THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[THIRD SERIES.]

No. 50. FEBRUARY 1862.

XII.—*Anatomico-physiological Investigations on the Respiratory Process in Insects.* By H. Rathke*.

I. Perfect Insects.

§ 1. Roesal, in the second volume of his 'Insekten-Belustigungen,' has noticed that in *Æschna grandis* the abdomen is alternately expanded and contracted, and that this movement is connected with the respiratory process. Carus subsequently made the same observation on *Locusta verrucivora*. These assertions led Rathke, in 1831, to examine all the larger insects which he could procure in the vicinity of Dorpat, to see whether they exhibited these movements of the abdomen. He found that, in the majority of insects which he could obtain for examination, the abdomen is alternately expanded and contracted; and fully convinced himself that in *Cetonia* and *Scarabæus* this movement has an effect upon the respiration.

§ 2. In all insects in which such movements of the abdomen may be distinctly perceived, these are not of the same kind, but in different insects they present many differences. These differences depend upon the peculiar organization of the wall of the abdomen. But whatever may be the kind of movement, it is always caused and rendered possible,—1, by the epidermis of the abdomen being solid and thick in some parts and soft and thin in others, so that those parts of the cutis on which the epidermis forms plates or bands of greater or less thickness may be pushed closer together and then again somewhat removed from each other; and 2, by the presence of peculiar muscles on the inner surface of the cutis of the abdomen, passing from one part of the cutis to the other, and capable of effecting a movement in it.

* This posthumous memoir, prepared by Rathke in 1835, has just been published by Dr. Hagen in the 'Schriften der Königl. physik. ökonom. Gesellschaft zu Königsberg,' 1st year (1861), p. 99. Translated by W. S. Dallas, F.L.S.

In general the cutis of the abdomen has several transverse bands, upon each of which the epidermis is harder and thicker than in the space between it and the next band; and it is only exceptionally that in some insects the spaces between the bands are either only represented by a constriction or completely unrecognizable. But when a thinner and softer skin is interposed between two bands, the posterior and smaller one is generally more or less immersed in the preceding, so that its anterior margin is more or less concealed by the posterior margin of the latter. Each band usually consists of two distinct halves, an upper and a lower one, united at the sides of the body, like the bands themselves, by a thinner and softer part of the cutis. In many insects, especially the Hymenoptera, the upper half or plate of most of the bands embraces the lower one more or less; but this is not the case in the majority, in which the softer part between the upper and lower halves may be recognized from without; this becomes broader and more distinct in proportion as the sexual organs are dilated by their products, or the intestinal canal is filled with food.

The muscles by which the hardened parts of the abdominal skin are united and moved are so arranged, in most insects, as only to approximate these parts; by which they only diminish the cavity of the abdomen, and produce an exspiration. Hence, in the following memoir, whenever the abdominal muscles are spoken of without any special qualification, those which relate only to exspiration are intended. The means by which the hardened parts of the skin are again separated, and the cavity of the abdomen again dilated, to produce inspiration, will be referred to hereafter.

§ 3. In most Coleoptera it is the superior wall of the abdomen that moves in respiration, being alternately depressed and elevated. This movement, however, does not extend in all over a relatively equal portion of the abdomen. In those whose elytra extend over the whole abdomen, all the belts or segments of this division of the body, with the exception of the last, usually take part in the movement; whilst in those, such as *Scarabæus* and *Cetonia*, whose elytra do not reach so far, the penultimate and even the antepenultimate segments take no part in it, which is indeed the case with all those segments which are of nearly equal thickness throughout and form a simple ring. Movement is observed in all those segments in which the epidermis of the ventral and lateral walls presents a firm plate, but in which that of the dorsal wall forms a thinner and usually smaller plate, separated by a membranous interspace at its ends from the above-mentioned larger plate, and at its anterior and posterior margins from the similar neighbouring plates. The movement is gene-

rally progressive, advancing rapidly from before backwards, rarely commencing in the middle of the abdomen and spreading both forwards and backwards.

The muscles by which these movements are producedare exceedingly simple. Each segment which takes part in it is furnished only with a single pair of muscles for this purpose, each of which is attached by one end to the lateral wall and by the other to the dorsal wall or plate, in both places close to the soft part of the cutis. All these muscles, therefore, run transversely across the softer and more flexible parts of the abdomen. When they contract, the dorsal wall of the segment to which they belong is drawn downwards more or less according to the extent of the soft interspace, by which the cavity of the abdomen is more or less diminished and the softer skin of the interspace more or less folded. The respiratory movements are stronger in some Beetles, weaker in others. In those which need strong respiratory movements the above-mentioned muscles are more coarsely fibrous, thicker, and generally larger in proportion to the size of the entire body than in those in which weaker movements are sufficient; but in all cases they form only short bundles, which are either of nearly equal thickness and breadth throughout or become narrower and thinner from above downwards. Besides the muscles just described, several other muscular layers occur in the abdomen, both on the dorsal and ventral walls. Between each pair of the upper plates which are moveable upon one another there is, on each side, a broader or narrower muscular layer, passing from the anterior margin of the posterior plate to the inner surface of the anterior one, and adhering at a greater or less distance from the anterior margin of the latter. Similar muscular bands, situated and attached in the same way, occur also on all the inferior plates which are mutually moveable. These lower bands are usually far thicker and more coarsely fibrous than the upper ones. Usually these two kinds of muscles only serve to bend the abdomen downwards and straighten it again; but, if they both act together, they may also shorten the abdomen a little, and if, as is usually the case, the upper wall is likewise drawn towards the lower one, diminish its cavity, and thus increase the quantity of air expelled. It must, however, be observed that such a universal contraction of the abdomen occurs but seldom, and not always even when the beetle is much alarmed.

The movement of the dorsal wall is not comparatively equal in all Beetles. The movement is greatest in those whose tracheæ possess many vesicular dilatations, such as *Cetonia* and *Scarabæus*, and less in those whose tracheæ run uninterruptedly without dilatations so as to produce a shrub-like appearance; it is least in those in which the tracheæ appear to be narrowest in

proportion to the whole body. The dilatations and contractions of the abdomen do not follow each other with equal rapidity in different Beetles; they appear generally to be rapid in proportion to the size of the air-vessels; in the Beetles examined by the author, they succeed each other most rapidly in *Cetonia* and *Scarabæus*. But here we have to consider whether the animal is quite quiet or in motion or troubled, and also whether it has lately taken a sufficiency of food or whether it is hungry; for when it has fed well or moves, the movements of the abdomen follow one another far more rapidly than when it is quiet or fasting.

Note I.—The above observations were made on species of the genera *Cetonia, Scarabæus, Cerambyx, Hister, Dytiscus, Carabus, Chrysomela, Tenebrio, Bruchus* and *Attelabus*. It is remarkable that in *Staphylinus*, in which, notwithstanding its differing so much in many respects from other Beetles, the structure of the abdominal segments and of their muscles is the same, no distinct movement of the upper pieces of the abdominal segments could be perceived. On the other hand, the upper part of the third thoracic segment was seen to rise and fall alternately, and often very considerably. The author could not ascertain whether for this movement there are peculiar muscles not occurring in other Beetles. He observed, however, that in *Staphylinus* the widest and most important air-vessels occur in the posterior half of the thorax. The above-described movements of the abdomen were not observed in *Coccinella*, in which, contrary to the general rule, the upper plates of the abdomen are larger than the lower ones. In the *Carabidæ* also (at least, in *C. granulatus*) the upper half of the last thoracic segment is moveable, and rises and falls a little during respiration, although less than the upper halves of the abdominal segments.

Note II.—In *Tenebrio molitor* the upper pieces of the abdominal segments are so transparent, that the intestines, and especially a quantity of tracheæ which run quite close beneath those pieces, may be distinctly seen through them. Many of these tracheæ, especially those which run from below upwards, may be seen in constant movement; they are observed sometimes to be alternately stretched out and again curved, and sometimes to be moved forwards and backwards. This movement is not proper to them, but is communicated by the dorsal vessel to which they are attached.

Note III.—In the vivisection of a *Scarabæus stercorarius*, the author, having removed the dorsal wall of the abdomen and drawn forth the intestinal canal a little, by which many small tracheæ were torn, was astonished to see several of these tracheæ move very briskly, like worms, in the water in which the Beetle was being dissected. For some minutes he supposed that the move-

ment was proper to the air-vessels themselves, but at last he perceived that several extremely delicate thread-worms issued from these vessels; others twisted about in some of the air-sacs of the abdomen.

§ 4. In the *Tabanidæ*, the different genera and species of which have a more or less depressed abdomen, the upper plate of the abdominal segment is somewhat larger than the lower one, and consequently assists more or less in the formation of the lateral walls of the abdomen, with which the lower plates have little or nothing to do. The thinner and softer portion of the skin intervening between the upper and lower plates is always of considerable breadth; it is always far broader at its anterior than at its posterior end, and possesses great extensibility and elasticity.

From the author's investigations of several species, and especially of *Tabanus autumnalis*, the respiratory movements of these animals are effected by the movement of the lower abdominal plates (especially those of the anterior segments) to and from the upper ones, during which the softer lateral portions appear alternately broader and narrower. But when the respiration is increased in force, the ends of the upper plates of the anterior segments, which assist in forming the lateral walls of these segments, are somewhat drawn inwards and then again pushed out. With a still more powerful respiration the lower plates are pushed a little over each other, and all drawn a very little towards the breast; so that the lower surface of the abdomen is somewhat shortened, but immediately returns to its former position.

In the *Tabanidæ*, as in the Beetles, peculiar muscles exist only for the contraction of the abdominal cavity, and these muscles coincide almost exactly in position and attachment with those of the Beetles. All these muscles are, however, both absolutely and relatively, very delicate and thin.

At the base of the abdomen there are two large air-sacs; the tracheæ are only of moderate width, and shrub-like in form. The canal which unites the tracheal stems on each side is also only of moderate size.

§ 5. In *Empis* the inferior pieces of the abdominal segments are comparatively smaller than in *Tabanus*; they form the entire ventral wall of the abdomen. Only the three or four anterior ones rise and sink alternately, but very weakly and scarcely perceptibly. The abdomen also frequently curves a little downwards.

In the *Tipulariæ* also the lower pieces of the three or four anterior segments, which are comparatively still narrower, move up and down scarcely perceptibly and but seldom. No movement that could be regarded as connected with respiration was de-

tected in the other abdominal segments of even the largest of these insects.

§ 6. The abdominal segments of the *Muscidæ* also possess two plates of hardened epidermis. In some of these animals, especially in the genus *Musca* itself, the upper plate assists to form a great part even of the ventral wall; in others it has but little to do with this. The lower plates are very considerably smaller, and in most of these insects resemble flat tiles. In some each lower plate is more elongated, and is then sometimes extremely narrow. But the most anterior of these plates is always the largest, and the rest generally diminish in size by degrees towards the posterior extremity. The interspace of soft skin on each side, between the upper and lower plates of each segment, is narrower or broader, according as the upper plate occupies more or less of the segment. It is usually very narrow, but becomes considerably enlarged when the alimentary canal is very full, or when the sexual organs, especially the ovaries, have attained a great size.

During quiet respiration only the lower pieces of the segments move a little up and down. When respiration takes place more violently, as, for instance, when a fly is held by the wings, the ends, or rather those parts of the upper plate which assist in forming the ventral wall, are alternately drawn in and pushed out, but at the same time the ventral wall, as it rises, becomes elongated, and afterwards, when it sinks, is again shortened; so that in the former case the abdomen is more straightly extended, and in the latter more curved downwards. When the fly is not troubled, the above-mentioned contraction and dilatation of the abdominal cavity takes place very rarely.

The tracheæ have a shrub-like form, and, like the canal which unites their stems on each side, are only of moderate diameter. In each side of the body, close to the thorax, there is a tolerably large air-sac.

§ 7. In *Panorpa* the upper and lower plates of each abdominal segment are of nearly equal size, and the interval on each side between the plates is proportionally very broad. Nevertheless the cutis, and especially the epidermis forming this interspace, are tolerably thick. Respiratory movements are very distinctly perceived in the three or four first segments of the abdomen: they consist in the alternate drawing in and pushing out of the skin between the plates, during which, however, the anterior half of the abdomen is scarcely perceptibly contracted from above and below.

§ 8. In the Lepidoptera the upper plates of the abdominal segments are not much larger than the lower ones. The intervening skin is tolerably wide, as in *Panorpa*, but somewhat

thinner and softer. The respiratory movements are of the same kind as in *Panorpa* but stronger, and extend throughout the whole length of the abdomen; in some species they are more distinctly visible in the anterior, in others in the posterior part of the abdomen.

§ 9. In *Blatta* the abdomen is broad and flat in proportion to its length. The upper halves of the segments are of the same size as the lower ones, and both extend to the rather acute lateral margins of the abdomen. Between them there is on each side a moderately wide space occupied by a soft skin, in which a series of constantly open stigmata is visible.

During respiration there is an alternate mutual approximation and removal of the upper and lower plates; but the respiratory movements do not take place rapidly.

§ 10. In the Dragon-flies it was observed that, when they are in perfect repose, that part of the abdomen on which the central nervous cord rests alternately rises and falls, although but slightly. This movement is most remarkable in the genera *Æschna* and *Libellula*, and weakest in *Agrion*; in the *Æschnæ* it is strongest in the posterior broader half of the abdomen. In *Æschna* and *Libellula* the alternate contraction and expansion of the abdomen is repeated eighty or ninety times in a minute. With more powerful respiration the abdomen is also alternately contracted and expanded at the sides, and then the lateral margins of the abdomen bend a little downwards during the contraction. This is very strikingly the case in the posterior part of the abdomen in the species of the genus *Æschna*. These respiratory movements are rendered possible partly by the peculiar structure of the abdominal segments, and partly by their tissues and the presence of peculiar muscular bundles in their interior. Each segment, except the first one in male individuals, consists essentially of two very elastic plates or shields of hardened epidermis, of which one forms the lateral and dorsal walls of the segment, and the other, which is much smaller, the ventral wall; these plates are separated at both sides by a space, occupied by a softer skin. At some distance from the posterior extremity of the lower plate there issues on each side a slender muscular bundle, which becomes somewhat broader as it passes upwards and outwards to the other plate of the segment, to which it is attached at some distance from the lower margin. When these bundles contract a little, the lower plate is moved inwards, and the cavity of the abdomen is contracted only from below. If they contract more strongly, not only is the lower plate drawn further in, but the parts of the upper plate which represent the lateral walls are somewhat drawn together and their lower margins pushed over the lower plate, by which the

cavity of the abdomen is contracted from below and also from the right and left. The subsequent dilatation of the abdomen is not effected by any peculiar muscles, but only by the elasticity of the skin.

This rhythmical contraction and expansion takes place even in the second abdominal segment of the male *Libellulæ*; and by this means the curious sexual apparatus occurring in this segment is set in motion.

The tracheæ have both stems and branches of considerable diameter, and are present in great numbers. Besides these air-vessels, several vesicles of considerable size, which collapse when pricked, belong to the respiratory system: the majority of these are placed in the abdomen.

§ 11. In the *Grylli* and *Acridia* the skin of nearly all the segments of the abdomen is likewise hardened into two separate plates, one of which forms the lateral and dorsal walls; the other, which is much smaller, belongs to the ventral wall. The latter piece is wanting in the first segment, which forms only a half ring; on the last segment it is present, but formed differently from the same part in the intermediate segments, and implicated in the sexual organs. On these intermediate segments there is on each side, between the upper and lower plates, a very considerable space in which the epidermis is soft and thin, and which possesses great extensibility, as may be seen in gravid female *Grylli*. In the genus *Gryllus* the ends of the lower plates reach only to this interspace; but in the *Acridia* the ends of these plates form longer and shorter processes, according to the different segments to which they belong, running upwards over the inner surface of the above-mentioned soft parts, and applying their free ends against the inner surface of the upper plates. The muscles attached to different parts of the abdominal skin, and serving for the most part to produce the respiratory movements, are very different both in number and attachment in *Gryllus* and *Acridium*. In *Acridium*, where they are most simple, we have,—1, a pretty strong muscle on each side springing from the base of the outer surface of the process into which each inferior plate is produced, passing upwards and somewhat backward to attach itself to the upper plate of the same segment; when these muscles contract, the abdomen is narrowed from below, the ventral wall being drawn a little upwards; 2, two other smaller muscles on each side, passing from the anterior margin of the lower plate of each segment thus furnished, forward to the next preceding lower plate; these muscles seem to shorten the ventral wall, and appear to have no essential part in the respiratory process; 3, a great quantity of muscular fibres forming a long and narrow band between every two

approximate upper plates, passing from the anterior margin of each posterior plate to the inner surface of the preceding one; these muscles also take no part in the respiratory movements, but seem to shorten the dorsal and lateral walls. The above description of the muscles applies only to the smaller species of the genus *Acridium*, and not to the larger ones, such as *A. stridulum* and *A. migratorium*. In these there is, on the outer surface of each process of the inferior plates, a tolerably strong, long, bandlike muscle, running from the apex of the process downwards and backwards, and attaching itself to the lower end of the upper plate of the same segment. If all these muscles contract, the ventral wall of the abdomen must be depressed, and the ventral cavity enlarged; so that these muscles must be regarded as inspiratory. Each segment likewise possesses a pair of exspiratory muscles, which are also of considerable size and form two flat, broad, and not very long bands, each of which springs from one of the outer margins of the lower plate, and, becoming broader, ascends upwards and outwards to attach itself to the lateral wall of the upper plate of the same segment. There are also muscles similar to those described under 2 and 3 in the smaller *Acridia;* but those of No. 1 are wanting.

In the various species of *Gryllus* (or *Locusta*) we have,—1, muscles which agree perfectly with those described under No. 3 in *Acridium*; 2, on each side of the abdomen there is a simple series of small muscular bundles, which, in position and attachment resemble those described under No. 2 in the *Acridia*. These and the preceding have no particular connexion with respiration. All the other muscles now to be mentioned, on the contrary, are probably devoted entirely to respiration: there is nothing like them in *Acridium*; and they spring from a small and tortuous fold, which is formed by the soft skin between the upper and lower halves of the abdominal segments, and projects a little inwards towards the ventral cavity. 3. A small muscle passes from the above-mentioned fold, inwards, forwards, and downwards, to the lower part of each segment, except the first and the last two. 4 and 5. In each of the same segments two somewhat larger muscles spring on each side opposite each of the preceding, from the fold, pass upwards and outwards, and attach themselves to the end of the upper plate. In the penultimate segment there is only one pair of such muscles. When the cavity of the abdomen is gradually extended, as especially in female insects by the products of the sexual organs, the soft space between the upper and lower plates increases considerably in breadth, and the muscles just described then not only become greatly elongated, but increase generally in size; but when these muscles and, simultaneously with them, those described

under No. 3 are contracted, the cavity of the abdomen is diminished from above and below. 6. A series of seven pretty strong muscular bundles, each of which always lies close behind the other, and has its axis directed from before backwards, covers the greater part of the above-mentioned fold on each side of the body. Each bundle corresponds with an abdominal segment; but whether it is connected with respiration is uncertain. 7. Lastly, wherever two segments are contiguous, a tolerably strong muscle passes transversely from the right to the left fold, and conceals on each side the contiguous extremities of each pair of muscles described under No. 6. When these muscles contract, the folds of skin to which they are attached are drawn a little inwards, and the cavity of the abdomen is narrowed laterally in the neighbourhood of these folds. These latter muscles also are greatly extended when, towards the close of summer, the generative organs are much enlarged and the abdomen is filled with an accumulation of fat, but they are not thereby weakened in their action. Between these muscles and the ventral wall there is a considerable space, in which the chain of ganglia and four very wide air-tubes are situated.

The tracheæ occur in greater number in the *Grylli*; and those which belong to the body-wall, with the exception of their final ramifications, are of considerable diameter, forming elongated and sausage-like tubes. Notwithstanding their width, they do not collapse when cut through, from their having strong and very elastic spiral fibres in them. They also become dilated again after being compressed. There are four or five pairs of vesicular dilatations immediately above the ventral wall of the abdomen, and a pair of much larger ones in the thorax above and behind the first pair of legs. In the *Acridia* the tracheal stems on the walls of the abdomen are fewer, but partly also much wider than in the *Grylli*, and, from their great diameter, their collapsing when cut, and their not expanding again completely when compressed, they form a sort of transition to the air-sacs. Their spiral fibres are comparatively thin and but slightly elastic.

§ 12. It is remarkable that *Acheta campestris*, although externally less nearly related than the *Acridia* to *Gryllus verrucivorus* and others of its genus, nevertheless resembles the *Grylli* much more than the *Acridia* in its respiratory apparatus.

This insect is essentially distinguished from the *Locustæ* (*Grylli*) in the structure of the skin of the abdomen, only by the lower plates of the abdominal segments being proportionally larger and especially longer, and by the first segment possessing a lower plate. Parallel to these plates, but at a tolerable distance from them, there are, as in *Gryllus*, several transversely stretched muscular bundles, passing from the soft parts of one lateral wall

to the same spot on the opposite wall; and of these, one is always placed where two segments are contiguous. Below them are the ventral chain and two long and wide tracheæ. When they contract, the abdomen is somewhat narrowed from each side. It is narrowed from below by numerous muscles, of which the first segment has two pairs, and all the rest, with the exception of the last, one pair. All these muscles unite the ends of the lower plates with those of the upper plates of the same segments: they lie close to the inner surfaces of the lateral soft spaces. Other much smaller muscles serve to draw inwards these soft spaces, which are of considerable width, and thus also contract the abdomen from above and below. Three of these small bundles pass up from each end of the lower plates and attach themselves to the soft skin; but one such muscle comes from the extremity of [the upper plate of] each of the same segments and attaches itself opposite to the first, also on the soft skin. The abdomen may be shortened by several muscles which unite together its individual segments: of these, one pair always goes from the end of the lower plate of each segment to that lying immediately before it, whilst others, forming long and slender bands, unite the upper plates of each two segments, as in the *Locustæ* (*Grylli*) and *Acridia*.

The respiratory movements themselves are probably effected exactly as in the *Locustæ* (*Grylli*); but the author had no opportunity of observing *A. campestris* alive.

In *Acheta Gryllotalpa*, Fab. (*Gryllus Gryllotalpa*, Lamk.), the skin of the abdomen is formed exactly as in *A. campestris*, but the muscular apparatus of this part is much simpler. The upper plates of the abdominal segments are united to each other as in *A. campestris*; this is also the case with the lower plates, but the muscles of these are absolutely and relatively much broader and stronger. The muscles uniting the upper and lower plates are not of the same kind in all the segments; in the two anterior segments they are of the same form as in *A. campestris*, but much stronger; in the other segments they form broad bundles, of which some fibres run from the upper plate, and others from the lateral soft skin, to the lower plate, and of which some take a straight course, while others appear to cross. The specimen examined had been for several years in spirit, and had become extremely hard.

The tracheæ in both species of *Acheta* are very wide, but never vesicularly dilated.

§ 13. In the broad and rather depressed abdomen of *Mantis religiosa* the lower plates of the segments are nearly of the same length as the upper ones. At the sides a blunt edge is formed by them and the soft skin uniting them. Each of the lower

plates is united to the next one by a pair of rather broad and strong muscular bands (the muscles uniting the upper plates are much weaker); so that the abdomen can probably be a good deal shortened. For the contraction of the abdomen upwards and downwards, several pretty long and almost bacilliform muscles pass from the upper to the lower plates in the vicinity of the lateral margin. The first two segments have each only one pair of such muscles; the segments from the third to the sixth possess each two pair, one close behind the other. The soft skin can also probably be drawn inwards; for on each side of the abdomen are several short muscular bundles, of which one always runs from one end of each lower plate, obliquely from before backwards, and a second, partly covering the former, from behind forwards to the soft skin, to which they are attached. Two other pairs of muscles on each side go from the upper plate to the soft skin—one of these, the largest, from the middle of each plate, the other from its posterior margin.

§ 14. In *Truxalis* the organization of the wall of the abdomen is almost exactly the same as in the larger *Acridia*.

§ 15. All the *Hymenoptera aculeata*, with the exception of the Ants, have, according to the author, essentially the same organization of the abdomen and respiratory movements.

Each segment, except the first, consists of two very firm plates, generally very broad in proportion to their length, both nearly of the same length, and united at the sides of the body by a softer skin in such a manner that the upper one projects over the ends of the lower one, and therefore the soft skin uniting the two plates cannot be seen from without. All these segments are also pushed into each other like the tubes of a telescope; so that the soft skin uniting them is likewise usually concealed. In most of these insects the anterior angle of each extremity of the lower plates of most of the segments projects greatly, forming a point, directed forwards. (The author observed in a Bee, the species of which he could not determine at the time of making the observation, that between each of these angles and the corresponding end of the upper plate there was a small and nearly lenticular cushion, consisting of a completely closed, white, opake, and rather firm sac, the walls of which were very thick in proportion to its cavity.)

The respiratory movements are effected with great quickness and vivacity, are rarely interrupted, and give the insect a restless aspect; they consist in an alternate abbreviation and elongation of the abdomen, the individual segments being drawn more deeply one into the other and again pushed out. In those which have the abdomen nearly straight, such as the Wasps, these movements usually take place in a straight direction; but in

those in which the abdomen is more or less curved downwards, as in the Humble Bees and Bees, the abdomen, when extended, is at the same time more strongly decurved.

The shortening of the abdomen diminishes its cavity and causes exspiration; its elongation enlarges the cavity, and is connected with inspiration. Sometimes, however, in this latter movement, especially when the insect protrudes its sting, the upper plates of the segments are pushed further over the lower ones, the cavity of the abdomen is contracted nearly as much as it is elongated, and thus the inspiration is hindered; nay, sometimes the upper plates may be so strongly pushed on the lower ones that an exspiration must be produced. The shortening of the abdomen (exspiration) is effected by peculiar muscles attached to the dorsal, ventral, and lateral walls of the abdomen. The ventral muscles are only of moderate size, and form cords, of which two always run (somewhat converging) from the anterior margin of each segment, nearly to the same part of the preceding one. The dorsal muscles take the dorsal vessel between them, as the ventral ones do the chain of ganglia, and are attached to the upper plates in the same way as these to the lower ones; they are, however, rather thinner. Of the lateral muscles one springs from the upper and anterior angle of each lower plate, except that of the first segment, and passes obliquely downwards and forwards, gradually becoming broader, to the lower plate of the preceding segment; and another, from the lower and anterior angle of each upper plate in the same segments, turning upwards and forwards, attaches itself to the inner surface of the same plate in the preceding segment. Both muscles reach from the segments from which they spring nearly to the anterior margin of the other.

The act of inspiration is effected partly by the elasticity of the softer skin between the segments, but still more by peculiar muscles, of which there are two pairs on each segment, except the first. In most (and probably in all) aculeate Hymenoptera these are much thicker than the muscles just described as being attached to the lateral walls and serving for exspiration. The inspiratory muscles are also placed in pairs on each lateral wall of the abdomen; they spring in each segment from the same spots to which the exspiratory muscles are attached, but lie behind these, and do not run, like them, obliquely forwards; but, supposing the abdomen in the act of inspiration, the muscle springing from the inferior plate of each segment passes straight down to the hinder margin of the inferior plate of the preceding segment; that springing from the upper plate goes straight up to the hinder margin of the upper plate of the preceding segment. In the state of exspiration both muscles are

directed somewhat obliquely backwards from their points of origin.

§ 16. In the Hymenoptera with an ovipositor (*Terebrantia*) the author's observations were made chiefly on *Ophion luteus*, *Ichneumon persuasorius*, and *Sirex gigas*. In these the upper plates of the abdominal segments are considerably larger than the lower ones, and form both the dorsal and lateral walls of the abdomen; the lower plates occupy only the ventral wall. The former also project a little beyond the latter, with perfectly free extremities.

In the respiratory movements the lower plates are usually somewhat elevated and again depressed; more rarely, and only when the respiration is very forcibly effected, the ends of the upper plates are also set in motion inwards and outwards.

The tracheæ are shrub-like; and no air-sacs ever occur.

Details.

In *Ichneumon persuasorius* the lower plate of each of the first eight segments of the abdomen is rather broad; the first is simple, the rest partly hard and partly soft. The harder and thicker parts form three longitudinal bands, of which the broadest occupies the middle of the plate, the others lying close to its lateral margins. Between these and the middle band are two softer bands, which in the specimen examined were a little bent in towards the ventral cavity; so that each plate, viewed from beneath, showed two moderately broad and deep furrows running in the direction of the length of the abdomen. During exspiration the entire plate moved upward, and during inspiration downward; and in the latter act the above-mentioned furrows were not unfrequently effaced, so that the plate became quite flat and a little widened. On the abdomen being opened it appeared that on the convex side of each of the furrows there was a longitudinal muscle running from the anterior margin of each plate to the same margin of the following one: from its position and attachment, its contraction must flatten the furrow-like part. A second, shorter and flatter muscle passed from each anterior angle of the lower plates, outwards, upwards, and backwards, to the upper plate of the same segment; these serve for exspiration. (Superior longitudinal muscles were also present.)

In the female of *Sirex gigas* the two hindermost segments of the abdomen have no inferior plates; in the other six segments the lower plates are present and very broad. From each anterior angle of these plates a moderately strong exspiratory muscle passes upwards, outwards and backwards to the upper plate of the same segment. Another much thicker and longer muscle, also serving for exspiration, passes from each posterior angle

of the lower plates upwards, outwards and forwards to the anterior margin of the upper plate, covering the broader upper part of the above-mentioned muscle. There are likewise upper and lower longitudinal muscles for the abbreviation of the abdomen. The lower ones are even doubled—two on each side of the lower plates. They are rather thick, but narrow. The upper muscles, on the contrary, are very broad, but thin and delicate. Notwithstanding these numerous muscles, however, the abdomen is not shortened and elongated for the purpose of respiration, as in Bees and Wasps.

§ 17. The author then discusses the question whether these movements of the abdomen, supposed to be connected with respiration, may not subserve some other fnnction.

1. The pulsation of the dorsal vessel cannot be essentially affected by these movements, as when they cease for a longer or shorter time the activity of the dorsal vessel does not stop. This applies also to the action of the digestive organs, for this likewise goes on, and movements (especially peristaltic) of the intestine and malpighian vessels take place even when the movements of the abdomen cease for some time. There can also be no particular relation between them and the function of the generative organs, as they occur both when the sexual organs are far from maturity and when their activity appears to be purely plastic. There are no other organs in the abdomen of most insects, except the respiratory organs, with which these movements can be connected.

2. As the latter organs are surrounded by structures far less compressible in their nature, it is clear that as the walls of the abdomen contract, the air contained in the respiratory organs must be set in motion and partly expelled through the stigmata.

3. The movements of the walls of the abdomen, in those insects in which they occur, take place, like the respiratory movements of higher animals, more rapidly when the insect makes, or endeavours to make, greater muscular exertions; hence we may conclude by analogy that there is a close relation between the movements in insects and those in vertebrate animals.

4. In *Cetonia aurata* and *Scarabæus stercorarius* the author convinced himself by observation that these movements truly act upon the respiratory organs. On cutting off first the wings and wing-cases and then the upper wall of the thorax from these Beetles, he saw that every time the dorsal wall of the abdomen was depressed the air-sacs contained in the thorax became tensely dilated, and when the dorsal wall again rose these air-sacs became a little smaller.

5. In *Acridium stridulum* he remarked that, whenever the abdomen contracted, the two pad-like and closely appressed lips of

each of the stigmata placed above the intermediate legs separated, indicating that a portion of the air contained in the thorax was driven out through them. The same phenomenon was observed in the stigmata above the posterior pair of legs in *Gryllus verrucivorus*.

§ 18. Distinct movements of the walls of the body are not seen in every perfect insect, even when observed for a long time; and hence it might be supposed that the tracheæ and air-sacs in many (or perhaps in all) insects may be capable of contracting and dilating themselves by the tone and elasticity of their tissue. Elasticity is certainly possessed in a high degree by all those tracheæ which are not too wide in proportion to their length, or too thin-walled in proportion to their width, as may easily be seen in any such vessel, even of a recently killed insect, by compressing it and then removing the pressure. All parts of the respiratory system also possess a greater or less degree of physical contractility according to their different nature. It is greatest in the tracheæ, as these, when extended in width, or still more in length, contract again to their previous dimensions; it is least in the air-sacs, which, when dilated, contract but little and scarcely perceptibly on the removal of the cause of the extension. A tone, or organic contractility, seems on the contrary to be entirely wanting in all these parts. This view the author supports by the following observations. Of several living insects, especially *Grylli*, *Acridia*, *Scarabæus stercorarius*, and *Carabus granulatus*, he opened the abdomen, and observed particular parts of their respiratory systems under the action not only of the air, but also of cold water, concentrated sunlight, and mechanical irritants, sometimes with a very strong lens and sometimes with the microscope, without ever remarking a contraction which indicated any tone of these parts. Nor could he observe any such contractions in the tracheæ of *Tenebrio molitor*, by examining them through the transparent parts of the skin of that insect. Hence he considers that we are justified in stating that respiration (and especially exspiration) is never effected in any insect by the proper powers of the tracheæ and air-sacs alone, but that they require a pressure exerted upon them by other surrounding structures. This pressure can be exerted only by the wall of the abdomen, or in some insects by that of the metathorax; for although some of the viscera by their own activity may be capable of exerting a pressure upon them, this must be much less than that of the wall of the body. If no respiratory movement of the wall be observed in a perfect insect, the cause of this may be various.

1. The insect may be too small, and the movement too slight, to allow its observation;

2. Or it may be too hairy or plumose to allow such a movement to be perceived by the eye;

3. Or it may have fasted for a long time, rendering the movements so few and weak as to escape observation;

4. Or the insect may be rendered dull and weakly by other causes.

Here the author remarks that in insects in general respiration by no means plays so great a part, and, although necessary, is not so important as in birds and mammalia*. Many proofs of this assertion are to be found, according to the author, in Sorg's memoir, 'Digestiones physiologicæ circa respirationem insectorum et vermium' (Rudolst.: 1804); and he cites the circumstance that many insects live in the earth or in rotten wood, where they cannot possibly obtain an abundance of pure air for their respiration. He also cites the observation of Sir Humphry Davy ('Consolations in Travel,' Dialogue 2), that on the small floating islands of Confervæ in a lake near Tivoli he found an immense number of the most various insects, although this lake exhales so much carbonic acid and sulphurous vapour, that the aquatic birds, which sometimes visit it, remain on its shores, because, on the lake itself, these vapours would be fatal to them. Moreover his own observations show that in many insects the respiratory movements are few and weak.

If the above-described movements of the abdomen have really an influence upon respiration, this must be a double one, in con-

* In a note subsequently written, the author observes:—"This is going too far, as appears from the experiments of Treviranus on the respiration of the lower animals (Treviranus and Tiedemann's 'Zeitschr. für Physiol.' Bd. iv.).

"Results.—1. The quantity of oxygen taken up and of carbonic acid exhaled by the same insect is very different in equal times, according as it moves or rests, according as it is exposed to a higher or lower temperature (greater in the former case), and according as it is full-fed or fasting.

"(In *Apis terrestris* the quantities of carbonic-acid gas exhaled at 9–12° R. and 14–23° R. are as 22 : 174.)

"2. The quantity of carbonic-acid gas produced in respiration differs in different insects. The most active insects exhale the most carbonic acid. Among these are the Bees, Humble Bees, and Lepidoptera. These are followed by the *Syrphi* and probably many other Diptera. Then come the *Libellulæ* and Beetles. The smallest amount of carbonic acid is exhaled by the larvæ of Lepidoptera and Beetles. A larva of *Cetonia aurata* does not exhale a fifth of that produced by the perfect insect of the same species.

"3. When the temperature of the air is 11½° R. the Bee produces nearly as much, and at a temperature of 22° R. far more carbonic acid than even the Dove. *Papilio Atalanta*, even when it has been for several days without food, exhales a far greater quantity of the gas at 15° R. than that bird. Cats, Guinea-pigs, and Rabbits are inferior to Humble Bees in strength of respiration at a temperature of 16–17° R. At this temperature *Syrphus nemorum* is about equal to those animals."

sequence of the structure and distribution of the respiratory apparatus.

1. In the abdomen itself. When its cavity is diminished, the tracheæ, and the air-sacs when they occur, must be somewhat compressed and a portion of the air contained in them driven out through the stigmata. But when the cavity of the abdomen enlarges again, and the pressure exerted upon the air-passages contained in it is removed, these must furnish an entrance for the atmospheric air, partly because the pressure of the external air overcomes that upon the outer surface of the air-vessels, and partly because the tracheæ at least may again dilate by their own elasticity.

2. As regards the head and thorax, which, if we except the thorax of the *Staphylini* and *Carabidæ*, cannot expand and contract. A portion of the air contained in the abdomen will be driven into them through the air-vessels when the abdomen contracts. A portion of this air then flows out through the stigmata of the thorax (as is seen in the *Locustæ*), but another portion inflates the air-passages of the thorax and probably those of the head to a greater or less extent. When the pressure on the abdomen ceases, the tracheæ and air-sacs of the thorax and head contract by their proper elasticity, and again expel a portion of their contained air, probably in part through the thoracic stigmata, at least in those insects whose stigmata are constantly open, and in part back into the abdomen.

The same applies probably to the movement of the air to and from the extremities.

§ 19. In all the insects examined, except the Hymenoptera, only the contractions, and not the dilatations, of the abdominal cavity are effected by the action of muscles. The means by which the cavity is enlarged and the inspiration effected, appear to be various in different insects and even in the same insect.

1. In those insects which only possess shrub-like tracheæ, the latter appear to be a principal means of the dilatation of the abdominal cavity during inspiration. The tracheæ, like the arteries of the Vertebrata, possess a high degree of elasticity, and, even after the insect's death, regain their volume, after being compressed, as soon as the pressure is removed. As they are undoubtedly compressed, directly or indirectly, by the walls of the abdomen during exspiration, it is to be expected that, when this pressure ceases, they will again expand, react upon the walls of the abdomen, and push these somewhat apart. This applies also to most of those insects which possess vesicular as well as ramified tracheæ, and especially to those in which the former are not too wide in proportion to their length. It is less applicable to those whose vesicular tracheæ are very wide in pro-

portion to their length, as is the case in the *Acridia*: these tracheæ, when compressed and emptied of air, do not completely recover their original diameter by the agency of their proper elasticity. The air-sacs, which exist in greater or less number in many insects in connexion with the tracheæ, usually consist of an extremely delicate membrane, in which no trace of a spiral fibre can be detected: when strongly dilated with air, they may certainly contract a little by their proper contractility, if the pressure from within ceases; but when compressed from without, they cannot dilate themselves again by virtue of any inherent elasticity. Consequently in those insects which have air-sacs or very wide vesicular tracheæ in the abdomen, these structures cannot contribute to the dilatation of the ventral cavity.

2. In those insects in which during exspiration the extremities of the upper halves of several abdominal segments are bent somewhat inwards (as in the *Grylli*, *Acridia*, *Libellulæ*, *Tabani*, some Beetles [*Carabus granulatus*] and many Lepidoptera), these extremities, when the muscles cease to act upon them, move apart again by their own elasticity, and thus assist in enlarging the abdominal cavity.

3. In those insects in which the softer skin between the upper and lower halves of the abdominal segments possesses considerable thickness and elasticity, and folds inwards during exspiration, it appears, during inspiration, to press outwards again by its own elasticity, recovering the plane in which it is stretched during repose, and pushing apart the upper and lower plates of the segments. In those, on the contrary, in which this skin is comparatively thin and does not fold during exspiration (as in *Tabanus*, *Musca*, *Tipula*, and the Beetles), it probably does not act in the above way in the dilatation of the abdominal cavity. For the contractility of this portion of the skin is very considerable, and it may therefore be supposed that when it has been somewhat compressed during exspiration, it will again extend itself on the cessation of the pressure.

§ 20. From the statements contained in the preceding paragraphs we may understand how the process of inspiration goes on in perfect insects.

1. In those which possess only shrub-like tracheæ, these expand by their own elasticity as soon as the direct or indirect pressure of the abdominal walls producing exspiration ceases, and by their proper force cause the atmospheric air to place itself in equilibrium with the air contained in them and penetrate through the stigmata. If the abdominal walls also expand by their own elasticity after the completion of exspiration, this dilatation can only be regarded as a removal of the obstacles to the independent dilatation of the tracheæ.

2. In those, on the contrary, which possess air-sacs as well as tracheæ, or in which some trachcæ are very wide in proportion to their length, the walls of the abdomen cause the inspiration, either by their proper elasticity or, as in the Hymenoptera, by muscular power.

§ 21. It is well known that insects when fully fed, and requiring a greater amount of oxygen for the purpose of digestion, respire far more frequently than when their alimentary canal is empty; the respiratory process also appears, at least in the greater number of insects, to take place more completely and powerfully. The movements of the abdominal plates and the extension of the soft skin uniting them are then far greater than when the alimentary canal is empty. The muscles moving these parts will be more stretched than usual, and therefore will contract to a far greater extent; so that the difference between the size of the abdominal cavity in inspiration and exspiration is increased, the air-passages are more strongly compressed, the air contained in them more completely evacuated at each exspiration, and a greater quantity of fresh air is taken in during inspiration, than under other circumstances. This at least must be the case with those insects which possess only ramose tracheæ. It probably applies also to these insects at the time when their generative organs, especially in the female, are much dilated and the abdomen inflated thereby; but it is not known whether at this time, if the alimentary canal be empty, the respiration goes on more rapidly than before, when the sexual organs had attained no great size. The same theory cannot apply to those insects which possess vesicular tracheæ or large air-sacs, as these vesicles are not so elastic as to be capable of dilating again by their own powers on the cessation of pressure. Perhaps these insects, under the above circumstances, breathe more rapidly than the others. The author considers that many of his observations are in favour of this view.

§ 22. Is that movement of the abdomen of insects which is connected with respiration a voluntary or an involuntary act? This question is to be answered in the same way as the similar one relating to the respiration of man.

After the decapitation of insects (*Grylli, Scarabæi, Tabani,* and Wasps) the abdomen has been seen to continue for a time contracting and dilating in the same way as before the injury, from which the author concludes that in these the respiratory movements may go on quite involuntarily. But these movements not unfrequently cease for a longer or shorter time in uninjured insects, or they are limited to one or two segments; and the contractions take place in these with unusual exertion, although the remainder of the segments which otherwise act in respiration

remain quite quiet: from this we may conclude that the will may exert some influence on the respiration.

§ 23. Certain phenomena lead to the belief that in many insects various viscera have a subordinate action upon the respiration of insects, or at least upon the *distribution* of air in them.

1. The pulsation of the dorsal vessel sets a number of tracheæ in motion, pushing them forwards and backwards, extending them in length, and then permitting them to contract or contort themselves again.

2. In those insects which possess a sucking-bladder connected with the anterior part of the alimentary canal, this must produce similar, but sometimes, by lateral pressure, still greater effects upon the tracheæ and air-sacs in its vicinity: in many such insects, especially Diptera, this bladder, which is sometimes of great size, may be seen, even through the skin, slowly but incessantly contracting and expanding alternately to a very great extent.

3. This applies also to the intestine and, although in a far less degree, to the malpighian vessels, which, as may be ascertained not only from opened insects, but also from many uninjured ones (such as some species of *Syrphus*), are constantly performing peristaltic movements. The strongest peristaltic movements, which indeed were perceptible through the walls of the abdomen, were observed by the author in *Ophion luteus*. In the first segment of the abdomen, in which the intestine was quite straight, they went on unceasingly, in such a manner that the portion of intestine contained in it always remained straight; in the remainder of the abdomen, in which the intestine is much contorted, they took place only at intervals, but each time with great rapidity and violence, the intestine undulating to and fro to a remarkable extent.

By the dragging of these viscera upon the neighbouring and attached tracheæ, and also by the pressure which some of them exert during their extension upon air-sacs in their vicinity, it cannot be but that the air contained in these parts will be set in motion. Partial movements of the air in the interior of the insect must also be produced during the action of the muscles of the limbs, as these muscles are penetrated and surrounded by many air-vessels.

II. Imperfect Insects.

A. *Of those which only undergo a partial metamorphosis.*

§ 24. The structure of the abdomen in the young of *Blatta*, *Gryllus* and *Acridium* is similar to that occurring in the perfect insects; so that it is probable that the respiratory process is the same in both.

B. *Grubs and Caterpillars.*

The tracheæ of these larvæ were examined immediately after they had been opened down the back, both with the simple lens and with the microscope, but no contractions could be observed in them even when irritated mechanically or with alcohol.

§ 25. The larvæ of *Vespa crabro* and *V. vulgaris*, both when within their cells and after removal therefrom, frequently shorten and elongate their bodies, at the same time curving them laterally either to the right or left. In the latter movement the convex half of the body also becomes smoother, and the concave half thicker than before, a portion of the fat and other structures contained in the body being pressed from the former into the latter.

The skin between each two contiguous segments is somewhat thinner and softer than in the segments themselves, and at the point where the upper and lower halves of each segment come together the skin is likewise thinner and softer, and forms a projecting fold. From the entire anterior margin of each segment, except the two soft spaces on the right and left sides and the spaces where the dorsal vessel and ventral ganglionic cord lie, there runs a great number of nearly straight and pretty thick muscular bundles, forming two superior and two inferior layers; these pass nearly to the corresponding margin of the preceding segment, and not only shorten the body, but also, by acting on one side, curve it to one side. Besides these, on each side, partly from the upper end of the lower half of each abdominal segment close to the soft skin, and partly from this soft skin itself, two delicate and closely approximated muscular bundles pass inwards and downwards to the lower half of the preceding segment, attaching themselves partly to the anterior margin of this in the vicinity of the ganglionic chain, and partly running further inwards and forwards to apply themselves to the upper surface of the straight muscles of the next anterior segment. These latter muscles may flatten the body, and appear to be antagonistic in the two halves of the body; so that when those of the left side contract, those of the right side are relaxed, and *vice versâ*. The straight longitudinal muscles are likewise antagonistic in the two sides of the body. When the entire body contracts in the direction of its length, during which the segments themselves, consisting only of a soft skin, are somewhat shortened, it is extended again, after the relaxation of the muscles, only by the elasticity of the cutis and of the contents of the cavity.

All the tracheæ are ramose, and all the stems of each side of the body are united, as in the perfect Wasps, by a com-

mon cylindrical and elastic canal, which, however, is only of moderate diameter.

The respiratory process in these larvæ can only be effected by the above-mentioned movements, both general and partial. If the larva contracts longitudinally, when it does not gain so much in breadth as it loses in length, the contents of the body-cavity, and therefore the tracheary system, must be compressed, and the air contained therein driven out of the stigmata, in larger or smaller quantity according to the shortening. On the cessation of the activity of the muscles, the air-vessels, being freed from the previous pressure, must dilate again by virtue of their elasticity, and cause the air to enter through the stigmata. The same process of exspiration must also take place when the larva bends strongly to one side; for as the convex side then becomes smoother, and the structures contained in it are partially driven over into the opposite side, it is more than probable that its tracheæ also are then compressed and partly emptied of air; and as the concave side is shorter and moreover filled with a portion of the structures from the other side, its tracheæ also must be compressed and compelled to part with their air.

§ 26. In the larvæ of the *Scarabæi*, or at least in that of the May Bug (*Melolontha majalis*), the epidermis of each abdominal segment, except the last, forms two moderately firm plates, the upper a little larger than the lower, united at each side by a thinner and more flexible part of the epidermis. In these softer parts are the stigmata. Both the upper and lower plates of every two segments move upon each other by means of several muscular bundles, of which some, and these the innermost, immediately surrounding the abdominal cavity, run straight forward from the hinder margin of one segment to the same margin of the other, whilst others take an oblique direction from within outwards and forwards, and others from without inwards and forwards. Of these oblique muscles some have the same insertions as the straight muscles, but others pass from the middle of one segment to the hinder margin of the preceding one. In each abdominal segment, except the last, there are also two, and in some even three pairs of pretty strong muscles, which all run from the ends of the upper plate, over the softer parts of the skin, inwards and downwards. Those of the inner pair pass straight to the lower plate of the same segment, and are attached to this; those of the other one or two pairs run obliquely forward, and attach themselves to the lower plate of the preceding segment. The hindmost segment has only one pair of muscles, and these are oblique.

By the muscles running obliquely from above downwards and

inwards the segments of the abdomen may be rendered flatter, and by the others it may be shortened. By means of these latter muscles, moreover, the larva is enabled to curve its body sideways, upwards, and downwards. It is also of great importance to the larva, both in shortening and bending its body, that the epidermis and cutis of each segment form several small folds directed towards the body-cavity.

In examining a living strong larva, it will be seen that it not unfrequently flattens its body greatly in places, and at the same time narrows it from the sides, and that this contraction of the body usually advances from before backwards over the different segments, no more than a few segments being contracted at the same time. The larva can likewise considerably shorten its body, when the increase of thickness does not appear to compensate fully for the abbreviation. But more commonly, and indeed when the larva endeavours to crawl, only partial shortenings of the body take place.

§ 27. The exspirations must take place, theoretically, as in the Wasps and other Hymenoptera, when the body shortens, the individual segments not gaining so much in width as they lose in length, and also when the body curves to one side, but still more when it is flattened from above and below. These views are confirmed by Bonnet's experiments on the respiration of Caterpillars. According to these experiments, when Caterpillars are immersed in water, more numerous and larger air-bubbles escape from the stigmata the greater the movements made by the animals. The inspiration must of course take place when the pressure upon the air-vessels, produced as above, ceases.

As, moreover, the movements perceptible in the body-wall of Caterpillars and the larvæ of Beetles and Diptera are chiefly connected with the locomotion of these animals, it follows that their respiration is also chiefly connected with their locomotion.

All respiration in these animals is subjected to the will, and never involuntary.

§ 28. The Caterpillars of the Lepidoptera can shorten and elongate their bodies considerably, but can neither flatten them nor contract them at the sides in the same way as the larvæ of the *Scarabæi*. When they shorten themselves, the individual segments increase in width, but by no means sufficiently to compensate for the shortening. This applies also to the narrowing of the segments when the Caterpillar elongates itself. Some segments are usually elongated at the same time that others are shortened; and the two processes take place progressively from before backwards. This at least is the case during the locomotion of Caterpillars.

C. *Pupæ and Nymphæ.*

§ 29. In undisturbed pupæ of Lepidoptera no movements of the body are to be detected, and therefore no movements that can be referred to the act of respiration. The same thing applies to the pupæ of Beetles, Hymenoptera, and probably of other orders of insects. Nor can it be perceived, on opening such pupæ and irritating their tracheæ in various ways, that these vessels contract or dilate.

From the absence of all such phenomena we might conclude that in the pupæ of the above-mentioned insects the tracheary respiration is entirely interrupted. But, according to Sorg's observations, pupæ of Lepidoptera and Ants die, although not for some time, when kept in small receivers from which the external air is completely excluded; and these creatures consume a small quantity of oxygen, and give out a little carbonic acid. According to the observations of Reaumur and Martinet also, pupæ die when their stigmata are covered with oil. If these observations be correct (and there seems no reason to doubt them), the phenomena in question may be ascribed to two causes. In the first place, it is possible and conceivable that the air may penetrate the envelopes of the pupæ as readily as those of birds' eggs, and then enter into a mutual action with the internal parts of the insects. The permeability of these envelopes by air and vapours is indicated by the fact that when dead larvæ or pupæ are exposed to the air, they dry and lose considerably in weight. In the second place, as the pupæ are not always exposed to the same temperature, the air contained in their tracheæ must undergo changes in its density; and in consequence the tracheæ must sometimes give out a portion of their contents, and sometimes draw in a portion of the external air.

In any case it is certain that the respiration of pupæ can only be very weak. This is shown by the observations of Sorg, and also by the circumstance that the pupæ of many insects, *e. g.* the Bees, are enclosed in a nearly air-tight case, whilst others lie deep in the earth. This weak respiration in pupæ is remarkable, inasmuch as it is in them that the most important changes in the form and number of the different parts of the body takes place. But it will not be difficult to give a satisfactory explanation of these phenomena.

During the evolution of an insect within the pupa-skin, nearly all the fat and likewise a quantity of muscles and other structures disappear, but the materials of these parts pass into new combinations and serve for the evolution or even for the formation and evolution of other organs. They contain more or less oxygen in their composition; and it is conceivable that this may suffice to

render the taking in of any considerable quantity of oxygen from the atmosphere unnecessary. Analogous phenomena are presented by hybernating Mammalia and Reptiles, as in these, during hybernation, respiration is almost entirely suppressed; and nevertheless whilst the fat so abundantly deposited almost entirely disappears, some of the other organs, especially the testes and seminal vesicles in the Mammalia and the ovaries and oviducts also in the Reptiles, are considerably increased in size and gradually prepare a great mass of their secretions. It is, as many phenomena indicate, the exaltation of nervous action and the activity of the muscles that give rise in animals to a greater consumption of atmospheric oxygen, and therefore to a more rapid and powerful respiration, in order to replace the wasted portions of the nervous and muscular systems; far less oxygen is required by the lower constituents of the organism to maintain themselves in action or even to develope themselves further.

§ 30. Lastly, the question is to be answered whether insects both inspire and exspire the air through all their stigmata.

Beautiful investigations for the solution of this question are to be found in one of Bonnet's memoirs*. Bonnet's principal observations are as follows:—

1. If a Caterpillar be immersed in water so that only the hindmost pair of stigmata are left free, it survives this experiment for some time, whilst it soon dies if entirely immersed.

2. It also lives for some time if immersed so that only its anterior pair of stigmata remain free.

3. When a Caterpillar is entirely immersed in water, an air-bubble is not unfrequently seen to issue from one or other of its stigmata, most commonly from one of the foremost or hindmost pairs, and this is then alternately drawn in and pushed out.

4. When the stigmata of the foremost and hindmost pairs in a Caterpillar are clogged with butter, and the rest left free, the animal is more uneasy than when the experiment is reversed.

From these experiments it follows that Caterpillars inspire and exspire by all their stigmata, but most through those of the foremost and hindmost pairs.

Moreover it is inconceivable that the whole mass of inspired air should be exspired by other ways than those through which it entered the body. This would be in opposition to the entire structure of the respiratory system; for in a great number of insects the stigmata are so constructed that they cannot be closed by the animal, and consequently furnish the air with a means both of entrance and exit.

* Mém. de Math. et de Phys., vol. v. In *Acridium stridulum* the stigmata above the intermediate pair of legs appear to exspire only, and not to inspire.