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II. Microporeuta. Stomach-wall with simple cutaneous pores (interstices in the parenchyma), without parietal canals.	A stock with many mouth-openings.	One person with one mouth-opening	2. <i>Olynthida</i> .
		Persons developed, all with mouth-openings	5. <i>Soleniscida</i> .
			6. <i>Tarromida</i> .
		Persons rudimentary, many without mouth-opening	9. <i>Nardopsida</i> .
		A stock with one mouth-opening	11. <i>Clistolythida</i> .
III. Orthoporeuta. Stomach-wall with straight, regular, radial parietal canals.	A stock without mouth-opening...	A stock without mouth-opening...	14. <i>Sycorrhizida</i> .
		A stock composed of persons and stocks of diverse genera	17. <i>Thecometrida</i> .
		One person with one mouth-opening	3. <i>Sycarida</i> .
		A stock with many mouth-openings	7. <i>Sycodendrida</i> .
		A person without a mouth-opening	12. <i>Sycocystida</i> .
IV. Cladoporeuta. Stomach-wall with crooked, irregular, branched parietal canals.	A stock without mouth-openings	A stock without mouth-openings	15. <i>Sycophyllida</i> .
		A stock composed of persons and stocks of different genera.....	18. <i>Sycometrida</i> .
		One person with one mouth-opening	4. <i>Dyssycida</i> .
		A stock with many mouth-openings	8. <i>Sycothamnida</i> .
		A stock with one mouth-opening	10. <i>Cænostomida</i> .
	One person without mouth-opening	One person without mouth-opening	13. <i>Lipostomida</i> .
		A stock without mouth-openings	16. <i>Sycolepida</i> .

XIX.—On the Parasitism of *Rhipiphorus paradoxus*.

By T. ALGERNON CHAPMAN, M.D.

I HAVE read Mr. Murray's papers on the economy of *Rhipiphorus* with much interest; and although he has not succeeded in converting me to his views of its life-history, he has added to our knowledge of its habits and raised anew an interest in the relations subsisting between the wasps and their parasites which will probably lead to observations in the coming season that will set at rest many of the points in dispute.

In the meantime I think it very desirable to form as correct an hypothesis of the life of *Rhipiphorus* as our facts admit of, since an approximation to the truth is a most valuable guide in making further investigations, while, on the contrary, an erroneous theory may blind us to very obvious truths.

I cannot better begin the remarks I desire to make than by rendering what appears to me to be but justice to the accuracy of the earliest record we have of the economy of *Rhipiphorus*, meagre and deficient in detail though this record is. The observations of Mr. Denison, brought to our notice by Mr. Smith from the papers of the Ashmolean Society, appear to me to

give an accurate sketch of the life-history of *Rhipiphorus*, and to be in harmony with all the facts yet recorded both of *Rhipiphorus* itself and of other parasites whose similar habits render their history fairly available in explaining that of *Rhipiphorus*. The account there given is that *Rhipiphorus* "deposits its egg upon the grub of the wasp at the moment it assumes the pupa (*i. e.* spins or covers itself in the cell); as soon as the egg is hatched, it devours the grub of the wasp entirely, and itself assumes the pupa- and imago-form in the cell of the wasp."

The mode of oviposition here noted of *Rhipiphorus* is, I believe, that followed by it, although it will be seen that I am here at issue not only with Mr. Murray, but also with Mr. Smith, with whom on all other points I agree. If Mr. Denison's view (but for the slight disagreement noted, I should here, as I shall in the rest of these remarks, have said Mr. Smith's view) of the history of *Rhipiphorus* is correct, the relation of *Rhipiphorus* to the wasp is, *mutatis mutandis*, precisely the same as that of *Chrysis bidentata* to *Odynerus spinipes*. The larva of *Chrysis bidentata* feeds on that of the solitary wasp, from whose cocoon emerges, not the wasp, but the *Chrysis*. Now in this instance the egg of the parasite is not laid until after the larva of the wasp has done feeding, and is spinning its cocoon. Before I ascertained this fact, I had formed the same theory as to the period of oviposition as Mr. Smith has done in the case of the *Rhipiphorus*, and made in consequence many a vain search for the egg of *Chrysis bidentata* beside the feeding larva of the *Odynerus*. The parent *Chrysis* has many more difficulties to overcome (what these are is not material to the present subject) in depositing her eggs than the *Rhipiphorus*, to whom it must be as easy to deposit an egg beside a full-fed larva, during or just before spinning, as in an empty cell. There are other instances recorded of parasites similarly depositing their eggs beside full-fed larvæ, none, that I know of, of an egg remaining dormant beside a feeding larva. Mr. Murray appears to interpret Mr. Smith's view to be that the larva of *Rhipiphorus* hatches at the same time as that of the wasp, and then walks off to find a full-fed larva to eat. I quite agree with Mr. Murray's comments on such a theory, but feel satisfied that Mr. Smith really meant that the egg lay dormant until its companion, the egg of the wasp, was a full-fed larva.

The two eggs found by Mr. Murray in some cells of the wasp both appear to me to be undoubtedly eggs of the wasp. I think it extremely improbable that the egg of *Rhipiphorus* should be precisely the same as, however similar it may be to,

that of the wasp. I have found two eggs so situated in nests in which I could see no trace, unless this was one, of *Rhipiphorus*. I have seen two young larvæ of similar size in the same cell; yet afterwards one of these must have disappeared, removed probably by the wasps, and not devoured by the other grub, whether that may have been a *Rhipiphorus* or not. I may mention an exaggerated, because abnormal, instance of more than one egg being in each cell. I had placed some pieces of wasp-comb with many wasps clustered about them in a box, and so made an artificial nest. After a period I found every otherwise unoccupied cell with two, three, or more eggs in it, several with as many as twenty. The cause of this I cannot explain. Whether I had so diminished the amount of comb that there were not sufficient cells for the queen to deposit her eggs, one in each, or whether I had destroyed the queen, and some of the workers had assumed queenly functions, which is said sometimes to occur, and the latter had not the same accurate instincts as a true queen, I am unable to say. But whatever may have been in a morbid instance the cause of this multiplicity of eggs in the same cell may fairly be assumed to be a possible cause in a healthy nest.

My argument, so far, is rather against the supposition that the *Rhipiphorus*-egg is laid in the cell with that of the wasp, on the theory of the latter being the prey of the former (Mr. Smith's view). On Mr. Murray's hypothesis, the egg of *Rhipiphorus* might be laid in a cell by itself; but, if laid in one with a wasp-egg also, we must suppose that the latter, either before or after it is hatched, is removed by the attendant wasps, or falls a prey to the young *Rhipiphorus*-larva. In either case it is a necessary result of the theory that the larva of *Rhipiphorus* should be found occupying a cell among the wasp-larvæ. No one has ever pretended to have found a *Rhipiphorus*-larva so situated, though it has often been looked for. I pass over as untenable Mr. Murray's suggestion that some of his wasp-larvæ were *Rhipiphori*; I have myself searched in vain for such a larva in nests infested by *Rhipiphori*. I shall leave Mr. Smith to show (which I know he has the means of doing) that a larva of *Rhipiphorus* so situated differs sufficiently from that of the wasp to be readily detected, though I think Mr. Stone's remark, that "the larva is a singular-looking one," would of itself sufficiently establish this, especially when we take into account the fact that he nowhere hints at any possibility of confounding it with that of the wasp.

The remaining difficulty in the way of supposing the larva

of *Rhipiphorus* to be reared in precisely the same way as those of the wasp, is the silken covering always found over the pupa of *Rhipiphorus*, just as over that of the wasp. I have never seen any difference between the silk covering a *Rhipiphorus* and that covering a wasp, though I have found it possible to guess the cell containing the beetle by the shining-through of the differently coloured inmate. It seems very probable, from what we know of the mimicry by guest-insects of their hosts, that its silk would closely resemble that of the wasp, did it spin silk at all. The only instances of beetles spinning any thing like silk, that I can call to mind, are *Cionus* and its allies, and the doubtful instances of *Coccinella* and *Donacia*.

In discussing the difficulties raised by Mr. Murray in the way of Mr. Smith's view of the economy of *Rhipiphorus*, I shall dismiss his objections to the supposition of the *Rhipiphorus*-larva devouring several wasp-larvæ, because I have no wish to defend such a theory, nor do I suppose that Mr. Smith has. But the objections he raises to the hypothesis of its devouring only one larva, viz. the one in whose cell the egg of *Rhipiphorus* is laid when the larva has done feeding, and is spinning or about to spin, all appear to me to be invalid. He first asks Mr. Smith if a meal of one animal can suffice to nourish another into as great dimensions as the animal eaten. Mr. Murray here stretches his point a little. The *Rhipiphorus* is not of as great dimensions as the animal eaten, although it is very nearly so. It is little if at all nearer to the dimensions of the wasp than *Chrysis bidentata* is to the dimensions of its host *Odynerus spinipes*, of which I have sufficiently proved it eats but one larva. Or I might put this in a still stronger form: *Chrysis neglecta*, differently from *C. bidentata*, eats not the wasp-larva, but the store of pabulum laid up for the larva of the *Odynerus*. It might certainly, then, so far as store of nutriment goes, be as large as the wasp; yet it is smaller than *Chrysis bidentata*, whose food is the larva of the wasp.

Mr. Stone found a "minute larva" grow to full size in forty-eight hours—on which Mr. Murray remarks that it is so opposed to every thing we know of the laws of development and assimilation that he cannot accept it. Now I am unable to give Mr. Murray any facts that will expand his faith in the laws of development and assimilation quite to the extent required; but I am able to give him some that will so nearly do so, that he will, I doubt not, like myself, be prepared to believe that Mr. Stone's account is literally true. I may first say that probably Mr. Smith felt little difficulty in accepting Mr. Stone's observations, as he must be accustomed to the

rapid feeding-up which occurs in so many Hymenoptera. I, on the other hand, was as much astonished at my own observations on the *Chrysides* as Mr. Murray can be incredulous of the facts recorded by Mr. Stone. The larva of *Chrysis bidentata* began to spin its cocoon in eleven days from the date of the egg-hatching. *Chrysis neglecta* took rather a shorter time. But in one instance in which I reared a larva of *Chrysis ignita*, and happened to know the date on which the egg was laid, I found, two days after that date, a "minute larva" ($\frac{1}{4}$ inch long, about one-thirtieth of the full-grown larva in bulk), and in four more days the larva was full-fed.

On Mr. Murray's next point, as I have no fresh light to throw on it, I will merely remark that, as I read the recorded facts, the larvæ that Mr. Stone found unemployed in eating wasp-larvæ were not larvæ that had still some eating to do, but were those that had, as Mr. Murray expresses it, eaten up their man and retired from active life; though not yet pupæ, they were about to enter that state. All larvæ take a prolonged rest at this stage of their existence. Mr. Murray, who will not allow that a larva can feed up in two days (not from the egg, but from a small size), surely does not ask us to suppose that the larva becomes a pupa the instant it has done feeding. *Chrysis*, which fed up in four days, remains before its change to pupa nearly ten months. Will he not allow *Rhipiphorus* a day or two?

I do not see that the question of size has much bearing upon the question at issue. In the one view the large specimens are large because they have eaten a queen instead of a worker larva, in the other the wasps have fed them more plentifully because they were in queen-cells. Still, if the capacity of parasites for varying in size which Mr. Smith mentions be not called in by Mr. Murray to account for those in the queen-cells being able to assimilate a larger supply of nutriment than the others, he must give us some other hypothesis. The case is obviously not parallel to that of the wasps, where the larger insects are queens, the larger *Rhipiphori* differing only in size. So much has this difficulty been felt, that I have seen it somewhere advanced that the larger specimens are always females—making the case parallel with that of the wasps themselves, which Mr. Murray has proved not to be the case. Why, if difference of feeding can produce the result, Mr. Smith should be asserted to be carrying his argument to the extreme in supposing that the mere difference between eating a worker-grub and a queen-grub is sufficient to account for the greater dimensions of the one in the queen's cell over the one in the worker's cell, I cannot at all understand. A

queen-grub must bear as a meal much the same relation to a worker-grub that the pabulum offered by the wasps to a *Rhipiphorus*-larva, on the supposition that it is a queen-grub because it is in a queen-cell, does to that they would offer to it in a worker-cell, where they must suppose it to be a worker-grub.

As to the difficulties which Mr. Murray finds in the *Rhipiphorus* beginning its repast at the head of its victim, he falls again into the error of supposing that Mr. Smith postulates that the larva of *Rhipiphorus* should perambulate in search of pabulum: this, however, only explains a part of his difficulty, as Mr. Stone's observations and the requirements of the theory that I accept from Mr. Denison show that the *Rhipiphorus*-grub really does begin his attack at or near the head. Here I cannot help suggesting, in parenthesis, somewhat mischievously perhaps, for Mr. Smith's consideration, that if the egg lies dormant during the feeding of the wasp-grub, it must remain so at the bottom of the cell; and then, of course, to the confusion of all parties, the attack of *Rhipiphorus* would "begin at the tail."

Mr. Murray clearly believes that he has here made a strong point. He assumes, with apparently logical accuracy, that if the *Rhipiphorus* begins to devour its victim at the head, it necessarily last eats the tail, and must thus, when it has completed its meal, have its head where its victim's tail was. Part of this error arises, as I have said above, from the supposition that the larva crawls about above the cells in search of a victim—a supposition that no one will object to my dismissing as untrue. But were it true, it would not alter my position that the wasp-grub can be easily (and is) attacked first near its head, yet the parasite assume the proper position in the cell. Let it be clearly understood that the wasp-larva is not to be eaten downwards, segment by segment, as though it were a carrot. It is doubtless eaten just as the larva of *Odynerus spinipes* is by that of *Chrysis bidentata*, viz. its juices sucked out, at first partially, of course, leaving it flaccid, so that both larvæ might easily be arranged side by side in the cell, the tail sucker of the victim now probably relaxing its hold of the cell-wall; afterwards more thoroughly; and, if the parallel holds good, the victim is reduced to very small dimensions indeed before any thing like eating takes place. I have often seen a larva of *Odynerus spinipes* reduced to very small bulk without any trace of even a microscopic opening in the skin being discoverable. In this way there is no difficulty in understanding how the *Rhipiphorus*-larva is found, when full-fed, with its head to the mouth of the cell. It

shows also how the remains (corneous head) of the victim would be beside the head, if not in the jaws, of its devourer, and, it being remembered that the mouth of the cell is downwards, might remain there after the *Rhipiphorus* had assumed the pupal state. But that a Coleopterous pupa should hold any thing in its jaws, whether previously held in the jaws of the larva or not, I can only, with Mr. Murray, regard as impossible; and if Mr. Stone means this, he has clearly committed some error. He uses the phrase "retain in their grasp," which, with perhaps a little forcing, may be supposed to mean the larval grasp, *i. e.* the grasp of the now cast larva-skin. Or we may suppose that the remains of the wasp lying at the top of the cell fell, on its inversion for examination, between the pupa and the wall of the cell, looking just as if held there by the pupa.

I must leave Mr. Smith to deal with the way in which Mr. Murray explains away Mr. Stone's observations, only observing that, in my opinion, if Mr. Stone committed half the errors imputed to him by Mr. Murray, he must henceforth be regarded as the most inaccurate observer on record.

It remains to consider the new facts brought forward by Mr. Murray, and which appear to have first led him to adopt the guest-theory of the life-history of *Rhipiphorus*. These are the three instances in which he found a pupa of *Rhipiphorus* and one of the wasp in the same cell. These are somewhat difficult to explain on either hypothesis, but they seem to me to be much less explicable on the guest-theory than on the parasitic. Mr. Murray finds it very difficult to imagine a wasp-larva turning round in its cell; and, though I have not found wasp-larvæ such completely helpless sacks as he appears to regard them, I agree that for a full-grown larva to turn round in its cell would be simply impossible. Yet, on the guest-theory, this must have occurred in two out of the three instances he mentions. And how the wasps could possibly feed the larva at the bottom of the cell, when the upper one was well grown, I cannot conceive. Mr. Murray has truly remarked that a full-fed wasp-larva, and equally therefore one of *Rhipiphorus*, completely fills the cell it occupies. Now, in the three cases in question, if the larvæ were fed by the wasps, why did one or the other not grow to its proper size, so as to fill the cell, and eject its companion? or why did one not eat the other?—an occurrence of which he elsewhere admits the probability, should a chance occur, which, on the guest-theory, must be but rarely.

On the parasitic theory, we have only to suppose that, for some accidental reason, of which several might easily be

imagined, the *Rhipiphorus*-larva ceased to feed before it had drained the juices of its victim to the point of death; the wasp-larva, being at a stage of its existence when it no longer eats, does not, of course, avenge itself. The struggles of the wasp-larva in these uneasy circumstances, and its semiflaccid condition, would easily account for, and render possible, its change of position in the two instances in which that had occurred.

The difficulties which have surrounded the elucidation of the life-history of *Rhipiphorus* may all, I think, be traced to the very short interval that elapses between the laying of the egg and the arrival of the insect at the pupal state. They appear to assume the pupal state almost as soon as the surrounding wasp-grubs; yet the eggs were only laid when these latter were beginning to spin. This allows a very brief period during which they must be found, if these stages are to be observed. Mr. Murray has failed to do so, probably because he did not examine the nests until such a period had elapsed after the nests were taken. I also failed, because, when my opportunities were most abundant, I did not know what to look for. As a similar instance among the *Chrysides*, I may mention the egg of *Chrysis neglecta*, which I have never been able to find. I find young larvæ only, and have satisfied myself that the egg-state does not last as much as twenty-four hours. In the instance I have mentioned above of *Chrysis ignita*, the egg-state cannot have lasted so long.

XX.—*Concluding Observations on the Parasitism of Rhipiphorus paradoxus.* By FREDERICK SMITH, Assistant in the Zoological Department of the British Museum.

WITH some degree of hesitation, I venture to reassert my belief in the views I put forth in reply to Mr. Murray's first paper on the relations between wasps and *Rhipiphori*. I have some fear of being considered dogmatic, and of not duly weighing the arguments offered to my notice by my friend Mr. Andrew Murray. I must, however, confess myself to be unconverted by his arguments, and unable to arrive at the same conclusions that he does when commenting upon the various phenomena which were presented to him when examining the comb of a wasps' nest. It will perhaps be a matter of astonishment that he has failed in his endeavour to bring me round; and it is equally surprising, but at the same time consolatory, to find Mr. Murray expressing the opinion that, should a larva of *Rhipiphorus* "fall upon a larva of the wasp,