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THE BIOLOGICAL SIGNIFICANCE OF THE ATTACHMENT OF  
IMMATURE STAGES OF *SIMULIUM* TO MAYFLIES  
AND CRABS.

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The attachment of the immature stages of SIMULIIDAE to other aquatic arthropods was evidently first noticed about 20 years before the association was regarded as other than fortuitous. In 1926, Ribeiro reported the finding of a Simuliid larva attached to a mayfly larva which had been collected in the eastern Himalayas, and remarked that the association was apparently accidental. Soon afterwards, F. W. Edwards (1928) recorded the occurrence of larvae and pupae of *Simulium nyasa-landicum* De Meillon (referred to by him as *S. hirsutum* Pomeroy) on a specimen of the crab, *Potamon niloticum* (H. M.-Edw.), collected in Uganda, and likewise concluded that the attachment must have been fortuitous. And in 1929, W. N. Edwards collected from the Victoria Falls a mayfly larva of the genus *Afronurus* to which were attached the pupa and cocoon of a *Simulium*, possibly *S. lumbwanus* De Meillon (see Freeman & De Meillon, 1953).

The specificity of the relationship was apparently recorded first by Rubtsov (1948, quoted by Grenier & Mouchet, 1958), who described the attachment of *S. ephemerophilum* Rubtsov to larvae of *Ecdyonurus* in Turkestan. Subsequently, and independently, Marlier (1950) and van Someren & McMahon (1950) reported similar associations with mayflies in West and East Africa, where several other examples have since been recorded (Freeman & De Meillon, 1953; Berner, 1954; M. T. Gillies, personal communication, 1958; Corbet, 1960). The specific attachment of members of the complex of *S. neavei* Roub. to freshwater crabs in Africa, noted by van Someren & McMahon (1950) and later by others seems to represent a relationship which is ecologically similar.

Several authors, particularly Rubtsov, have discussed the possible biological significance of these associations, and have suggested various respects in which the *Simulium* might be expected to benefit from them. This subject has recently been reviewed by Grenier & Mouchet (1958), who have provided a useful summary of the available information. It is my view, however, that, although sufficient evidence necessary for a tentative solution of the problem has now been published, the most plausible of the permissible inferences has not yet been drawn from it, and the purpose of the present communication is to call attention to the one which I consider the evidence unequivocally supports, and then to discuss some of its implications. For conciseness, I shall confine the detailed arguments to the association involving *Simulium* and mayflies, and then briefly explain why essentially the same considerations apply when crabs are involved.

Characteristic features of the association are that larvae or pupae of *Simulium* are attached, in a more or less constant position, to the larva of a mayfly which lives amongst stones on the bed of a fast-flowing stream or river. Species of *Simulium* exhibiting this habit usually attach themselves only to those mayfly larvae which are dorso-ventrally flattened, and which cling tightly to the stones amongst which they live. Examples of such mayflies are members of the HEPTAGENIIDAE (*Afronurus*, *Ecdyonurus*) and OLIGONEURIDAE (*Elassoneuria*).

It was Rubtsov who pointed out that in Turkestan the majority of attached examples of *Simulium* are either pupae or large larvae; and subsequent enquiry and examination have shown that this is true elsewhere. To my mind, this

indicates that the biological significance of the association is to be found in some adaptive requirement peculiar to *older larvae* or to *pupae*, since otherwise it is presumably the *smallest* larvae that would be the most numerous. One thing with which, in their different ways, both large larvae and pupae are concerned, is the location of a suitable site for pupation. Thus the most likely explanation seems to be that the pupa is the stage towards which the adaptation is primarily directed. *A priori* this is equally probable. Being immobile in an environment where the stones of the river bed may frequently be changing position owing to violent water movement, the *Simulium* pupa has need of a support which will (a) adopt a constant orientation with respect to the current, and (b) reduce the chances of its being crushed or buried when stones are displaced. As Rubtsov remarked, certain lithophilic mayfly larvae, which tend both to face the current and to seek sheltered crevices, answer these requirements well. Furthermore, it is evident that the ones most suitable will be those which have a dorsal surface sufficiently large and even to accommodate the pupal cocoon.

Hitherto, this interpretation has been mentioned as merely one of several advantages that the *Simulium* might derive from the relationship. In the light of the evidence, however, I consider that it is more appropriately to be regarded as the principal selective factor which has determined the association. Certainly, such a hypothesis simplifies a problem which writers hitherto have been inclined to regard as complex. It resolves, in particular, the confusing question of whether or not the *Simulium* larva *per se* benefits from the association. Previously it had been suggested that, in an environment where organic matter in suspension was scarce, the larvae might obtain significantly more food by exploiting the detritus dislodged by the mayfly or crab, and also that, as a result of the attachment, they might obtain shelter from the current and enjoy enhanced opportunities for respiration. If, however, the pupa provides the *raison d'être* of the association, then, as explained above, the presence of attached larvae is to be expected simply on the grounds that it is they who must select the pupation site. Were attachment to have any selective value for the early stages, one would expect *Simulium* larvae to be represented in proportion to their abundance—the smallest being the most numerous—whereas in fact the reverse is the case.

To sum up, I consider the evidence supports the hypothesis that the determining factor in the evolution of this association has been the need for *Simulium* in fast-flowing, unstable watercourses to secure a pupation site which gives protection against disorientation and damage.

In the case of associations involving *Simulium* and crabs, the evidence is similar and leads to the same conclusion. The associations usually occur in swiftly flowing streams or rivers, and the attached examples of *Simulium* comprise mainly pupae and large larvae. If, as sometimes happens, small larvae are represented, then they are disproportionately rare (see Browne, 1960). Like certain mayflies, crabs present a smooth, even surface for pupal attachment, and also presumably give adequate protection against disorientation and damage. It should perhaps be stressed here that physical damage due to displacement of stones is more than a theoretical possibility in some habitats. Barnley (1960) noticed that, after heavy rainfall had caused abrupt flooding in highland streams in Uganda, many of the *Simulium* pupae found on the stones were crushed or dead.

It has been suggested that, where streams are liable to dry up or become otherwise unsuitable, crabs may assist the *Simulium* larvae by transporting them across land to a more favourable habitat (see Lewis, 1960). Once again, however, the size-distribution of the attached examples of *Simulium* militates against this being more than a secondary advantage of the relationship, although it is possible that in some habitats selection pressure may now be acting upon it in this way. When this happens to a significant extent, however, we may expect to find small larvae attached in greater numbers.

A second, and separate question may now be considered, namely the means by which *Simulium* larvae locate and select their carriers, and then become attached to them.

The location of a mayfly larva, as such, may perhaps depend upon the slight gradient in water velocity produced by the activity of its abdominal gills. Heptageniid mayfly larvae commonly live beneath stones, in relatively sheltered sites, the dorso-ventral flattening of their bodies being regarded as a crevice-seeking, and not a current-resisting, adaptation (Nielsen, 1951; Stuart, 1958). In such places the contrast between their respiratory current and the water movement of their immediate surroundings might be enhanced, and thus become discernible to a searching *Simulium* larva. Water velocity is known to be one of the most important physical factors determining the micro-distribution of *Simulium* larvae in watercourses (Phillipson, 1956; 1957), and it would therefore seem possible that *Simulium* larvae seeking an attachment site might be able to locate a mayfly larva by responding to short-range current gradients set up by its gill movements.

The point has already been made that most of the attached *Simulium* larvae are large ones. But it can be seen that there is no obvious reason why larvae should not attach themselves in instars other than the final one. Indeed, by exploiting a premature encounter, they would extend their chances of finding a suitable mayfly. To judge from the material of several species I have examined in the British Museum (Natural History) and elsewhere, a few larvae begin to attach when they are about half grown, and others do so in increasing numbers after this. It must be borne in mind, however, that attachment need not be irrevocable, and that, as the time for pupation approaches, attached larvae may perhaps become more critical and may change their supports.

If attachment is to be an insurance against displacement during the pupal stage, then it is clear that the mayfly larva selected as a carrier should neither be about to moult nor about to emerge, since in either event the *Simulium* pupa would then be stranded on the mayfly exuvia and in all probability be swept downstream. Thus the mayfly larvae most suitable for attachment in this respect would be those which had just entered a late instar, *i.e.*, one with a relatively long duration, though not necessarily the last (see Corbet, 1960). There are two physical attributes which are peculiar to such mayfly larvae, and which accordingly might enable *Simulium* larvae to recognise them. These are first, a soft cuticle; and second, a relatively large, even, dorsal surface. It would be interesting to discover whether searching *Simulium* larvae (especially those in the last instar) respond positively to objects possessing these two properties.

It was originally believed that the emergence of the *Simulium* and that of its mayfly carrier were closely synchronised, a conclusion based on the observation that the emergence of captive *Simulium copleyi* Gibbins took place within one or two hours of that of the *Afronurus* carrying them (van Someren & McMahon, 1950). It has recently been shown, however, that so long as the adult of *Simulium* can emerge *before* the moult of its carrier, no synchronisation of this kind is necessary, a conclusion amply supported by the finding of empty pupae attached to penultimate-instar mayfly larvae (Corbet, 1960). To obtain final confirmation of this, I examined the preserved material of attached *Simulium* in the British Museum (Natural History), and found that the majority of pupae or pupal exuviae of *Simulium* (including a specimen of *S. copleyi*—the species in which van Someren & McMahon reported synchronisation to occur) were attached to mayfly larvae in the penultimate instar. It may be concluded that grounds no longer exist for regarding synchronisation of emergence as a feature of this association.

Most of the remarks above have equal force when applied in principle to the association involving *Simulium* and crabs. *Simulium* larvae could probably locate and recognise crabs in similar ways; and here also it would be advantageous for

a larva seeking a pupation site to select a crab which was at the beginning of an instar (*viz.*, a crab with a soft cuticle), although there would evidently not be the same need for the instar to be a late one. What little information exists indicates that all but the earliest instars of crabs have a duration many times longer than that of the pupal stage of *Simulium*. Hence, whereas it might still be necessary for the *Simulium* larva to select a crab of above a certain size (a phenomenon noted recently by Browne (1960) in *S. neavei*), the range of suitable instars available to it would presumably be much greater than is the case in the mayfly. A recent observation which may be of great significance in relation to this question has been made by Barnley (1960), who remarked that final-instar larvae and pupae of *Simulium* predominated on soft crabs.

If the attachment of *Simulium* to freshwater arthropods has the biological significance which has been attributed to it in this paper, then it is obviously appropriate to describe the association as phoresis.

#### Summary.

It is suggested that the attachment of the immature stages of certain species of SIMULIIDAE to mayfly larvae and to crabs is primarily an adaptation whereby the immobile *Simulium* pupa can obtain protection against disorientation with respect to the current, and against damage, in an environment where available inorganic substrata are liable to be displaced by violent water movement.

The principal evidence for this is that these associations typically occur in fast-flowing streams or rivers, and that the attached stages of *Simulium* include a disproportionately high number of pupae and large larvae. Any direct benefit the *Simulium* larvae themselves may derive from the association is regarded as a secondary feature of it.

Certain responses to physical factors, which might be expected in *Simulium* larvae achieving successful attachment, are briefly discussed.

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