

CHAPTER V.

LINEAR SERIES—*continued.*

HOMŒOTIC VARIATION IN ARTHROPODA.

THE occurrence of Homœosis among the appendages of Arthropoda is illustrated by a small but compact body of evidence. To this evidence special value may be attached, not because it is likely that in the evolution of the Arthropods variations have really taken place, in magnitude comparable with those now to be described, but rather because these cases give a forcible illustration of possibilities that underlie the common and familiar phenomena of Meristic Repetition. Of these possibilities they are indeed "Instances Prerogative," salient and memorable examples, enunciating conditions of the problem of Variation in a form that cannot be forgotten. Facts of this kind, so common in flowering plants, but in their higher manifestations so rare in animals, hold a place in the study of Variation comparable perhaps with that which the phenomena of the prism held in the study of the nature of Light¹. They furnish a test, an *elenchus*, which any hypothesis professing to deal with the nature of organic Repetition and Meristic Division must needs endure.

INSECTA.

- *75. **Cimbex axillaris** (a Saw-fly), having the peripheral parts of the left antenna developed as a foot. The right antenna is normal, ending in a club-shaped terminal joint. In the left antenna the terminal joint is entirely replaced by a well-formed foot, having a pair of normal claws and the *plantula* between them (Fig. 16). This foot is rather smaller than a normal foot, but is perfectly formed. The rest of the antenna, so far as the point at which the club should begin is normal in form, but is a little smaller and thinner than the same parts in the right antenna. KRAATZ, G., *Deut. ent. Ztschr.*, 1876, xx., p. 377, Pl.

¹ See the well-known passage in *Nov. Org.*, II. xxii.

This specimen was most kindly lent to me for examination by Dr Kraatz, but to this description I am unable to add anything¹.

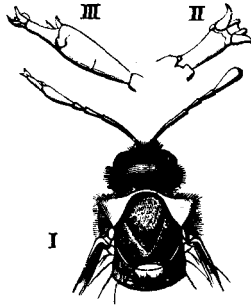


FIG. 16. *Cimbex axillaris*: right antenna normal; left antenna bearing a foot. II. the left antenna seen from in front. III. the same from above. After KRAATZ.

It should be noted that the plantar surface of the foot was turned rather forwards as shewn in the figure, and not downwards like the normal feet.

- *76. **Bombus variabilis** ♂ (a Humble-bee). A specimen taken beside the hedge of a park in Munich, having the left antenna partially developed as a foot. The first two joints were normal. They were followed by two joints which were rather compressed and increased in thickness and breadth. Of these the first was oblong and somewhat narrowed towards its apex by two shallow constrictions, giving it an appearance as of three joints united into one; below it presented a projecting and tooth-like point. This joint was only slightly shiny. The next joint to it was almost triangular, and was reddish-brown, shiny, and having hairs on its lower surface. Posteriorly it was prolonged inwards, covering the previous joint so that both seemed to form one joint: the posterior edge was somewhat thickly covered with hairs. The upper part of the first of these two joints and the prolongation of the second were together covered by a hairy, scale-like third joint, which seemed to be only attached at its base. From the apex of the second joint arose a shortened claw-joint, like the claw-joint of a normal foot. This joint was reddish-brown and shiny, bearing a pair of regularly formed claws, like the claws of the foot. KRIECHBAUMER, *Entom. Nachr.*, 1889, xv. No. 18, p. 281.

¹ Some to whom I have spoken of this specimen, being unfamiliar with entomological literature, and thus unaware of the high reputation of Dr Kraatz among entomologists, have expressed doubt as to its genuineness. I may add therefore that the specimen, when in Cambridge, was illuminated as an opaque object and submitted to most careful microscopical examination both by Dr D. Sharp, F.R.S., and myself, and not the slightest reason was found for supposing that it was other than perfectly natural and genuine. The specimen was also carefully relaxed and washed with warm water, but no part of it was detached by this treatment.

The two following cases must be given here, inasmuch as they relate to Homœosis of the appendages in Insects; but in the case of the first the evidence is unsatisfactory, and in the case of the second there is considerable doubt whether the variation is really of the nature of Homœosis.

77. **Prionus coriarius** ♂: having elytra represented by legs.

The following is a translation of an announcement in the *Stettiner Ent. Ztg.*, 1840, vol. I. p. 48, which is copied from the original communication to the *Preussische Provinzial-Blätter*, Bd. xx. [The latter journal not seen, W. B.]:—"One of my pupils brought me to-day a male *Prionus coriarius*, Fbr., the thorax of which is remarkably constructed. The horny covering of the mesothorax is absent, and in place of the elytra is a pair of fully developed legs which are directed upwards and backwards. These legs are inserted at the points of articulation of the elytra. The metathorax supports the wings as usual and the abdomen is not hardened more than it usually is. In trying to fly, the creature moved these upwardly directed legs simultaneously with its wings. The scutellum is absent and the prothorax has only two spines; other parts normally developed." Dr SAAGE, Braunsberg, 1839:—Hagen, in quoting this case, mentions that the specimen was afterwards seen by von Siebold, but gives no reference to any writing of von Siebold on the subject.

[If this specimen still exists, it is to be hoped that a description of it may be published. In the absence of further information there seems to be no good reason for accepting the case as genuine.]

- *78. **Zygæna filipendulæ** ♂. Specimen possessing a supernumerary wing arising in such a position as to suggest that it replaced a leg. This specimen was originally described by RICHARDSON, N. M.,

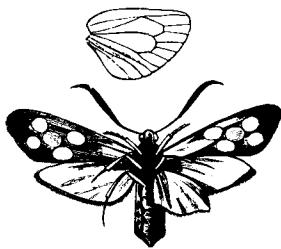


FIG. 17. *Zygæna filipendulæ*, ♂, having a supernumerary wing on the left side. The upper figure shews the neuration of the supernumerary wing. From drawings by Mr N. M. RICHARDSON.

Proc. Dorset Field Club, 1891, and was exhibited at a meeting of the Entomological Society of London, 1891, *Proc.* p. x. The extra wing was in general form and appearance like a somewhat folded

hind wing but its colour was rather yellower, though it was more red than yellow. I have to thank Mr Richardson for allowing me to examine this specimen in company with Dr Sharp. In compliance with Mr Richardson's wish we did not strip the wing or remove the thick hairs which surrounded its base, and it is therefore not possible to speak with certainty as to its precise point of origin. The following description of it was drawn up for me by Dr Sharp: "The supernumerary wing projects on the under side of the body, and at its base there intervenes a space between it and the dorsal region of the body about equal to the length of the metathoracic side-piece. The exact attachment of the base of the supernumerary wing cannot be seen owing to the hairiness of the body, but so far as can be seen it is to be inferred that the wing is attached along the length of the posterior coxa, the outer edge of the point of attachment may be inferred to extend as far as the suture between the coxa and thoracic side-piece; if this view be correct the abnormality may be described as the absence of the hind femur and parts attached to it, and the addition of a reduced wing to the hind-margin of the coxa. It is, however, just possible that if the parts could be clearly distinguished it might be found that the real point of attachment of the abnormal wing is the suture between the metathoracic side-piece and the hind coxa."

It should be distinctly stated that there is no empty socket or other suggestion that the rest of the leg had been lost, and it was in fact practically certain that it had never been present. There is thus a strong *prima facie* case for the view that the leg has been developed as a wing, however strong may be the theoretical objections to this conclusion. On the other hand, as will be shewn in a later chapter, supernumerary wings are known in specimens having a full complement of legs, and it is conceivable that one of these supernumerary wings may have arisen in such a way as to prevent the proper development of the leg from the imaginal disc. If the specimen were carefully stripped of hairs some light might perhaps be thrown on this question. The figure (Fig. 17) is from a drawing kindly lent me by Mr Richardson.

CRUSTACEA.

- *79. **Cancer pagurus.** Specimen having the right third maxillipede developed as a chela. This animal was brought by a fisherman to the Laboratory of the Marine Biological Association at Plymouth. It is a male, measuring five inches from one side of the carapace to the other. All the parts appear to be normal with the exception of the third maxillipede of the right side. This structure, however, has the form shewn in Fig. 18, A, differing entirely from the ordinary condition of the appendage. Fig. 18, B, is taken from the third maxillipede of the left side and shews the ordinary structure of the same parts. On comparing the two figures it will be seen that the protopodite does not differ in the

limbs of the two sides; that the exopodite of the right side is

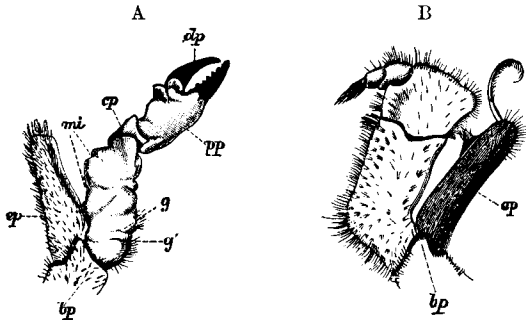


FIG. 18. *Cancer pagurus* ♂; the right and left third maxillipedes, that of the right side having the endopodite in the likeness of the endopodite of a chela. *bp.* basipodite, *cp.* carpopodite, *dp.* dactylopodite, *ep.* epipodite, *g.* groove between parts representing ischiopodite and meropodite, *g'.* groove representing the suture at which a normal chela is thrown off if injured. From *P. Z. S.*, 1890.

essentially like that of the left, but that it lacks the inner process and the flagellum which are borne by the normal part. There was some indication that this branch of the limb had been injured, and perhaps the flagellum may have been torn away, but the appearances were not such as to warrant a conclusion on this point. The branchial epipodites (not shewn in the figures) were normal in both cases. The endopodite of the right side was entirely peculiar, and was, in fact, literally transmuted into the likeness of one of the great chelæ. It consists of a single joint (*mi*), articulating with the basipodite centrally and bearing the carpopodite. This single joint represents, as it were, the ischiopodite and meropodite of an ordinary chela, but these two parts are ankylosed together and the articulation between them is only represented by a groove (*g*). Another groove (*g'*) represents the groove upon the ischiopodite of the chela, at which the limb is commonly thrown off by the animal if it is injured. The carpopodite, propodite and dactylopodite are freely moveable on each other and hardly differ, save in absolute size, from those of the normal chelæ. The shape, proportions and texture are all those of the chela. BATESON, W., *Proc. Zool. Soc.*, 1890, p. 580, fig. 1.

80. A similar case¹ of *Cancer pagurus* ♀. 4 inches across carapace, mature, right pedipalp [*i.e.* 3rd maxillipede] normal, left pedipalp modified into a chela having all the joints clearly defined, CORNISH, T., *Zoologist*, S. 3, VIII. p. 349.

*81. **Palinurus penicillatus.** The left eye bearing an antenna-like flagellum, growing up from the surface of the eye as shewn in the figure (Fig. 19). The eye-stalk and cornea, as represented, appear to have been of the normal shape but reduced in size.

¹ Similar cases since published by RICHARD, *Ann. Sci. Nat., Zool.*, 1893.

MILNE-EDWARDS, A., *Comptes Rendus*, LIX. 1864, p. 710; described and figured by HOWES, W. B., *Proc. Zool. Soc.*, 1887, p. 469.

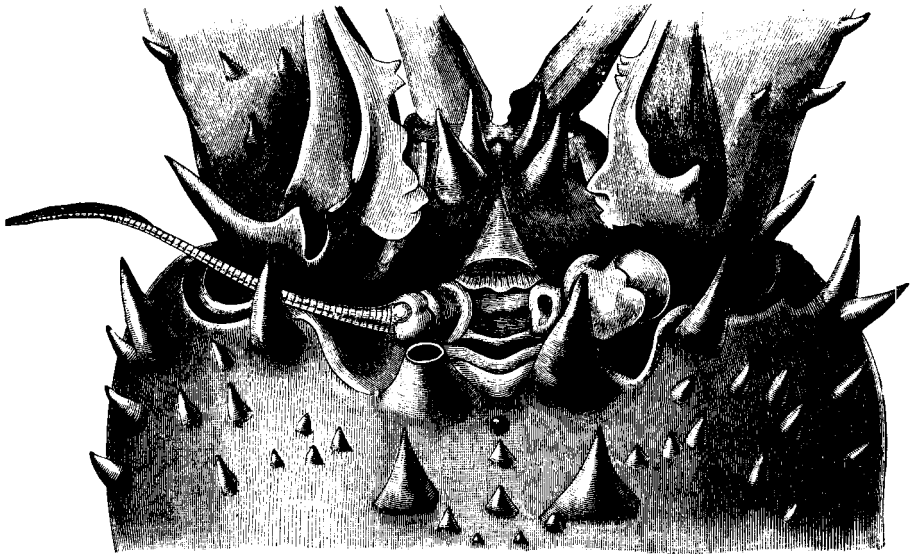


FIG. 19. *Palinurus penicillatus*, the left eye bearing an antenna-like flagellum. After Howes.

82. **Hippolyte fabricii** differs from other species of the genus in being usually without epipodites at the bases of all the cephalothoracic legs except the first pair, while in the other species these appendages are usually present upon the bases of the first and second, or upon the first, second and third pairs, and on this character it was placed by KRÖYER in a separate section of the genus.

Of 52 individuals (18 males varying in length from 27 mm. to 39 mm. and 34 females varying from 16.5 mm. to 50 mm.), from various localities on the New England coast, 47 had the normal number of epipodites, while 5 had epipodites on one or both of the second pairs of legs. Of the latter 3 were from the Bay of Fundy; one ♂, 35 mm. long, has well-developed epipodites on each side of the 2nd pair of legs; another ♂, 36 mm. long, has a short epipodite on the left side and none on the right; the other, ♀, 47 mm. long, has a well-developed epipodite on the left side and none on the right. The two others were from Casco Bay; a ♀, 36 mm. long, with a short epipodite on the left side, and a ♂, 28 mm. long, with a rudimentary one on the right side. As the measurements shew, the presence of these epipodites is not characteristic of the young. SMITH, S. J., *Trans. Connecticut Acad.*, v. 1879, p. 64.

Variation in the number of generative openings in Crayfishes.

- *83. **Astacus fluviatilis.** A female having the normal pair of oviducal openings on the bases of the *antepenultimate* pair of walking legs, and in addition to them another pair of similar openings placed upon the corresponding joints of the *penultimate* pair of walking legs. On dissection it was found that the ovary was normal, and that from each side of it a normal oviduct was given off; but each of these oviducts divided a little lower down to form two smaller oviducts, one of which went to each of the four oviducal openings. DESMAREST¹, *E., Ann. Soc. Ent. France*, 1848, Ser. 2, VI. p. 479, *Pl.*
- *84. **Astacus fluviatilis** ♀, having a supernumerary pair of oviducal openings placed on the *last pair* of thoracic legs. The normal oviducal openings were in the usual position and of the usual shape and size, but in addition to them there was an extra pair placed on the last thoracic legs. It should be remarked that though these are the appendages upon which the openings of the male organs are placed, the oviducal openings were not in this case situated at the posterior surface of the joint as the male openings are, but were placed relatively to the leg in the same situation as the female openings on the antepenultimate legs. The penultimate legs and the abdominal appendages were normal. On dissection it was found that each oviduct after passing for the greater part of its course as a single tube, divided into two parts, one of which went to each oviducal opening. The ovary itself was normal. BENHAM, W. B., *Ann. Mag. N. H.*, 1891, Ser. 6, VII. p. 256, *Pl.* III. [I am greatly obliged to Mr Benham for an opportunity of examining this specimen. Attention is called to the fact that in this specimen Homœosis occurs in an unusual way, leaving a gap in the series; for the openings are on the *antepenultimate* and *last* thoracic legs respectively.]

Desmarest's observation stood apparently alone until lately, when the specimen just described and several others presenting the same or similar variations were observed by BENHAM. Mr Benham was kind enough to send me the following specimens for examination: one female having a *single extra* oviducal opening on the left side upon the penultimate thoracic leg (Fig. 20 C), and two females having a similar extra opening in the same place on the right (Fig. 20, B); in both of these the normal oviducal openings were unchanged. Together with these Mr Benham also sent a female having *only one* oviducal opening on the right side and another having *only the left* oviducal opening (Fig. 20, A), the corresponding leg of the other side having no trace of an opening.

¹ DESMAREST had this specimen from ROUSSEAU (*l. c.*, p. 481 note): Faxon quoting the case (*Harr. Bull.*, VIII.) accidentally represents it as two cases, but the note to Desmarest's paper shews that the description referred to a single specimen only.

*85. After receiving these specimens I made an attempt to ascertain the degree of frequency with which such variations occur in

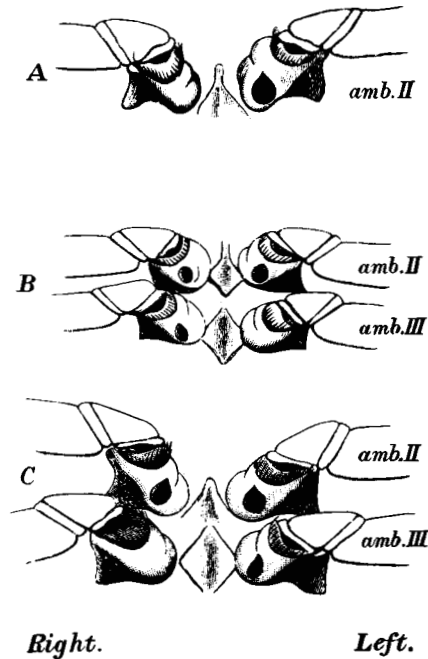


FIG. 20. Females of *Astacus fluviatilis* having an abnormal number of oviducal openings. N.B. The form with *three* pairs of openings is not figured.

A. Right oviducal opening absent. B. Extra opening in right penultimate leg. C. Extra opening in left penultimate leg.

the Crayfish, and though the total number examined is too small to give a percentage of much value it may be well to record the result.

In all, 586 female *A. fluviatilis* have been examined: of these 563 were normal in respect of the number of oviducal openings, and 23 were abnormal, as follows:

1. Extra oviducal opening on left penult. leg	7
2. ditto.....right.....	10
3. ditto.....on both penult. legs	1
4. ditto.....on both penult. & last legs	1
5. Single oviducal opening on left side only	3
6. ditto.....right ¹	1

Total abnormal specimens 23

¹ Mr R. ASSHETON sends me word of a similar specimen found among 80 of both sexes; Prof. W. B. HOWES of another among 144 of both sexes.

In all cases of supernumerary oviducal openings the normal openings were also present.

These cases are in addition to those received from Mr Benham. So far, therefore, the cases of extra opening amount to over 3 per cent. of females examined.

Of 714 *males* examined, only one was abnormal, having no trace of a generative opening on the right side, the vas deferens ending blindly and hanging free in the thoracic cavity. There was no female opening in this specimen, and the abdominal appendages had the form characteristic of the male on both sides. The base of the last thoracic leg on the right side bore no enlargement for the genital opening, but was plain and like that of the penultimate leg¹.

In cases of females which lacked one of the openings, the basal joint for the leg which should have been dilated and perforated for the opening, was undilated and resembled the basal joint of a penultimate leg. The oviduct upon the imperforate side was more or less aborted and hung loosely in the thoracic cavity.

In the abnormal females with extra oviducal openings, the oviduct divides generally into two just before it enters the legs, the fork being placed at the level between them. In some few cases no branch of the oviduct could be traced to the extra opening. In one specimen the extra opening led into a short tube which ended blindly, not communicating with the oviduct. The specimen (4) with extra openings on the penultimate and last legs had thus in all six oviducal openings. Those in the normal position on the antepenultimate legs were of normal size, those on the next pair were smaller but still of fair size, while those on the last pair of thoracic legs were very small, that on the left side being the smallest and admitting only a fair-sized bristle. In this specimen the single oviduct of each side forked in its peripheral third, giving a duct to each of the first two pairs of openings, but I failed to find any connexion between it and the openings on the last thoracic legs, which were very short blind sacs.

In all cases of extra oviducal opening the basal joint of the leg is expanded like those of the normal antepenultimate legs, the degree of expansion being proportional to the size of the opening. The normal openings are always the largest, but the extra ones are sometimes almost as large and would easily allow the passage of ova, but occasionally they are too small to let an egg through.

As regards principles of Homœotic Variation illustrated by these cases, three points should be especially remarked:

¹ Compare the following: *Astacus fluviatilis*. Amongst 1500 specimens 3 were found in which the tubercle through which the green gland opens was entirely absent. The opening itself was not formed and the green gland of the same side was absent. In another specimen the opening was deformed, probably owing to some mutilation. In this and the previous cases the green gland of the other side was considerably enlarged. STRAHL, C., *Müller's Archiv für Anat. u. Phys.*, 1859, p. 333, *fig.*

1. That this Variation may be bilaterally symmetrical, but that the evidence goes to shew *that it is more often unilateral*.

2. That there is a clear *succession* between the several oviducal openings, those of the antepenultimate legs being the largest, the penultimate the next, and those of the last legs the smallest.

3. That Homœosis may occur between segments which are *not* adjacent, as in the case of extra oviducal openings on the last thoracic legs, none being formed on the penultimate (No. 84).

4. That the Variation may be *perfect*.

With the foregoing, the following evidence may be compared, though it is very doubtful whether it properly belongs here¹.

86. ***Cheraps preissii*** [an Australian freshwater Crayfish, nearly allied to *Astacus*]. Of seven specimens received one was a normal male and three were normal females. The other three had on the basal joint of the third [antepenultimate] pair of legs a round opening, having the size and shape and situation of the normal female openings. These apertures were closed with soft substance. The fifth legs bore the usual male openings, from which the ends of the *ductus ejaculatorius* protruded. The coiled spermatid ducts were normal; but no ovary was found and no internal structure was connected with these female openings. VON MARTENS, E., *Sitzb. Ges. naturf. Fr. Berlin*, 1870, p. 1.
87. ***Astacus pilimanus*** ♂, a single specimen, and ***A. braziliensis*** ♂, a specimen collected by HENSEL in Southern Brazil, a similar opening was found on the third pair of legs; but in other specimens of these forms there was only a slight though sharply defined depression in the chitinous covering at this point. VON MARTENS, E., *l.c.*

¹ See also NICHOLLS, R., *Phil. Trans.*, 1730, xxxvi. p. 290, figs. 3 and 4 describing a Lobster (*Homarus vulgaris*) having male organs on the left side and female organs on the right.