that it is not possible to place the Scorpions and the Merostomata in separate classes, if by the use of the division known as a 'class' we are to indicate as nearly as possible, in different parts of the pedigree of animals, an equal break or unrepresented interval of structural change. At the same time the Scorpions, having once been developed, appear to have given rise to the whole series of living Arachnida, to the Pedipalpi first, and through these to the Araneina, and through the Araneina to the Acarina.

Galeodes is probably a special development from the Scorpionina, as in a different direction are the Opilionina and Pseudoscorpions.

This conclusion, if it be well founded, justifies some important inferences of a secondary character. In the first place we have to admit a very extensive process of degeneration in the course of development, leading from the Scorpion to such Acarina as Demodex, or even Hydrachna. In the second place we obtain a definite answer as to the mode of origin of tracheæ, in so far, at least, as the tracheæ of the Arachnida are concerned. The vascular lamelligerous appendages of the Limuloid ancestor of the Scorpion became dry and filled with air in place of with blood. From this blood-sinus, converted into an air-sinus, the air appears gradually to have made its way, encroaching upon pre-existing blood-canals, and converting them into air-canals. The highly developed condition of the blood-vascular system in the Scorpions renders it probable that the tracheæ of the tracheate Arachnida are not *new* vessels specially developed as an aërial vascular system, but are the modified and adapted blood-vascular channels, just in the same way as the air-containing lamelligerous appendages of the Scorpion are not new organs, but the modified and adapted blood-containing appendages of a Limuloid ancestor.

The relationship of the groups of Arachnida to one another thus suggested may be best indicated by means of a genealogical tree (see last page). I have also drawn up the names and arrangement of groups suggested in a tabular form.

I have further thrown into the form of a genealogical tree the conclusions to which I am led in reference to the relationship to one another of Peripatus, the Crustacea, and the Arachnida.

In this pedigree of the Arthropoda no place is assigned to the two great tracheate groups of Insecta Hexapoda and Insecta Myriapoda. In the present state of knowledge it appears to be impossible to assign to either of them one position rather than another. We have not even sufficient ground for concluding that they are closely related to one another. The antennæ of Hexapods and of Myriapods *may* be, as probably are those of Peripatus, non-appendicular prostomial antennæ, which would be, in addition to the presence of tracheæ, a reason for considering both to have been developed from such a form as Peripatus. On the other hand, possibly only the Myriapoda are derived from Peripatus-like ancestry, and, probably enough, neither one nor the other. It seems to be in the highest degree probable, and is not difficult of admission, that there is no such a group to be recognised as the Tracheata. Tracheæ have probably developed independently in Peripatus and in the Insecta, and again in the Arachnida. Nevertheless, the view is capable of being defended that all tracheate Arthropoda have a common tracheate ancestor; in which case it will be necessary to derive the Insects, the Myriapods, and, to be consistent, Peripatus also, from the tracheate Arachnida, through such a form as Galeodes. The derivation of Galeodes through the Scorpions, from the branchiate Arachnida, is, relatively speaking, a well-grounded conclusion; and if tracheæ are to have but one starting-point, it is of necessity here that we must look for it.

Insuperable difficulties are, however, found in the derivation of Hexapoda from Galeodes, in spite of curious homoplastic agreements between the two. Such a difficulty is the absence of appendages corresponding to the antennæ of Insects in Galeodes, and in the whole line of its Arachnidan ancestry, which absence has to be recognised if the pincers of Galeodes are identified with the mandibles of an Insect.[1]

[1] I do not admit the truth of this identification.

In deriving the Hexapods and Myriapods from Galeodes we should have to suppose the antennæ of the former to arise *de novo*—a supposition which is contrary to one of the fundamental principles of phylogeny, viz. that new organs do not arise *de novo* as new parts, but by the modification of pre-existing parts.

Hence it seems that in any case the tracheate Arachnida must be left apart from the other tracheate Arthropods as the extreme modification of the series originating in the Limuloids.

This conclusion is, however, in opposition to the view that the renal Malpighian tubes are of phylogenetic significance. It is a very striking fact that all well-developed tracheate Arthropoda (except Peripatus) have not only tracheæ as respiratory organs, but also have these Malpighian cæca growing from the proctodæum. Either the Hexapods and Myriapods are closely related to the air-breathing Arachnids or these Malphighan cæca have, like the tracheæ, appeared more than once independently in divergent lines of the Arthropod family-tree.

A minute comparative study of the structure and development of these cæca is wanting; at the same time it appears that certain of the Isopod Crustacea possess organs comparable to them. If this be so, another possible place of attachment for the Hexapods and Myriapods to the Arthropod family-tree is indicated, which, on independent grounds, has much in its favour. Supposing that the antennæ of Hexapods and Myriapods should prove not to be identical with the prostomial antennæ of Chætopods but should be shown by the examination of the development and structure of their connected nerve-ganglia to be like those of Crustacea, originally post-oral appendages, or supposing on any other grounds that the antennæ of these forms could be identified with one pair of the Crustacean's antennæ, then it would not be difficult to conceive of such a modification of the post-oral appendages of an Isopod as would give the disposition characteristic of them in either Myriapods or Hexapods.

And it is to be noted that among existing Isopods, terrestrial forms are known with peculiar lung-like pouches adapted to aërial respiration.

A strong argument in favour of the derivation of the Hexapoda from Crustacea appears at first sight to be afforded by the minute structure of the compound eye of the two series of organisms.

Amongst all the possible points of genetic connection of the Hexapoda and of the Myriapoda with the other large groups of Arthropoda, there is probably more hope of a definite indication being obtained as the result of a critical study and comparison of the structure of the *eyes* than from any other source. The eyes of Arthropods are elaborate in the histological details of their structure, and at the same time have not been inherited from a common ancestor in one and the same elaborate form by all the members of the group, as have been the eyes of craniate Vertebrata for example. Accordingly we may expect that the elaboration of the eye has taken a somewhat different course in different lines of descent within the limits of the Arthropod phylum, and we should be justified in concluding a common line of descent for classes of Arthropods showing identity in numerous details of the optical structure, which details had been ascertained not to be a common inheritance from the primæval Arthropod ancestor.

Whatever may be the conclusion arrived at in the future in reference to the affinities of Hexapoda and Myriapoda, the result of the recognition of the intimate relationship of Scorpio and Limulus must be, I think, to break up the artificial group of "Arthropoda Tracheata" by the separation of the Scorpions, Spiders, and Mites, from any special connection with it.

Phylum.—APPENDICULATA.

Branch 3.—Arthropoda (Gnathopoda).

Class.—Arachnida.

Arthropoda developed from ancestral forms, in which a 'prosoma' formed by the union of the prostomium and six anterior segments was sharply marked off from the rest of the body, both by the confluence of its terga to form a carapace and by the special character and size of its appendages. The six pairs of appendages (including the foremost of the whole series) were arranged round the mouth, and all subservient to the purpose of prehension and mastication of food. In the later developed forms of Arachnida either the number of these appendages may be reduced (Eurypterina, Trilobita), or the functional relation to the mouth of the more posterior of the six pairs may be lost. Whatever their number, the foremost pair is free from a jaw-like enlargement of the coxa. The palps of all six pairs of appendages exhibit a wide range of adaptational form, as prehensile, tactile, ambulatory, natatory, or fossorial organs.

The generative apertures are placed far forward—ancestrally in the first segment of the 'mesosoma' or region following the prosoma, and are covered by a fused pair of appendages, or, when these have aborted, by the corresponding sternite.

The appendages of the mesosoma posterior to the generative apertures carry peculiar respiratory lamellæ, which expose the blood circulating in them to the dissolved oxygen of natural waters in the more archaic members of the group, but are perforated, invaginated in recesses of the ventral integument, and filled with atmospheric air in terrestrial forms (Scorpions, Spiders, &c.), or may be altogether aborted and replaced by tracheæ.

Except in the Trilobita the segments and paired appendages of the mesosoma are not more than six in number, and the same is true of the metasoma or terminal region of the body, which is devoid of appendages (except in Trilobita), and may either have the appearance of a simple continuation of the mesosoma (macrourous forms), or may have its segments fused with one another, but separate from those of the mesosoma (Trilobita); or, again, may be more or less completely aborted and fused with the mesosoma (Limulus), when the segmentation of the mesosoma itself may also become partially (Spiders) or completely (Acarina) obliterated.

In all the larger known forms (Limulus, Scorpio, Mygale) a large free sclerite, the entosternite, is found within the prosoma, giving attachment to muscles inserted into the sternites of the mesosoma.

Tabular view of the Orders of Arachnida.

GRADE A.—HÆMATOBRANCHIA (= MEROSTOMATA):

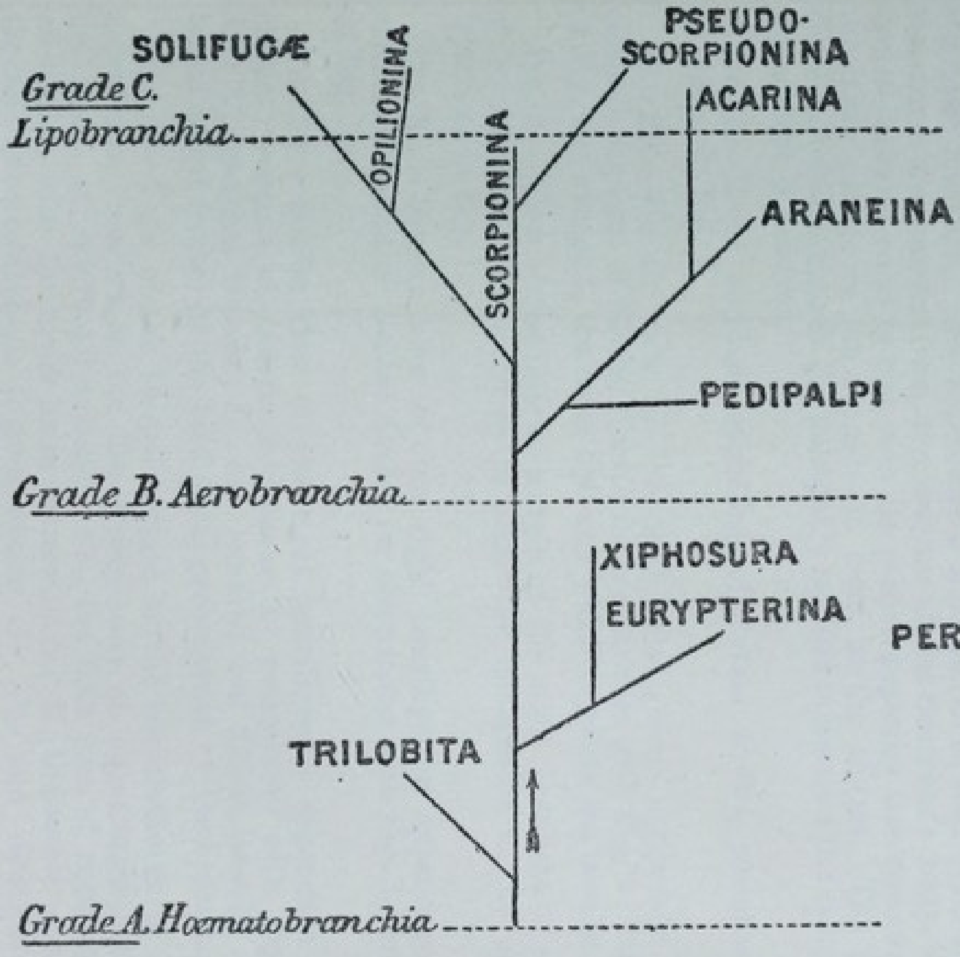
Order 1	Trilobita.
,, 2	Eurypterina.
,, 3	Xiphosura.

GRADE B.—AEROBRANCHIA:

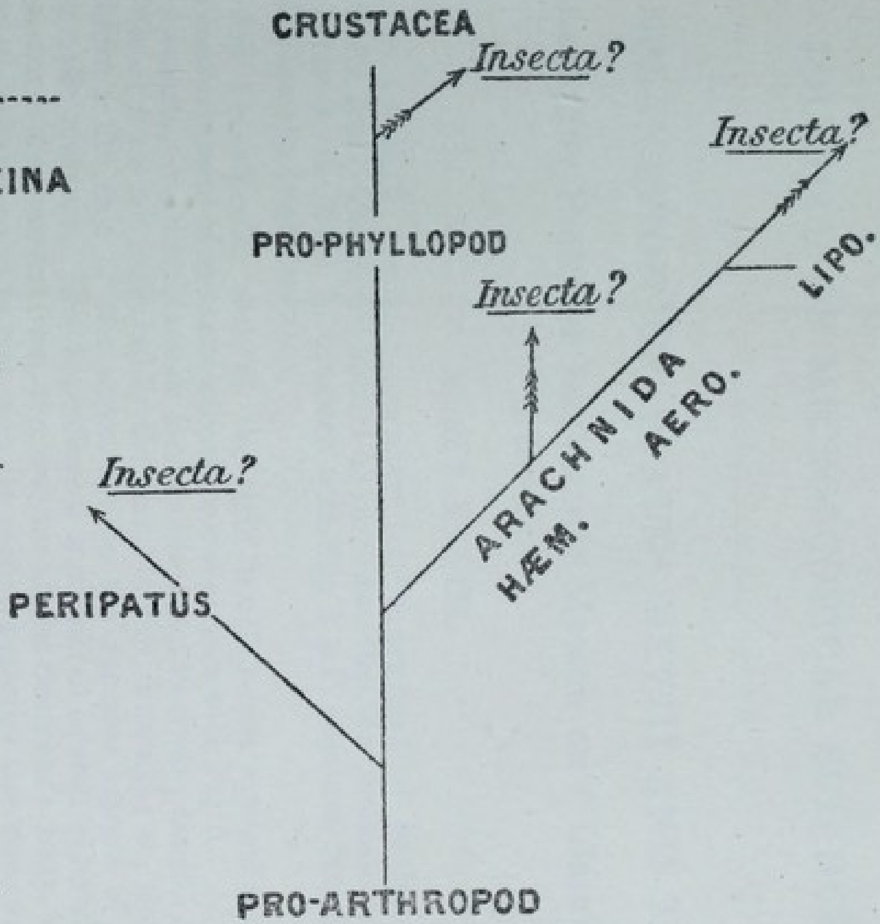
Order 1	Scorpionina.
,, 2	Pedipalpi.
,, 3	Araneina.

GRADE C.—LIPOBRANCHIA:

Order 1	Solifugæ.
,, 2	Pseudoscorpionina.
,, 3	Opilionina.
,, 4	Acarina.



Genealogical Tree of the Arachnida



Genealogical Tree of the Arthropoda.

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EXPLANATION OF PLATES XXVIII AND XXIX,

Illustrating Professor Lankester's Memoir on "Limulus an Arachnid."

PLATE XXVIII.

Fig. 1.—Right pectinate appendage (eighth segment) of *Buthus Kochii*, anterior face. This figure should be turned so that the pectinate border is uppermost, in order to compare with Fig. 1 *a l'*, proximal lamella; *lx.*, distal lamella (eighteenth).

Fig. 1 *a*.—Similar view of the right lamelligerous appendage of the eleventh segment of the same animal for comparison with Fig. 1. *l.'*, proximal lamella; *lx.*, distal lamella (one hundred and thirtieth; the full number of lamellæ are not indicated by the lines in the drawing); *m.*, membrane attaching the axis of the appendage to the superior margin of *st.*, the stigmatic aperture. The appendage is represented as seen when all other structures are removed from the interior of the Scorpion's body, it is reflected forwards so as to rest with its proper posterior face downwards on the inner surface of the sternite in front of the stigma. The delicate membrane which bounds the pulmonary sac and represents the invaginated integument is removed.

Fig. 2.—Right pectinate appendage of *Buthus Kochii*, posterior face; letters as in Fig. 1.

Fig. 2 *a*.—Similar view of the right lamelligerous appendage of the eleventh segment of *Buthus Kochii*, for comparisom with Fig. 2; letters as in Fig. 1 *a*, except *b*, the canal-like axis which supports the lamellæ.

Fig. 3.—View of the inferior margin of the right pectinate appendage of *Buthus Kochii*, so placed as to show the imbrication of the lamellæ; letters as in Fig. 1.

Fig. 3 *a*.—Similar view of the right lamelligerous appendage of the eleventh segment of *Buthus Kochii*, for comparison with Fig. 3; letters as in Fig. 1 *a*.

Fig. 3 *b*.—Similar view of the right lamelligerous appendage of the eleventh segment of *Limulus polyphemus* for comparison with Fig. 3 and 3 *a*: *l.'*, proximal lamella; *lx.*, one hundred and fiftieth lamella; *ex.*, external lappet (exite) of the bifid distal prolongation of the appendage.

Fig. 4.—View of the sternal surface of the cephalothorax of *Limulus polyphemus*, from which the five hinder pairs of appendages have been detached. *sf.*, subfrontal sclerite; *Ch.*, the first pair of appendages or chelicerræ; *cam.*, the upper lip or camerostome; *M.*, the mouth; *pmst.*, the thoracic promesosternite (representative of pro- and mesosternite as separately developed in the spiders, see woodcut, fig. 9); *metst.*, thoracic metasternite or chilaria, homologous with the pentagonal metasternite of Scorpio, see woodcut, fig. 8, *met.*

Fig. 5.—Entosternite of bird's-nest spider (Mygale, sp.), dorsal face.

Fig. 5 *a.*—The same, neural face.

Fig. 6.—Entosternite of a Scorpion (*Buthus*, sp.), posterior face.

Fig. 6 *a.*—The same, neural face.

Fig. 7.—Entosternite of *Limulus polyphemus,* neural face. Compare with Fig. 5 *a* and Fig. 6 *a.*

Fig. 8.—A single lamella of the right lamelligerous appendage of the eleventh segment of *Buthus Kochii,* formed by two closely adherent plates : *a. b.*, the base or line of attachment. Note the marginal setæ.

Fig. 9.—A single lamella of the right lamelligerous appendage of the eleventh segment of *Limulus polyphemus,* for comparison with Fig. 8 : *a. b.*, the base or line of attachment. Marginal setæ are present, but more numerous than in Fig. 8.

Fig. 10.—View of the posterior face of the conjoined pair of lamelligerous appendages of the eleventh segment of *Limulus polyphemus* : *st.*, soft sternal lobe or plate which unites the two appendages ; *md.*, median process or soft papilla of the sternal plate ; *epst.*, epistigmatic sclerite ; *stg.*, parabranchial stigma (invagination to give attachment to the thoraco-branchial muscle) ; *app. m.*, protractor muscle of the appendage, seen through the the soft integument ; *l.*, branchial lamellæ ; *l.′*, the proximal lamella ; *app.*^{1}, the proximal division of the appendage carrying the lamellæ and extending beyond them ; *app.*^{2}, *app.*^{3}, *app.*^{4}, second, third, and fourth sclerites, forming the jointed axis of the distal prolongation of the appendage ; *ex.*, exite or outer ramus of the appendage.

Fig. 11.—View of the pair of lamelligerous appendages of the ninth segment of *Limulus polyphemus,* seen from in front. The chitinised integument has been removed from the surface of the proximal portion of the appendages, so as to expose the bases of the hollow lamellæ, and the soft integument of the median sternal area ; and the retractor muscles have also been removed so as to expose the inner face of the corresponding integument of the posterior face, and the insertions of the thoraco-branchial muscles : *st.*, sternal lobe ; *stm.*, thoraco-branchial muscle of the left side ; *Bl.*, bases of the laminæ, open to the branchial blood-vessels.

Fig. 12.—A semi-diagrammatic view of one of the respiratory appendages of a Scorpion, to show *Bl.*, the bases of the lamellæ exposed, as in *Bl.*, fig. 11, by the removal of the integument of the axis, the remnants of which are seen at *m.* The drawing further shows the gradual narrowing of the bases of the laminæ in the series as the distal region is approached until the free projecting portion of the axis (x) is reached ; *l.*, proximal lamella.

Fig. 13.—A tendon-sac of *Limulus polyphemus* detached from the parabranchial stigma, the homologue of the investing pulmonary sac of Scorpio.

PLATE XXIX.

The drawings on this plate are diagrammatic, and illustrate the hypothesis as to the derivation of the lamelligerous appendages of Limulus, and Scorpio from a common ancestral form. All the figures, except 4, 5, 6 present the appendages as seen when the ventral surface of the animal is facing the observer.

Fig. 1.—Hypothetical intermediate form. *R.* axis of appendage ; *l.*

lamella; *stg.*, parabranchial stigmata on the sternal surface; *b.*, bases of the lamellæ supposed to be seen through the axis of the appendage by transparency.

FIG. 2 *a.*—Hypothetical form leading on to Limulus. Letters as before, excepting R′ R″ pointing to the distal region of the appendage now prolonged beyond the lamelligerous region, and *ex.* the exite. The parabranchial stigmata are now in proportion to the size of the appendages much smaller than in fig. 1. The median sternal tubercle seen in fig. 1 has now grown up into a fold uniting the bases of the appendages.

FIG. 3 *a.*—The form realised in Limulus. The appendages no longer diverge, but converge, and the median sternal fold or lobe widely unites their proximal segments, and overlaps the parabranchial stigmata, *stg.*, which are indicated by dotted lines, as though showing through the sternal fold by transparency.

FIG. 2 *b.*—Hypothetical intermediate form leading from that represented in fig. 1 to the condition realised in Scorpio. The letters have the same significations as in fig. 1. The parabranchial stigmata are now greatly enlarged, and the appendages reduced in size, so that the latter hang, as it were, from the anterior margins of the former.

FIG. 3*b*.—A further approach to the condition found in Scorpio and the pulmonate Arachnids is shown. The margins of the parabranchial stigmata have contracted, enclosing within the sunken sternal surface the reduced lamelligerous appendages. On the right hand side of the figure the appendage is represented as though the integument covering it in were quite transparent. It has rotated on its base line, so as to present what was the concealed or posterior face.

FIGS. 4, 5, 6.—Diagrams of sections of the sternal wall of the three stages drawn in figs. 1, 2 *b*, and 3 *b.*; *ch.*, the integument; *R.*, axis of the appendage; *l.*, lamellæ of the appendage; *stg.*, cupped surface of the sternum or parabranchial stigma; *m.*, thoraco-branchial muscle attached to the cupped integument.

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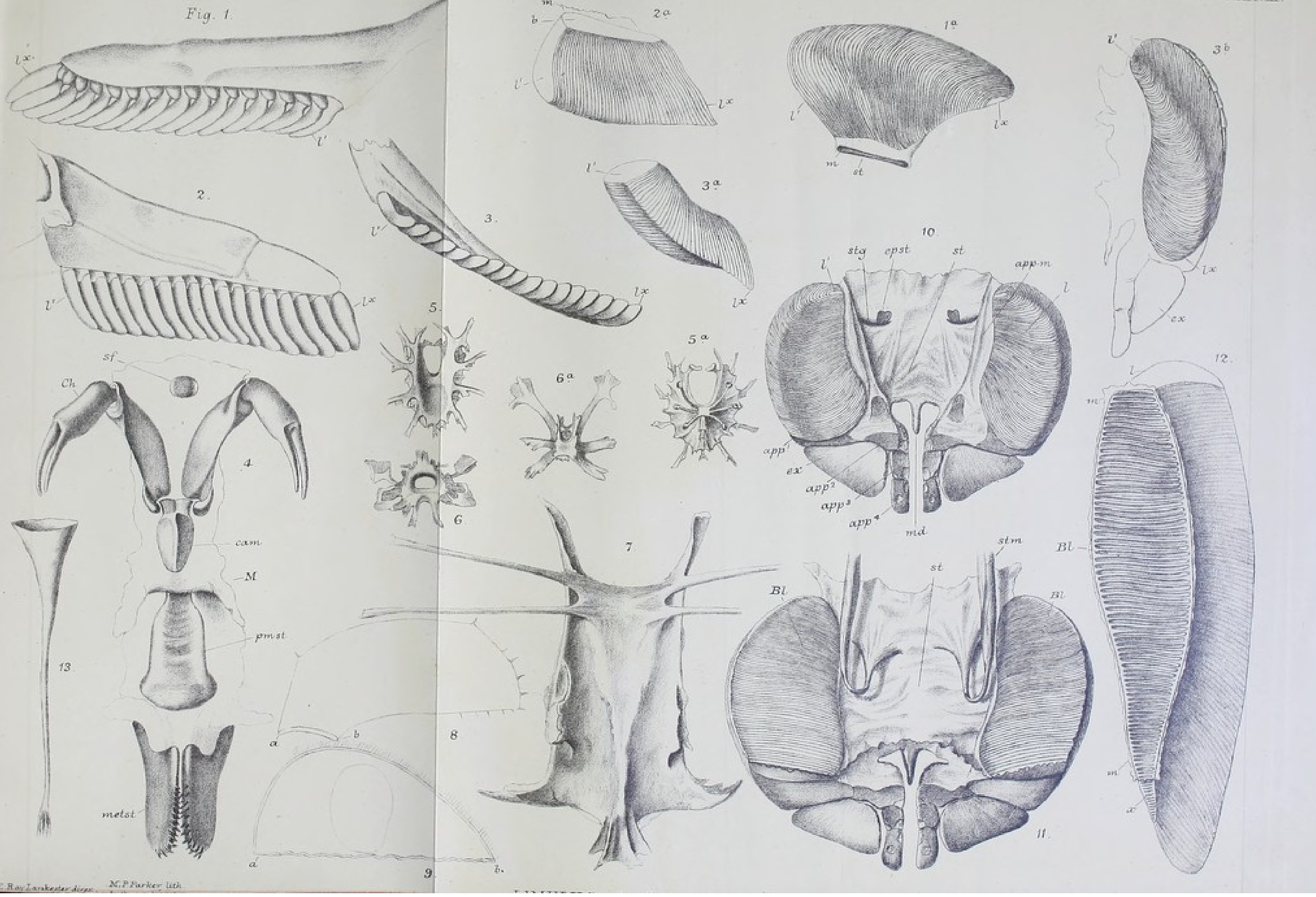

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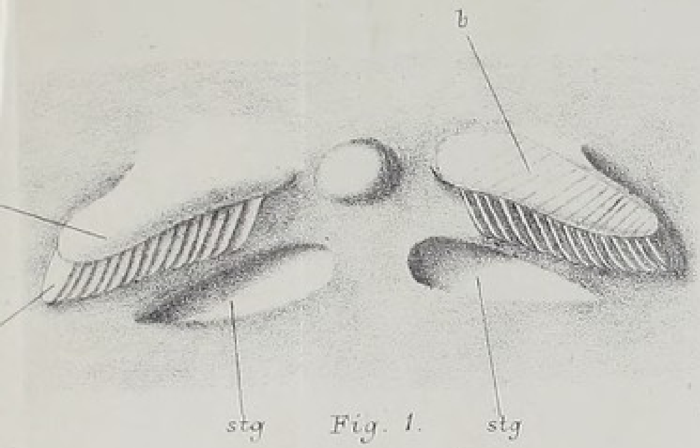

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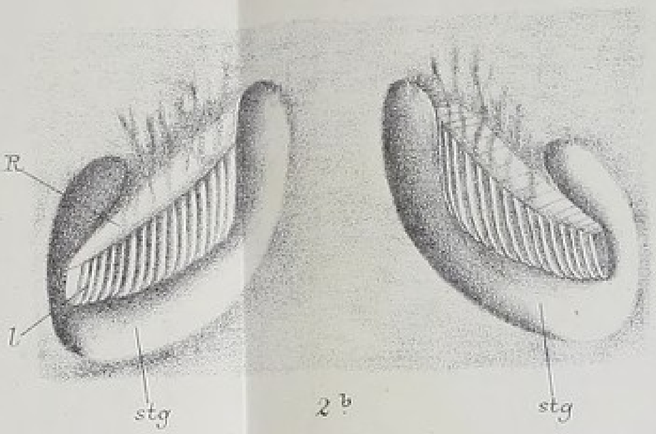

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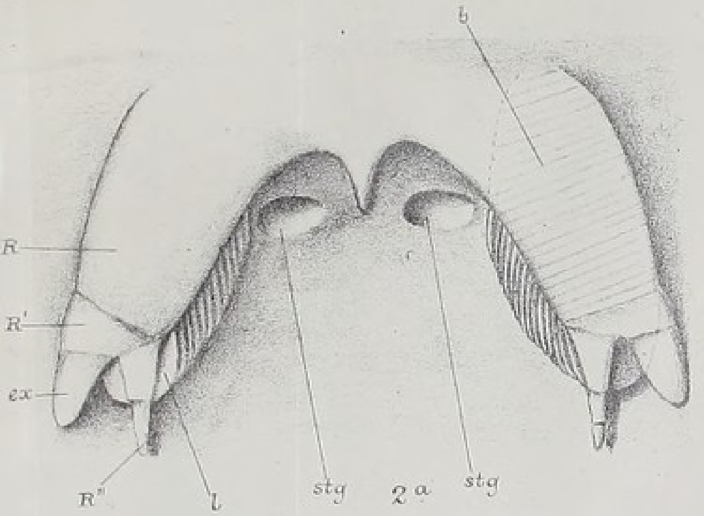

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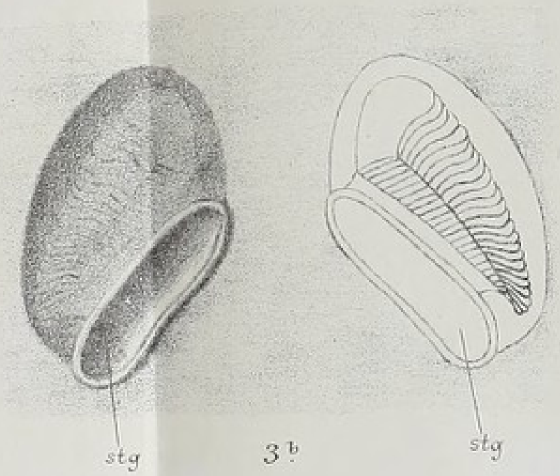

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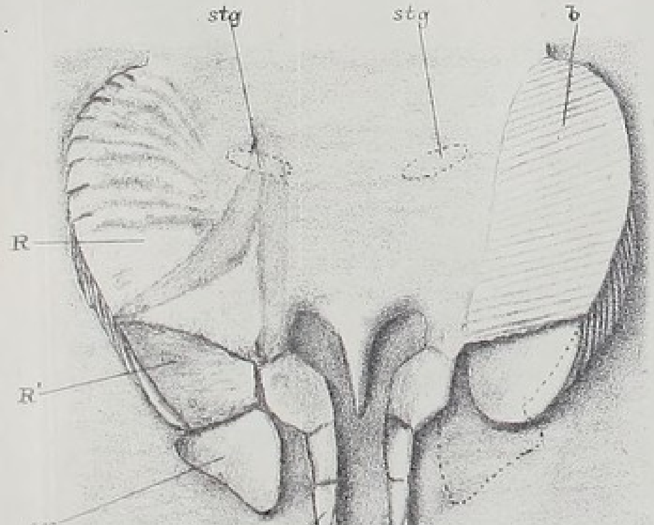

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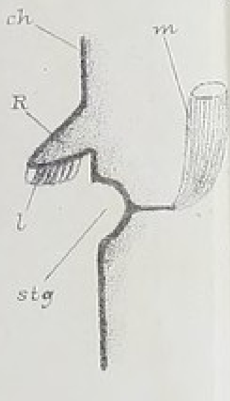

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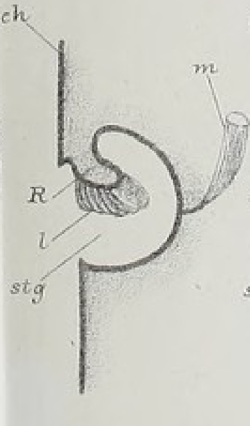

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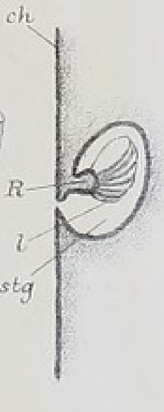

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E. Ray Lankester del.
M. P. Parker lith.

LIMULUS & SCORPIO.

West, Newman & Co. imp.