On Mr. Portchinski's publications on the larvae of Muscidae

including a detailed abstract of his last paper: Comparative biology of the necrophagous and coprophagous larvae

by

C. R. Osten Sacken.

For many years past Mr. Joseph Portchinski (at present Secretary of the Entomological Society in St. Petersburgh) has been devoting a great deal of time to the study of the life-habits of carnivorous and coprophagous larvae of Muscidae, and several valuable publications on that subject are due to his pen already. But as most of these publications are written in russian, they have remained less known than they deserve.

In 1874 appeared the Observations on the natural history of *Cynomyia mortuorum* (Trudy of the Russian Entomological Society Vol. VII, p. XXXII—XXXVI). In order to ascertain the successive appearance of different necrophagous flies with the advancing season, the author used to lay out dead bodies of small vertebrates, birds, rats etc. and to breed the maggots that speedily accumulated in them. *Cynomyia* was abundant in the spring; *Calliphora vomitoria* began to appear about the middle of June only. Thus two sparrows laid out on June 8 gave 41 specimens of *Cynomyia mortuorum*, 9 *Lucilia caesar*, 56 specimens of different *Anthomyiae* and only three *Calliphorae*. After that *Cynomyia* began to disappear and was gradually replaced by *Calliphora;* (we shall return to this subject further on).

In 1875—76 Mr. Portchinski published an elaborate paper, entitled Materials for the natural history of the flies which, in their larva-stage, cause diseases among men and animals (Trudy etc. Vol. IX, p. 3—180 with three plates). A condensation of a portion of this paper, concerning *Sarcophila Wohlfahrti*, was published in the Horae Soc. Ent. Ross. Vol. XI, 1875, p. 123—160 in german under the title: Krankheiten, welche im Mohilewschen Gouvernement von Larven von *Sarcophila Wohlfahrti* entstehen, und deren Biologie.

In 1884 a monographic essay on *Sarcophila Wohlfahrti* appeared (Horae etc. Vol. XVIII, p. 247—314, with 33 woodcuts), containing some new observations, and comparative descriptions of this fly and its next relatives.

The principal result which science owes to these papers is the elucidation of the history of *S. Wohlfahrti* as a dangerous but hitherto unrecognized enemy of men and animals, the european substitute of the celebrated *Lucilia macellaria* (Syn. *L. hominivorax*) of America. In 1768 Dr. Johann August Wohlfahrt, physician in Halle, published a paper: Observatio de vermibus per nares excretis, describing a case where peculiar worms in the nose of an old man produced intolerable headache, and almost drove him to madness. Wohlfahrt succeeded in breeding the fly of these larvae and gave a description, accompanied with figures sufficient for the recognition of the species. Numerous similar cases have been observed since, and either altogether misunderstood, or else ascribed to different other species of common carnivorous flies, species of *Sarcophaga*, *Lucilia*, *Calliphora*. To Mr. Portchinski belongs the merit of having pointed out that the great majority of the cases of the malum verminosum observed on men and animals are produced by that particular species, described more than a century ago by old Wohlfahrt, and so far overlooked since, owing probably to its close resemblance to other species, that it was described for the first time by Schiner in 1862 only, who had no idea of its dangerous propensities, nor of its identity with the species described, but not named by Wohlfahrt. Mr. Portchinski shows, that *S. Wohlfahrti* occurs all over Europe, that it attacks animals, domestic and wild, and that occasionally it causes horrible sufferings and even death among men. In the work of Dr. Megnin: „Les parasites et les maladies parasitaires" Paris 1880, the author acknowledges Mr. Portchinski's conclusions and says: „that every time he succeeded in breeding the fly from such larvae, it was the *Sarcophila Wohlfahrti* which escaped from the pupa; he adds: „Il y a donc lieu de compter avec ce parasite à l'avenir" (l. c. p. 46). We fully sympathise with Mr. Portchinski when he insists upon calling this fly *S. Wohlfahrti* in honor of its first real describer, notwithstanding the name given to it by Schiner (*S. magnifica*), in ignorance of the earlier description.

The new article of Mr. Portchinski, Comparative biology of the necrophagous and coprophagous larvae (Horae etc. Vol. XIX, p. 210—244, 1885), brings us a series of important observations, and illustrates the wonderful power of adaptation of these larvae to

their environment, an adaptation which, in a certain measure, destroys the parallelism which we naturally expect to exist between the systematic characters of larva and imago. Such apparent want of parallelism has been observed in the order of Diptera before, but an abundance of new facts are found in Mr. Portchinski's paper. Distantly related species, belonging to different genera, issue from larvae almost undistinguishable from each other. And again closely related and almost undistinguishable imago's, species of the same genus, differ in their oviposition (size and number of eggs), and their larvae follow a different law of development (as to the degree of maturity the larva reaches within the body of the mother and the number of stages of development it passes through). In one case even *(Musca corvina)* larvae of the same species were found to have a different mode of development in northern and in southern regions.

The following abstract reproduces the facts and merely condenses the statements. We begin with the carnivorous larvae[1]).

Calliphora erythrocephala (the blue-bottle fly). Its development has been thoroughly investigated in the well-known work of Mr. Weissmann. — It lays its eggs on meat and on dead animals. The elongated eggs are remarkably small, only about one millimeter long. Mr. Portchinski found as many as 450 to 600 in the body of a single fly; that is 225 to 300 in each of the ovaries, counting the last row of ripe eggs only, as it is very probable that the undeveloped eggs of the second and following rows never come to maturity. About 24 hours after the egg is laid, the larva is hatched, in the first stage of its existence, easily distinguished by the shape of the posterior stigmatic horny plates; they are exceedingly small, and have a single, characteristic heart-shaped breathing-fissure. In the second stage, the stigmatic plates are much larger, each with a pair of straight, subparallel fissures in the middle. In the third and last stage before becoming a pupa, the larva has still larger stigmatic plates, each with three subparallel breathing-fissures. (Fig. 1. I quote the figures of Mr. Portchinski's original article.) When the larva is about to pass from the second to the third stage, the stigmatic plates of the third stage are distinctly visible through the integuments of the larva, behind those of the second stage; the larva seems then to have two pairs of posterior stigmata.

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1) It must be borne in mind that most of the observations of Mr. P. were made in St. Petersburgh and environs; those made in the south of Russia are specially mentioned.

The larva of *Lucilia caesar* (the green bottle-fly) passes through the same stages of development, and its larvae, except in size, are undistinguishable from those of *C. erythrocephala*. Still it would be premature to conclude from the resemblance of the larvae to the close relationship of the mature flies, and to infer that flies of a more distant systematic position would necessarily have very different larvae. *Cynomyia mortuorum* is structurally very different from *Calliphora*, so different in fact that it is usually referred not to the group of Muscinae, but to the Sarcophaginae. Nevertheless, instead of being viviparous, like the Sarcophagae, *Cynomyia mortuorum* is oviparous, and its larvae are, in all their structural details, so much like those of the *Calliphora* (blue-bottle fly) that it is impossible to discover any distinctive character.

The larvae of these three flies are true carrion-eaters; they are exactly alike and have the same mode of development.

In order to test the food-habits of these larvae, they were bred from the egg. The flies, being confined within a closed receptacle containing a small piece of meat, soon begin to lay eggs in quantities[1]); — it is an easy matter afterwards to transfer them for hatching in different other substances, according to the nature of the experiment to be tried on them. Eggs of the blue-bottle fly and of *Cynomyia* were placed at the same time on meat, on cattle-dung and on decaying mushrooms, and it soon became evident that they could thrive on meat only; in the two other environments they grew very slowly and finally perished. The same result was obtained with *Lucilia caesar*, except that the larvae put in cattle-dung did not perish, but grew slowly.

We have said that the larvae of these three flies are almost undistinguishable from each other, and pass through the same three larval stages. Still, there is one important difference between their life-histories: the blue-bottle and the green-bottle lay from 300 to 600 eggs, while *Cynomyia* does not lay more than 150. All the specimens of the fly which were dissected did not contain more than 150 eggs, generally less. All other conditions being equal this difference in numbers is a disadvantage for the fly, and hence among the three carrion-flies *Cynomyia* is the rarest. In the spring of certain years *Cynomyia* is unusually abundant, and then the blue-bottle is rare and appears in the beginning of June only. Carrion,

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1) Some species of flies do not like to lay eggs in confinement, and for this reason the observation of their habits is much more difficult.

laid out at intervals during such years, produced the largest number of *Cynomyiae* from the middle to the end of May, with a minimum about the beginning of June, from which time the blue-bottle began to grow in numbers at the expense of *Cynomyia*, which ceased to appear about the end of June. The only chance for *Cynomyia* therefore is in the spring, as long as its competitors are less numerous, and especially in such years when, for some reason, the blue-bottle is rare, or appears later. We have here an instance of the dependence of the propagation of a fly on the number of eggs it is capable to lay. —

Now about flies developing in dung (coprophagous 1).

We begin with *Musca domestica*, the common house-fly, although on account of its favored, domestic position, it does not, as will be shown, follow the common rule of other dung-flies. Notwithstanding the difference in the environment, the development of *M. domestica* shows some resemblance to that of the blue-bottle fly. It lays about 120—160 small eggs, from which in about 24 hours the larvae in the first stage of development are hatched; they are characterized by very small stigmatic horny plates, with a single, heart-shaped breathing-fissure (like that of the blue-bottle); the larva remains in this state about a day, and then enters the second stage, characterized by stigmatic plates with two fissures, almost exactly like those of the blue-bottle. After another day the larva reaches the third stage, with still larger stigmatic plates, each of which has two breathing fissures of a peculiar shape, distinctive of the species: a meandering, serpentine line running parallel to the outer ring of the horny plate (Fig. 2). In other respects the larva of *Musca domestica* is exceedingly like that of the field-fly *(Musca corvina)* and also of the meadow-fly *(Dasyphora pratorum)*. The differences are slight. The larva of *Musca domestica* differs from that of *M. corvina* in the shape of the anterior spiracles, which have six rays in the former, and twelve in *M. corvina*. The posterior stigmatic plates of *Musca corvina* are very large, in comparison to those of the two other species; in *M. domestica* they are small and more distant from each other; in *Dasyphora pratorum* they are also smaller than in *M. corvina*, and still nearer to each other. In the perfect state *Musca domestica* and *corvina* are exceedingly alike; there is a slight difference only in the structure of the front and in the coloring.

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1) The authors researches extend merely to the fecal matters of men and horned cattle.

Considering the great resemblance between these two flies in the imago-state and in that of the mature larva, the very important differences in their mode of development are the more astonishing. *Musca corvina* lays on dung only 24 comparatively large eggs of a very peculiar shape, and not, like the house-fly 120—160 very small eggs of the ordinary shape. — These eggs are about one and a half millimeters long, and have, beyond that length, an elongated, curved appendage, about two-thirds of the length of the egg, which, in the mature state has a dark color (fig. 5).

Musca corvina is not the only one among the dung-flies which lays a small number of large eggs. *Pyrellia serena* and *Graphomyia maculata* do not lay more than 44 eggs, but they too are of a large size. *Sarcophaga haematodes*, viviparous like its congeners, lays 40 large larvae; *Myospila meditabunda*, *Mesembrina mystacea* and *Spilogaster angelicae* lay only 24 eggs each, and often less; the size of the eggs is 1,5 mm. for the first (the fly being 6 mm. long); 4 mm. for the second (length of the fly 12,5 mm.); 2 mm. for the third (length of the fly 6,5 mm.). The hatching of these large eggs, and the further development of the larvae, was observed on specimens of *M. meditabunda*, a fly which very easily lays its eggs in captivity. The egg of *M. meditabunda* is not unlike that of *M. corvina*, only the characteristic black appendage of the latter is much shorter here and its curvature much stronger; from this appendage a black stripe runs along the ventral side of the egg to its opposite end (fig. 6); a heap of these eggs look to the naked eye more like a heap of minute pupae. In about 24 hours larvae are hatched, with the posterior spiracles already described before as characteristic of the first stage. But the next stage of the larva is not the second, but the third, characterized by posterior spiracles with three straight, slightly converging, slits. The passage from the first to the third stage is immediate, because a short time before it takes place the stigmata with the three slits become visible under the integument, alongside of the characteristic stigmata of the first stage. After a very short larva-period, the pupa-state begins.

From the great resemblance of the eggs of *M. corvina* to those of *M. meditabunda*, in their shape and size, as well as in their number, the inference may be drawn that the development of their larvae follows the same rule, that is, that the second larva-stage is omitted in *M. corvina* as it is in *M. meditabunda*. And thus, although *M. corvina*, as imago, is very like *M. domestica* its metamorphosis is very different:

M. domestica lays 120—160 small eggs, producing larvae which undergo three stages of development.

M. corvina lays only 24 large eggs, of a peculiar structure, and the larvae undergo only two stages of development, the first and the third, omitting the second. This shortened mode of development enables larvae to reach their maturity quicker and this rapidity of growth, in the struggle for existence, is a compensation for the small number of eggs laid by the imago.

We have seen that the carnivorous larvae of diptera are very prolific and that the struggle for existence among them depends principally on the number of the eggs laid; it remains to point out the causes which prevent the coprophagous larvae from enjoying the same fecundity. — The number of species of carnivorous flies in our regions (that is of flies living on the soft and semiliquid parts of carrion) is not large, some nine species, if we take some rare ones into account (*Calliphora*, several *Luciliae* and *Pyrelliae*, two or three viviparous *Sarcophagae* and *Cynomyia mortuorum*). They have it all to themselves; their action must be rapid; food is plentiful; all there conditions favor multiplication. The numerous Coleoptera and coleopterous larvae (Staphilinidae, Histri, Silphae etc.), occurring about carcasses, compete very little with the dipterous larvae, but rather prey upon them, destroying multitudes and thus making room for new broods. The large number of eggs laid involves their small size, and plentiful food favors a comparatively long period of development.

Quite different circumstances attend the development of the dipterous larvae living in dung; here, instead of plenty of elbow-room, there is a severe competition, and instead of abundance, scarcity. Numerous coleoptera (belonging at least to 14 genera) live on dung, but equally numerous are the genera and species of dung-flies (31 genera at least). This, from the very beginning, was a check to fecundity which, in the course of time, must have kept down and crowded out the too prolific species, while those with a less numerous progeny survived, because with the diminution of the number of eggs there was an increase of their size and a shortening in the period of development. Other conditions being equal a large egg gave a large larva, which required less food for its full development. This was an advantage which enabled the less prolific flies to crowd out the more prolific ones. „The coprophagous flies offer us an instruc-„tive lesson of natural selection and of the law of mutual succour, „in virtue of which living animals of various species and genera, as „if by common consent, diminish their fecundity, to prevent a common „ruin and render cohabitation possible."

The coprophagous diptera do not form a single, compact group;

on the contrary they occur in various families, among species living upon entirely different substances. Mr. Portchinski argues therefore that if the biological conditions of the coprophagous diptera are so peculiar as he represents them, it follows that in whatever family or group they occur, their biology would necessarily be different from that of the other species in the same group. He goes on to show that coprophagous diptera, in whatever family they occur, incline to viviparousness. Among the viviparous diptera par excellence, the Sarcophagae, there is a coprophagous species, *S. haematodes;* the coprophagous *Mesembrina meridiana* is viviparous[1]), while the other species *M. resplendens* lays eggs; the coprophagous *Dasyphora pratorum* is viviparous, while *D. lasiophthalma* lays a quantity of eggs. The Hylemyiae lay eggs, but among them there is a coprophagous species, *H. strigosa* which is viviparous. Even in other families systematically distant from the Muscidae, the biology of coprophagus species is peculiar. The most striking example is *Chironomus stercorarius*, which forms a remarkable exception among all the *Nemocera* in being viviparous.

There are different modes of viviparousness, most interesting to study. The coprophagous species of *Sarcophaga* do not lay more than 40—60 larvae, but of large proportions; these larvae in developing in fecal matters go through all the three stages of development. *Hylemyia strigosa*, which is only 5 mm. long, deposits in fecal matters a single larva (very seldom two), which develops within the body of the fly from an egg of a proportionate size. One might expect, from the comparatively enormous size of the larva, that it is brought forth in the last stage of its development. But this is not the case. This at its birth gigantic larva, is still in the first stage, and has the characteristic heart-shaped opening of the stigmata; it soon passes into the second stage, with two fissures to the stigmata, and then into the third, with three fissures (figure 7).

These various modes of development of coprophagous diptera (viviparousness, or oviparousness, with omission of the second stage of the larva, or laying of a single very large larva), — all have the same end in view, — the gain of time, the shortening of the period of growth. And it is remarkable that, within one and the same genus, different species take different roads towards that end; for

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1) The observation on the viviparousness of *Mesembrina meridiana* was made in the Crimea. A larva 3 mm. long was found in the body of a female, and alongside of it an egg of the same length. The further development of the larva has not been investigated.

instance *Mesembrina meridiana* and *Spilogaster divisa* are viviparous, while *Mesembrina mystacea* and *Spilogaster angelicae* lay only a small number (24 or less) of large eggs, the larvae omitting the second stage of development 1).

The biologies hitherto discussed were those of flies belonging to the northern regions of Russia, principally the environs of St. Petersburgh. But Mr. Portschinski extended his observations to the south of Russia also, and brought home very remarkable results. — One of the most common coprophagous flies in the south of Russia is *Dasyphora pratorum*; we have already stated above that its larva shows but trifling differences from that of *Musca corvina;* the imago's resemble each other likewise, although less than the larvae. There must necessarily exist a severe competition between the two so closely related flies, and this competition must have had its influence on the biology of *Musca corvina* in those southern regions. Now the mode of larval development of *Dasyphora pratorum* is very peculiar. A comparatively large, usually oblong egg detaches itself from one of the ovaries and remains in a matrix-like receptacle; there the larva is hatched and begins to grow; the structure of its posterior stigmata indicates the first stage; upon further growth, the second stage is reached, provided with stigmata with double fissures; and finally the third (with the three fissures). It is in the third stages that the larva is laid by the fly, and deposited in the dung of horned cattle; it very soon reaches its full growth and goes underground for its further development. It is very probable that, one larva being laid, a new one is soon developed within the body of its mother; the ovaries show its beginnings.

The biology of this fly is not unlike that of *Hylemyia strigosa*, as, in both cases, a single large larva is laid; but with this great

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1) This latter fact is not explicitly stated, but must be inferred from the context, especially in connection with the passage beginning at the bottom of p. 14: „Thus the larvae of coprophagous flies, *Musca corvina*, *meditabunda* etc. that lay a small number of very large eggs, do not pass through the second stage." On p. 13 the coprophagous flies laying a small number of large eggs are enumerated as follows: *M. corvina*, *meditabunda*, *Mesembrina mystacea*, *Spilogaster angelicae*, *Pyrellia serena* and *Graphomyia maculata.* Therefore we have a right to infer that the author's meaning is that all these larvae omit the second stage of development. But it is not quite clear at the same time whether this generalization is a mere inference, or is based on actual observations; the only observation expressly mentioned by the author is that on *Musca meditabunda*, which he saw pass directly from the first to the third stage.

difference that the larva, when laid by *H. strigosa*, although large, is still in its first stage, and therefore has not grown within the body of the mother; it passes its three stages outside of it.

Musca corvina is exceedingly common in the Crimea and the Caucasus. Early in the spring (rarely in summer) specimens were observed that multiplied according to the mode already explained, that is by laying about 24 eggs with their peculiar appendages. Towards the end of the spring, and in summer almost exclusively, specimens were taken, subject to an entirely different process of propagation. Within the matrix-like expansion in the body of the female a single, very large egg, is found; it has the ordinary oval shape, without any appendages (fig. 8). It is very like the egg of *Dasyphora pratorum* in shape, but is larger (although the imago of *M. corvina* is smaller than the *Dasyphora*); it is in its first stage, as is proved by the shape of the stigmata; like the larva of *D. pratorum* it grows[1]) within the body of its mother, but passes immediately into the third stage, with its characteristic spiracles. This, as far as known, is the only instance of a shortened larval development among viviparous species, as they usually undergo the three stages. Supposing therefore that the specimens observed belong to the same species, of which, after careful and repeated comparisons, no doubt was entertained, *Musca corvina* has two different modes of larval development; one seems to prevail in the north, the other in the south; the latter may be due to the increased numbers of coprophagous species in the southern regions. *Musca corvina* thus forms the connecting link between the flies to which either of these modes is exclusively peculiar.

Hitherto the Pupipara had an isolated position among the Diptera. The modes of larval evolution of *Musca corvina* and *Dasyphora pratorum*, discovered by Mr. Portchinski bridge over the interval. He even ventures the hypothesis that the Pupipara began by being coprophagous in their larval state, and laid an almost full-grown larva, like that of the two above-mentioned flies. Later, owing

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1) Mr. Portchinski observes at this place that as his researches are not quite completed he cannot as yet stop to examine some important questions, for instance: on what do larvae feed in the body of their mother? He did not notice in *M. corvina* ♀ that large development of the adventitious glands which, according to Leuckart, secrete the food of the larvae of Pupipara. It is also worthy of notice that the larvae of *M. corvina* and *D. pratorum* when squeezed out of the body of a female come out with their tail first, while in the Sarcophagae they emerge head foremost.

to the parasitic mode of life of the imago and the diminution of the powers of flight necessary for providing the proper environments for the larvae, those changes in the mode of evolution of the larvae were produced which distinguish the Pupipara now.

A far distant past must have witnessed the evolution of the different modes of larval development of coprophagous flies; an abundance of forms must have existed at that time, and an intense struggle been going on among them, in order to produce the variety of larval development existing at present. The few palaeontological data in our possession tend to confirm this view; for instance, Oswald Heer's Tertiary Fauna of Oeningen is remarkably rich in coprophagous insects.

There are species nevertheless, among the typical coprophagous diptera, which are in open contradiction to the general result which we have reached about that group: the diminution of their fecundity. In this respect, the common house fly *(Musca domestica)* deserves our especial attention. It lays a comparatively large number of small eggs (120—160) and its larvae pass through the normal three stages of growth. It remains to explain how the house fly can, under such circumstances, compete with the other coprophagous flies? The explanation may perhaps be found in the very domesticity of the house-fly. Unable to compete with the other flies, it sought a refuge around human dwellings, where it had no dangerous competitors. Its dependence on human society is so great, that it is very seldom found in abundance in uninhabited districts. (Zetterstedt mentions such an instance; another was observed in North-America; comp. Psyche, Vol. III, p. 339.)

It would be most interesting to study the life habits of european flies in extra-european regions. *Musca corvïna* for instance, as has been shown, has a two-fold mode of development; it would be worth while to inquire about its life-history in Taity or the Philippine Islands. — *Musca domestica*, in New-Zealand, crowds out the native blue-bottle fly; what are its advantages in that struggle?

Whether Mr. Portchinski's very ingenious generalizations are accepted or not, it must be acknowledged that he has discovered a great number of interesting biological facts, and has opened a new field for most important inquiries.

List of the species of diptera mentioned in this paper.