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XXVII.—*On Abdominal Appendages in Hexapoda.*

By E. HAASE *.

IN his celebrated memoir upon the development of the Great Water-Beetle (*Hydrophilus piceus*) A. Kowalewsky, in 1871, first called attention to the fact that in the embryo of an insect stages might occur in which certain abdominal segments bear appendicular structures homologous with the thoracic legs. He first observed such leg-rudiments on the first two abdominal segments, and then saw the posterior pair disappear, while the anterior remained longer in the form of small tubercles. These results of Kowalewsky's were extended by K. Heider in 1886 † so far that "at a certain period of development indications of the rudiments of extremities may be recognized on all the abdominal segments."

In 1877 V. Graber ‡ succeeded in establishing the occurrence of rudimentary appendages homologous with the legs on the first and second abdominal segments in a *Mantis* (*M. religiosa*).

In 1884 H. Ayers found that in an American Cricket

* Translated from the 'Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin,' Jahrg. 1889, pp. 19-29.

† Abhandl. d. k. preuss. Akad. d. Wiss. in Berlin, p. 42.

‡ 'Die Insecten,' i. fig. 1; and see Morphol. Jahrb. xiii. (1888), tab. xxv. fig. 18.

(*Œcanthus niveus*), soon after the segmentation of the blastoderm, an indeterminate number of paired tubercles are formed upon the abdomen, which exactly correspond to the first traces of the true thoracic legs, but of which only those on the first and last (?) segments are retained for any length of time.

Further, in 1884, W. Patten observed in a Caddis-worm (*Neophylax concinnus*) that, when the thoracic legs are about half-grown, a pair of rudimentary appendages are developed upon each of the first three abdominal segments. He also found * that in the embryo of the House-Cockroach (*Blatta germanica*) a considerable number of abdominal appendages are originally developed, but that they rapidly disappear down to the first pair.

Finally, V. Graber † has recently recognized within the eight pairs of abdominal stigmata the same number of undeveloped limb-rudiments, of which the appendages of the first abdominal segment especially, both in their position and their histological structure, were perfectly homologous with those of the thorax.

From these statements we obtain a fresh support for the supposition *that the existing Hexapoda are to be derived from polypodous myriopodiform ancestors.*

After Balfour (1880) had adopted this view, the author sought (in 1881) to determine that primitive form of the Tracheata from which both Myriopoda and Hexapoda were to be derived, and came to the result of adopting as such a hypothetical form, nearly allied to the recent order Symphyla, which is represented only by the single genus *Scolopendrella*, and this he named *Protosymphyla*.

The more accurate investigations of last year, specially furthered by B. Grassi's labours, already enable us to attempt the closer definition of the characters of these hypothetical forms by the elimination of such peculiarities as appear to have been acquired secondarily by the existing orders which come under consideration.

Notwithstanding that in the indefiniteness of the parts of its mouth, the simplicity of its body-segments, &c., it far exceeds all known Tracheata, *Scolopendrella* itself is to be regarded as a form secondarily developed in several directions, especially degeneratively. Thus its tracheal apertures are confined to the lower surface of the head, its visual organs are aborted, and its thirteenth pair of legs converted into a tactile organ, which yet possesses no ganglion. If the sexual

* Quart. Journ. Micr. Sci. 1884, p. 48.

† Morphol. Jahrb. xiii. (1888), p. 598.

organs by their being paired, as also by their rather ventral position on each side of the intestine, show a primitive condition, their opening in an unpaired slit *, placed behind the third pair of legs, appears to be of secondary origin.

The order Chilopoda also, as already urged by V. Graber and the author in opposition to F. Brauer, is above all excluded from being regarded as a direct ancestor of the Insecta, by the decided drawing up of the first pair of legs to form part of the mouth-organs, and, further, the asymmetrical development of the dorsally-placed sexual organs is to be regarded as secondary, although their aperture, situated close in front of the anus, shows the original type, still represented by the Annelid-like *Peripatus*.

To decide the question whether the postembryonal increase from 9 or 7 to 17 † or 13 leg-bearing segments common to the Chilopoda Anamorpha (e. g. *Lithobius*) and *Scolopendrella* is to be regarded as a phyletic repetition, or, as is more probable, as a secondary larval phenomenon, our knowledge is still insufficient; at any rate, in *Scolopendrella* the gemmiparous zone is situated in front of the subsequent thirteenth pair, and therefore, as in the Chilopoda, immediately before the preanal segment, and the insertion of new somites occurs from before backward, so that in both the hindmost pair of ambulatory legs is also the youngest.

The order Diplopoda stands in the closest relation to *Scolopendrella* by the intimate fusion of the last two pairs of jaws into a gnathochilarium, which appears as a simple appendage even in the first embryonic rudiment, and by the anterior, although separated, opening of their paired and decidedly ventrally-situated genital sacs (behind the second pair of legs); and their apparently double segments are to be accounted for by the union of two individual segments effected by the fusion of their dorsal plates, as demonstrated by Newport and since, among others, by the author, Latzel, and, recently, Heathcote. In point of fact the resemblance of the embryo *Iulus* to an insect-larva, which is so often referred to, is also so far purely superficial, that one of the thoracic segments‡ has no appendage, and consequently the

* Successful serial transverse sections now enable me to confirm the union of the germ-sacs with the anterior unpaired slit, as stated by B. Grassi in 1884, in both sexes.

† In the Chilopoda referred to the poison-gland segment and also the preanal genital segment, which also bears jointed appendages, are included in the number 17.

‡ By analogy with *Scolopendrella nothacantha*, Latz. & Haase (= *Isabellæ*, Grassi), and *Pauropus*, and in accordance with Heathcote's view (Phil. Trans. vol. clxxix. (1888) p. 159), we must regard the *first* thoracic segment as the footless one.

third pair of legs of the Iulidæ must be referred to the abdomen.

As to the Pauropoda, they can only be regarded as ramifications of the great Protodiplopodan stem, degenerated by a subterranean mode of life, among other things the tracheal system having been completely lost, but which also in their genitalia and development still show throughout the fundamental form of this type, represented in a minor degree by *Polyxenus*, whilst their buccal organs and antennæ are aborted.

The examples of polypodism in the embryos of insects cited at the commencement had in common *the comparatively long persistence of the rudiments of the first pair of abdominal legs*, and recent investigations have even shown that, before their final disappearance, these may undergo special transformations. As long since as 1844 Rathke had observed peculiar "pilzhutartige Korper," also afterwards detected by Korotneff and V. Graber, and regarded them as "branchiform respiratory arrangements." Ayers also subsequently discovered on the same segment of the embryos of *Œcanthus* lateral excrescences of the ectoderm, which he described as vesicular appendages, united with the body by a short peduncle and lined with a layer of large cells, the cavities of which were connected with that of the body, and which he characterized as "branchiæ."

Further, in *Blatta*, W. Patten described the transformation of the leg-appendages of the first abdominal segment into similar "pear-shaped structures," but urged against their interpretation as branchiæ their thick cell-lining, and ascribed to them rather a sensorial function and a glandular one to their lining. The author has found similar appendages also on the first abdominal segment of tolerably mature embryos of *Periplaneta orientalis*.

While in *Hydrophilus*, according to V. Graber, the appendages of the first abdominal segment persist in the rudimentary state, on the embryo of the Cockchafer they show, according to the same naturalist, a considerable increase in size. As early as the seventeenth day * they have become comparatively stronger in growth than the typical legs, while "the originally very inconsiderable rudiments of the other (abdominal) segmental appendages have entirely disappeared"—nay, they finally become much longer than the thoracic legs and almost three times as broad. They then form a soft sac which is united with the body by a short peduncle, lined with large ectodermal cells and filled internally with meso-

* Morphol. Jahrb. xiii. (1888) p. 599.

dermic elements, but which possesses neither muscles, nerves, nor tracheæ. With the thirtieth day commences the retrogression of the abdominal sacs, and "on the excluded embryo we can find only the closed-up scar of its peduncle."

Conditions like those of the embryonic development of the insects just referred to are to be found *persistent* in the mature representatives of a section of Hexapoda, which, although nearly related to the Orthoptera, has been justly separated by F. Brauer from the other insects as "Apterygogenea," which never have possessed wings.

Thus in *Campodea*, the genus of Thysanura which in general stands nearest to the primitive form, there are leg-like appendages upon the first abdominal segment, and these in young animals are comparatively more strongly developed than in the adults; at the same time the whole ventral surface of this segment, by the abundance of cells and staining faculty, reminds one of embryonic tissue. The appendages are seated in the same direction as the thoracic legs, and also show an indistinct articulation into two or three joints. Thus only the portion of the ventral plate which is situated between them is to be regarded as the "ventral shield." The aborted musculature of these leg-rudiments, which completely resemble the developing extremities of the Symphyla, is also to be deduced from that of the thoracic legs, and in their segmental division, such as appears characteristic of mesoblastic appendages, it is traceable to the last joint of the rudiment. On the next (second) abdominal segment instead of the leg-like appendage there appears externally a cheliform movable piece, and within a cutaneous sac lined with very large hypodermic cells in part glandularly developed, which is protruded by the inflow of blood and retracted by special longitudinal cutaneous muscles attached to it at the apex. Towards the end of the body, at least to the extremity of the seventh abdominal segment, the planing down of the duplicatures and their fusion with the ventral shields gradually becomes more and more intense, at the same time the cutaneous sacs decrease in size, and the cheliform spur increases, so that even on this account the former may be claimed as older formations. At the eighth abdominal segment the saccules return within the body and at the same time come together in the middle in front of the opening of the sexual organs; as in *Japyx*, the movable abdominal spurs are wanting from this segment onwards also in *Campodea*.

In the largest representative of the Thysanura, *Japyx gigas*, there is on each side of the narrow, unpaired ventral shield of the first abdominal segment a tripartite mass of

glandular cells, immersed like a pocket, and united with retractor muscles and nerves, the efferent ducts of which lead into peculiar hollow capillary processes, so that one is reminded of the scent-glands of *Periplaneta* and *Corydia*; in *Japyx solifugus* the glandular mass is simple and less developed. In all species of *Japyx* there is at the margin of the duplicature which represents the rudiment of a leg, and amalgamates with the ventral shield, an unjointed movable chitinous appendage, exactly like an ordinary *terminal spur* (calcar).

As in *Campodea*, there are also in *Nicoletia*, according to B. Grassi *, ventral sacs and spurs from the second to the eighth abdominal segments; with regard to the important conditions in the first abdominal segment Grassi unfortunately says only:—"the false feet, and, I believe, also the vesicles, are wanting." In *Lepismina*, which, according to Grassi, possesses abdominal spurs only on the three penultimate segments, there is on each of the abdominal segments 1–8 "a pair of organs comparable with the segmental vesicles" (ventral sacs). In *Lepisma* the ventral sacs are entirely wanting, while the abdominal spurs may occur from the seventh to the ninth segment.

The ventral sacs and spurs are most highly developed and have been longest known in the genus *Machilis*, which was regarded by P. Mayer as particularly near to the primitive insects. The ventral sacs were described as long ago as 1836 by Guérin, as delicate, protrusible vesicles at the hinder margins of the ventral plates, which he regarded simply as resembling the branchiæ of the lower Crustacea. After the discovery of the tracheæ by H. Burmeister and C. T. von Siebold, this interpretation was rejected by the latter, but it has been revived by the most recent investigator, J. T. Oudemans. On the first abdominal segment there is one, on each of the four following segments two, and on each of the others a pair of delicate membranous sacs of considerable size, which are protrusible by the inflow of blood. They are covered with a transparent, perfectly smooth and solid chitinous cuticle, the partly glandular matrix-layer of which contains distinctly limited, flat cells with large nuclei, and they have their own nerves and strongly transversely striated retractor muscles; tracheæ never enter them. On the first abdominal segment the movable spurs which are elsewhere articulated outside the sacs are wanting, but this is probably to be regarded less as a primitive condition than as a sup-

* Boll. Soc. Ent. Ital. xviii. (1886), p. 6, and xix. (1887), p. 7.

pression of the structure, due to the bending of the abdomen, which is angularly applied to the thorax.

Organs which we may regard as homologous with these ventral sacs are met with first among the Chilopoda in the genera *Lithobius* and *Henicops*, standing still nearer to the Protosymphyla, in the coxæ of the last four, or more rarely five, pairs of ambulatory legs, where they occur as thread-spinning coxal glands. In the Scolopendridæ and Geophilidæ, derived by elongation from the shorter primitive forms, analogous organs, here characterized as pleural glands (on account of the union of the coxæ with the pleuræ), occur in the last leg-bearing segment.

Among the Symphyla a lobiform plate appears in *Scolopendrella immaculata* on the coxæ of the second pair of legs, and this in the next segment is transformed into a ventral sac which is only slightly protrusible. The distal part is covered with a transparent homogeneous chitinous cuticle, and lined with a few gland-like hypodermic cells. Below this layer of cells lies the reticulated tissue of the adipose mass, through which blood-corpuscles pass into the ventral sac. Outside of this coxal saccule, as we must call it here, there is to the thirteenth segment a claw-like appendage increasing in size posteriorly, which can by no means be regarded as the rudiment of a leg, but only as the product of transformation of a joint-spur, and which occurs similarly on the two posterior pairs of coxæ in *Machilis* *. On the twelfth segment the coxal sac is reduced to a softer, oval, membranous piece; in the undeveloped legs of young animals we find no trace of appendages on the coxæ.

In the order Diplopoda also protrusible sacs situated in the coxæ are often present; thus they occur in the anterior segments in Chordeumidæ and *Lysiopetalum*, as well as in the section of the Colobognatha derivable from the Chilognatha, in *Polyzonium* and *Siphonophora*, and indeed they appear first, and at the same time most strongly developed, on the third pair of legs, the somite of which would therefore correspond to the first abdominal segment of the Hexapoda.

As these ventral sacs in the coxæ of the Myriopoda, or at the posterior margins of the ventral plates of the Thysanura, usually occur at the end of partially unconnected developmental series, we are compelled to assume their probably polyphyletic development within the order. And yet, in their position, in their origin, and at the same time in their

* To what extent such structures, originally equivalent to the ordinary cutaneous setæ, can become developed, is shown especially by the tibial spur, *e. g.* of the Heterocera.

histological structure they show so many common features, that we may, with H. Eisig *, think of them as repetitions of old inherited tendencies. To this may be added that in the pterygote Insects referred to they likewise occur during embryonic life in a position relatively to the limbs which corresponds with that demonstrated in the Thysanura and Symphyla, inasmuch as the vesicular sac is always situated within the coxal joint or the leg-like abdominal spur, just as V. Graber has indicated in the development of *Hydrophilus* †.

Now to glance at the physiological significance of the ventral sacs, it seems probable, from the developmental history of *Œcanthus*, and especially of the Cockchafer, as already assumed by H. Ayers and V. Graber, that in these Insects they perform secondarily a *respiratory* function, which can only be regarded as a special development of cutaneous respiration (the above-mentioned embryos, in the egg, lying generally in moist earth), as the dorsal vessel and tracheæ are not yet in action when these ventral sacs possess their highest development. That in the Symphyla and Thysanura also the ventral membranous sacs have a similar *respiratory*, and perhaps a specially excretory significance, is supported by the defective or aborted development of the tracheal system and the ventrally concealed position of the stigmata in these forms.

Thus *Scolopendrella* has only cephalic stigmata, the tracheæ from which extend exactly into the third segment, onward from which the coxal membranous sacs occur. So also *Campodea* has stigmata only on the three thoracic segments, and these lead into feebly developed tracheæ; and *Nicoletia*, according to Grassi, forms only delicate dorsal longitudinal trunks, and feeble ventral transverse anastomoses, so that here also the tracheal system appears to be only feebly developed. In *Machilis*, again, the longitudinal trunks are entirely wanting, and the feeble abdominal tracheæ present only a slight ramification. According to the observations of J. T. Oudemans (and the same thing was observed by the author in the open) *Machilis* in captivity extruded its ventral sacs, especially if it were in a warm and at the same time moist atmosphere, but always only when it was perfectly quiet; this is against the one-sided conception of the ventral sacs as defensive arrangements analogous to the fleshy forks of the Papilionid larvæ, for example, seeing that the latter come into action only when their bearer is disquieted.

* Monographie der Capitelliden &c. in Fauna und Flora von Neapel &c. xvi. (1887), pp. 371–403.

† Morphol. Jahrb. xiii. (1888), p. 605.

In favour of at least the partially respiratory function of their ventral sacs, the feeble development of the tracheæ in the above-mentioned Diplopoda and Collembola may be cited; in the latter the ventral tube, which is often very extrusible, corresponds to the first pair of ventral sacs of the Thysanura, and stigmata occur at the utmost (*Sminthurus*) on the anterior margin of the prothorax. Further in favour of this function is the fact of the deficiency of the ventral sacs in those Thysanura which possess a more highly developed tracheal system of the Orthopterous type, with strong ventral longitudinal trunks, such as *Japyx gigas* and *solifugus*, *Lepisma* (and *Lepismina*?). On the first abdominal segment of *Japyx*, the decidedly glandular function of the ventral sacs, as in the Chilopoda, which, according to H. Eisig (*l. c.* p. 392), is to be regarded as the primitive one, has apparently alone persisted. Any special glandular functions of the ventral sacs in other forms still need more accurate observations, which the author hopes to make very shortly.

That in reality the ventral sacs, of the Collembola for example, perform other functions is rendered probable by some observations upon the living animal, the results of which, however, are contradictory; thus Nicolet, Olfers, Lubbock, and Tullberg ascribe to the ventral tube the action of an adherent organ, while O. Reuter regards it as an arrangement for the reception of water; in *Macrotoma*, again, A. Sommer has described large, unicellular glands, opening by a pore.

The ventral sacs of *Machilis* also show upon the dorsal surface a special glandular epithelium of much thickened, sharply defined cells, the plasma of which breaks up into fine, close cords, just as has been demonstrated by A. Weismann and C. Grobben for the excretory antennal glands of the Crustacea.

XXVIII.—*On the Nomenclature of the Oral Folds in the Shells of* Clausilia. By Edgar A. Smith, F.Z.S., and B. B. Woodward, F.G.S.

[Plate XI. A, figs. 1–4.]

It is well known to all conchologists that among the distinguishing features of the genus *Clausilia* the folds (*plicæ* and *lamellæ* as they are variously termed) within the aperture or mouth of the shell are especially characteristic.