the 5 percent level. From Category A, the least number of eggs were obtained though the differences from B, C, and E are not significant.

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PHORETIC ATTACHMENT OF *SIMULIUM* LARVAE AND PUPAE TO MAYFLY AND DRAGONFLY NYMPHS[1]

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BACKGROUND. Phoresy among insects is a type of relationship in which an insect is carried on the body of another, larger insect, but does not feed on the latter (Torre-Bueno, 1962). Phoretic attachment of *Simulium* larvae and pupae to mayfly and dragonfly nymphs has been reported mostly in Africa. The attached form may be designated as the "epizoite," and its host a "carrier." (Clausen, 1962; Grenier and Mouchet, 1958). Both terms "larvae" and "nymph" appear in the literature in reference to aquatic stages of Odonata and Ephemeroptera. Chapman (1969) states that the stage which succeeeds the egg is a larva, and that the nymph is a larva of a hemimetabolous insect which basically resembles the adult, in contrast with the radically different larva of a holometabolous insect. Phoretic attachment of *Simulium* species in Africa occurs also upon crabs and prawns, but will not be reported here.

The nymphs of many species of mayflies and dragonflies inhabit fast-flowing water, and hence occur in large numbers in the same places where blackfly larvae develop. A blackfly larva which has sufficient food carried to it by the current in a favorable and undisturbed environment,

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will generally remain and pupate upon or near the site of attachment. If the food supply is greatly diminished, if the larva is disturbed, if the curent velocity fluctuates as a result of becoming too slow or too rapid (Tarshis and Neal, 1970; Burton and McRae, 1965; Yakuba, 1959), if the turbidity increases (Yakuba, 1959), or if the larva is iritated by insecticide (Burton, 1964; Burton *et al.,* 1964), it will often detach and migrate either by moving like a measuring worm along the substratum, or at the end of a silken thread, or break loose and reattach elsewhere (Rubtsov, 1964). Exposure to too much insecticide will often, of course, result in its death. Yakuba (1959) found that the 4th instar larva was the most common stage among the migrants as a result of water level and turbidity increases.

Although some attachments may be accidental or incidental, certain *Simulium* groups have evolved either to a fully phoretic or facultatively phoretic behavior. The phoretic species *S. berneri, S. diceros, S. copleyi,* and *S. lumbwanus* all have similar respiratory filaments (Freeman and de Meillon, 1953; Freeman, 1954). Lewis (1961) considered *S. copleyi* to be a facultative epizoite because sometimes the larva does not exhibit phoresis. Disney (1971a) found that the mayfly *Elassoneuria* occurs only in rivers having abundant *Simulium* breeding, thus ensuring its availability for phoresis. A summary of phoresis involving *Simulium* eggs, larvae, and pupae upon mayfly and dragonfly larvae mostly in Africa, is given in Table 1. The constancy of association of epizoite and carrier can be seen: *S. berneri* on *Elassoneuria, S. lumbwanus* on *Afronurus, S. copleyi* on *Afronurus* and *Baetis,* and and *S. adersi* and *S. hargreavesi* on dragonfly nymphs only, the former on *Zygonyx* species. Outside Africa attachments have been recorded only on nymphs of the mayfly genus *Iron,* in India and the U.S.S.R. Attachment of *Simulium* pupae to pupae of Blepharoceridae (Diptera), reported by Hora (1930), may be accidental due to overcrowing on the same substratum.

Since the *Simulium* pupa is a fixed stage, it is obviously the larva which effects the attachment by migrating to the carrier. The silken thread of the blackfly larva may catch upon the nymph, or the larva may progress directly upon it if it is close to the *Simulium* attachment site. An example of this was seen in the case of *S. hargreavesi* [4] which is reported here: at Nalerigu Dam the stones were covered with the larvae, and underneath these stones were hundreds of *Zygonyx torrida* nymphs. Disney (1971b) concluded that attachments are effected by the 1st or very early instar larvae. *Simulium* egg attachments have been reported only once, *S. adersi* eggs upon the dragonfly nymph *Aeshna rileyi* Calvert (Lewis *et al.,* 1960).

The sites of attachment are diversified. Disney (1971a) recorded the numbers and distribution of *S. berneri* larvae and pupae on *Elassoneuria:* on wing covers or pads, head, thoracic tergites and sternites, abdominal tergites and sternites, and gills. Attachments are also seen on legs (Corbet, 1962). Sometimes the epizoites are as long as or longer than the carrier (Disney, 1971b). Most authors report finding only 1 to 3 epizoites per infested nymph. Disney (1971a) found 10 *S. berneri* larvae on a nymph of *Elassoneuria.* Corbet (1962) found 13 cocoons on an exuvia of *Zygonyx natalensis.* Crosskey (1965) recorded 11 larvae and 1 pupa of *S. berneri* on an *Elassoneuria nymph.* Disney (1971b) found 12 instances of both *S. afronuri* and *S. lumbwanus* attached to the same *Afronurus* nymph, concluding that multiple epizoites occurred upon larger nymphs.

Although attachments appear to be random in most cases, many investigators have found pupae on the right side of the carrier, particularly on the wing pads, although left-side attachments also occur (Corbet, 1960a). In certain associations

[4] Lewis (1964) designates this as a full species. Previously most authors followed Freeman and de Meillon (1953), i.e. *S. medusaeforme* form *hargreavesi.*

TABLE 1.—Summary of reported phoretic associations between *Simulium* species and dragonfly and mayfly nymphs, including country where collected.

Classification of Carrier	Phoretic *Simulium* Species	Country	Reference
Dragonfly Nymphs—Odonata			
Aeshnidae			
Aeshna rileyi Calvert	*S. adersi* Pomeroy (eggs only)	Southern Rhodesia	Lewis *et al.* (1960)
Libellulidae			
Libellulid nymph (no genus)	*S. hargreavesi* Gibbins	Nigeria	Lewis *et al.* (1960)
Zygonyx natalensis (Martin)	*S. adersi*	Uganda	Corbet (1962)
	S. vorax Pomeroy	Uganda	Corbet (1962)
	S. damnosum Theobald	Uganda	Corbet (1962)
Zygonyx torrida Kirby	*S. adersi*	Ghana	Burton & McRae (1972) (This paper)
	S. hargreavesi	Ghana	(This paper)
Mayfly Nymphs—Ephemeroptera			
Oligoneuridae			
Elassoneuria sp.	*S. berneri* Freeman	Ghana	Berner (1954)
	S. berneri	Southern Cameroon	Grenier and Mouchet (1958)
	S. berneri	Uganda	Gillies, M. T. in Crosskey (1965)
	S. berneri	Uganda	Crosskey (1965)
	S. berneri kumboense Grenier, Germain & Mouchet	West Cameroon	Germain and Grenier (1967)
	S. berneri	West Cameroon	Lewis *et al.* (1965)
	S. berneri	West Cameroon	Disney (1971a)
Baetidae			
Baetis sp.	*S. copleyi marlieri* Grenier	Congo	Marlier (1950)
Baetid (no genus given)	[1] *S. diceros* Freeman & de Meillon	Congo	Marlier (1950)
Heptageniidae			
Iron sp. (?)	Simuliid larva	India	Ribeiro (1926)
[2] *Iron* sp.	*S. ephemerophilum* Rubtsov	Tadjikistan, U.S.S.R.	Rubtsov (1948)
Afronurus sp.	*S. copleyi marlieri*	Belgian Congo	Marlier (1950)
Afronurus peringueyi Esben-Petersen	*S. copleyi* Gibbins	Kenya	van Someren and McMahon (1950)
Afronurus sp.	*S. lumbwanus* de Meillon	Southern Rhodesia	Edwards, W. N., in Freeman and de Meillon (1953)
Afronurus sp.	*S. lumbwanus*	Uganda	Bertram, D. S., in Freeman and de Meillon (1953)
Afronurus negi Corbet	*S. copleyi marlieri*	Uganda	Corbet (1960a)
Afronurus ugandanus Kimmins	*S. lumbwanus*	Uganda	Corbet (1960b)
Afronurus sp.	*S. vickenbachi* Germain, Grenier & Mouchet	West Cameroon	Germain, Grenier and Mouchet (1966)
Afronurus sp.	*S. afronuri* Lewis & Disney	West Cameroon	Disney (1971b)
Afronurus sp.	[3] *S. lumbwanus*	West Cameroon	Disney (1971b)
"Mayfly nymphs"	*S. copleyi* (?)	Kenya	van Someren (1948) in McMahon (1951)
"Mayfly nymphs"	*S. lumbwanus*	Kenya	McMahon (1951)

[1] Marlier erroneously determined this to be *S. neavei* Rouband, which it resembles.

[2] This genus has been reported as *Ecdyonurus,* but a translation of Rubtsov's paper, and his illustration, shows it to be *Iron.* Burks (1953) lists *Iron* as a subgenus under the genus *Epeorus,* but Day (1963) lists it as a valid genus.

[3] Disney designates this as *S. lumbwanum.*

there is a definite specificity of attachment site. Van Someren and McMahon (1950) found *Simulium* larvae attached at the base of the coxa of either metathoracic leg, with the head and body directed posteriorly. Marlier (1950) found the larvae of *S. copleyi marlieri* and *S. diceros* attached at the first abdominal segment on either side, the head between the hind legs of the *Afronurus* nymph; in each case the pupa attached to the wing covers. Berner (1954) found *S. berneri* attached between the legs, between the gills, and just behind the labium of *Elassoneuria.* Disney (1971b) found 44.7 percent of *S. lumbwanus* epizoites on the mesonotum and wing covers of *Afronurus,* and 40 percent of *S. afronuri* on the 2nd abdominal segment.

With few exceptions, phoretic *Simulium* pupae are oriented with the cocoon aperture facing posteriorly, i.e. in the direction of flow of the current. This obviously protects the pupa from the force of the current, and makes it easier for the emerging fly to reach the surface. Since the carrier usually faces upstream, the posterior orientation of the epizoite is assured. Corbet (1960) observed that the epizoite developed more rapidly than the mayfly carrier, emerging before the final exuvia is cast off. Van Someren and McMahon (1950) found that whenever the *Afronurus* nymph molted, the blackfly larvae detached temporarily, then reattached to the new integument; when the final nymphal skin was cast off, the fly emerged also. Mayfly nymphs undergo many instars, often between 20 and 30 (Burks, 1953). Murphy (1922) stated that the nymphal life of *Baetis vagans* McDunnough lasted for 6 to 9 months, and involved 27 instars. The nymphal span of *Hexagenia* is said to be about 2 years (Burks, 1953). The nymphal period of *Afronurus* appears to be much shorter, based on the mutual timing of the *Afronurus* and phoretic *Simulium* aquatic stages (van Someren and McMahon, 1950). Corbet (1961) disagreed with this synchronization concept, as *Simulium* empty pupae were attached to mayfly penultimate instar nymphs.

In phoresy the attachment benefits only the epizoite. Berner (1954) concluded that the phoretic association was an outgrowth of identical feeding habits and a paucity of places in the stream for attachment and pupation of the epizoite. Mayfly larvae are generally herbivorous, as determined by gut dissections of representative genera (Muttkowski and Smith, 1929; Jones, 1950). Marlier (1950) found that the gut contents of *S. copleyi marlieri* and *S. diceros* matched those of the carrier, and concluded that the attached *Simulium* larvae trapped in their fans vegetable fragments which were being torn up or raked up by the nymph during its own feeding activities. One of us (G.J.B.) found that there are generally sufficient plankton and other food materials in flowing rivers to sustain *Simulium* larvae, and this was noted also by Grenier and Mouchet (1958). Most observers have stressed the benefit of shelter for the epizoite, which otherwise might be affected by torrential currents or natural enemies. The mayfly nymph itself is often preyed upon by almost every aquatic predator (Day, 1963), including dragonfly nymphs (Smith and Pritchard, 1963; Imms, 1960). Epizoites upon them may thus be destroyed. Those upon dragonfly nymphs are better protected, since few predators will attack the larger ones (Corbet, 1962), except when they become cannibalistic, such as *Aeshna* (Smith and Pritchard, 1963). Some mayfly nymphs remain closely attached to and flattened against stones and small rocks, such as *Afronurus* (Disney, 1971b), *Heptagenia* (Day, 1963), and *Elassoneuria* (Disney, 1971a), as well as the dragonfly nymph, *Zygonyx* (Corbet, 1962). On the other hand, *Aeshna* (Smith and Pritchard, 1963) and *Baetis* (Day, 1963) are free-ranging and very active, and might therefore become involved in a phoretic association to a lesser extent, except when a blackfly larval migration thread might catch upon them. Barnard (1932) stated that in South Africa *Elassoneuria* occurs in slowly flowing rivers.

The attachment of *Simulium* larvae and pupae to dragonfly and mayfly nymphs may be regarded as unusual in that they thus affix themselves to natural enemies. Cameron (1922) reported that dragonfly and mayfly nymphs, especially *Heptagenia,*

fed extensively upon larvae of *S. arcticum* Malloch (=*S. simile*). Zivkovic (1955) found remains of *S. columbaszense* in nymphs of *Heptagenia sulphurea* Müller. Crisp (1956) found that *Afronurus* and *Baetis* spp. nymphs fed on *S. damnosum* larvae, but *Elassoneuria* fed mainly on algae in Ghana. Peterson and Davies (1960) observed nymphs of *Aeshna umbrosa* Walker devouring *S. venustum* Say larvae, approaching them from behind while the larvae were oriented down stream in feeding position. Miall (1912) also reported that *Baetis* and *Heptagenia* were carnivorous. Burks (1953) described the mayfly nymphs *Isonychia, Anepeorus,* and *Metreturus pecatonica* Burks as being predaceous, the former also feeding on other mayfly nymphs.

PRESENT STUDY. In the Red Volta River, at Nangodi, immediately east of Bolgatanga in the Upper Region of Ghana, an empty cocoon of *S. adersi* Pomeroy was found attached to the left side of the head of a nymph of the dragonfly *Zygonyx torrida* Kirby, between the compound eye and the trochanter of the left prothoracic leg. The axis of the cocoon was at about a 70-degree angle to the ground, its aperture directed upwards and partly posteriorly (Fig. 5). In Fig. 6 the view is directed into the cocoon aperture, the cocoon itself being slanted downwards away from the observer. This cocoon had the loose-meshed construction typical of *S. adersi.* The nymph measured 15/16-inch (23 mm) long and 3/8-inch (9 mm) wide at the abdomen. A second nymph of the same species and size bore upon its outer wing pad a complete pupa of *S. adersi,* with its respiratory filaments directed posteriorly (Fig. 1 and Fig. 2).

At Nalerigu Dam spillway, in northeast Ghana, immediately east of Gambaga, a partially-eaten or partially-deteriorated pupa of *S. hargreavesi* was found upon a nymph of *Zygonyx torrida* which was also 23 mm long, being situated upon the right outer wing pad. Although the respiratory filaments were gone, the pupa was identified by comparison of the cocoon construction with that of the only *Simulium* species found breeding upon the entire spillway, namely *S. hargreavesi.* The nymph was covered with a heavy layer of red silt, and was found buried in the bottom mud beneath a stone which was covered with larvae of this species. The immersion in the mud may have contributed to the death of the pupa, and it may also have been partially eaten by some predator.

These findings are similar to those of Corbet (1962) who reported finding pupae and empty cocoons of *S. adersi, S. vorax,* and *S. damnosum* attached to exuviae of nymphs of *Zygonyx natalensis* in Uganda. Almost all of the cocoons of *S. damnosum* and *S. vorax* were attached at the right side, all facing more or less posteriorly. One *S. damnosum* cocoon was attached at the right side of the head on the antero-dorsal surface of the compound eye and the vertex. This should be compared with the site of the *S. adersi* cocoon in the present study, but which was on the left side. Corbet (1962) also found *S. adersi* attached to the left underside of the abdomen. Lewis *et al.* (1960) found eggs of *S. adersi* on the abdomen behind the wing pads of a 25 mm nymph of *Aeshna rileyi* Calvert in Southern Rhodesia. As regards *S. hargreavesi,* Lewis *et al.* (1960) also found two larvae of this species attached to a libellulid dragonfly nymph 18 mm long, one on the frons and the other on the left wing pad.

Phoresy also occurs with *Simulium* pupae in the role of carriers instead of epizoites. Edwards (1929) found larvae and pupae of the midge *Eukiefferiella* attached externally to pupae of *S. ornatum* Meigen. He cited the findings of Falkner regarding a midge whose larval and pupal stages were passed completely within the cocoons of *S. nigritarsis* Coquillett (=*S. latipes* Meigen) and *S. aureum* Fries as a means of shelter. Bequaert (1934) observed similar chironomid behavior in the cocoons of *S. callidum* (Dyar and Shannon) in Guatemala. Grenier (1948) also noted such an association, citing a chironomid larva which lives in large num-

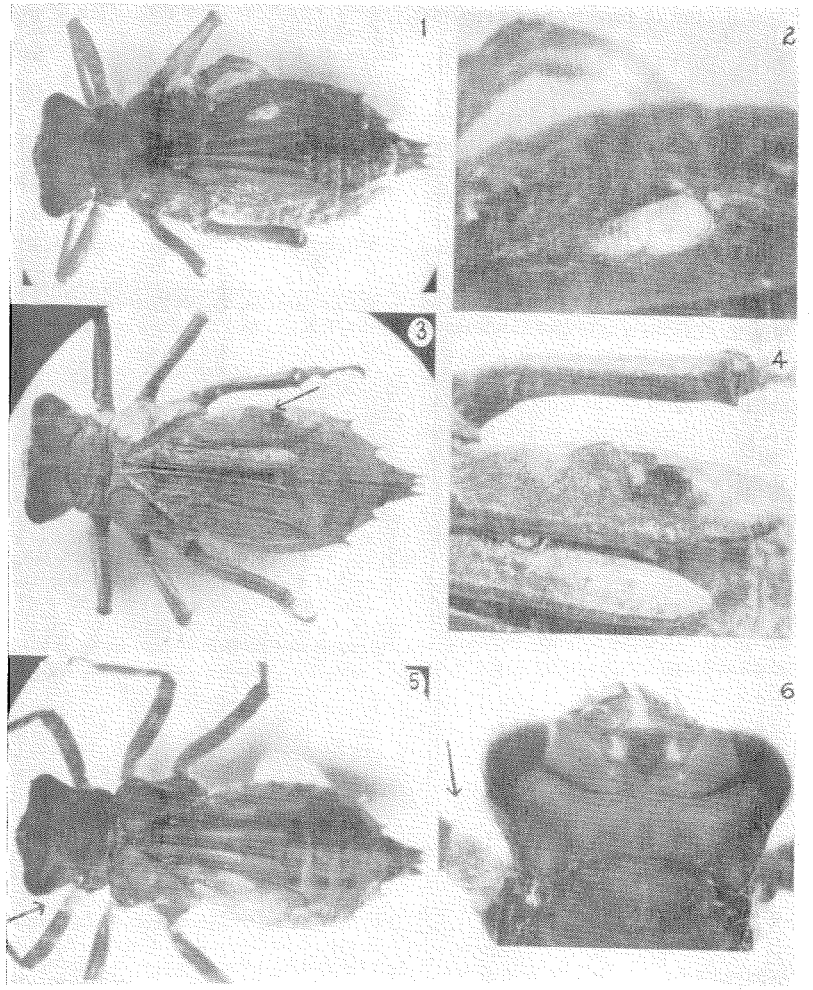

FIG. 1.—*Zygonyx torrida* Kirby nymph with pupa of *S. adersi* Pomeroy attached to right outer wing pad. 8.5 X; FIG. 2.—Closeup of *S. adersi* pupa shown in Fig. 1. 29.5 X; FIG. 3.—*Zygonyx torrida* nymph with deteriorated or damaged pupa of *S. hargreavesi* Gibbins attached to right outer wing pad. 8.5 X. Note that attachment site is identical with that of *S. adersi* pupa; FIG. 4.—Closeup of pupa shown in Fig. 3. 21 X; FIG. 5.—*Zygonyx torrida* nymph with empty *S. adersi* cocoon at left side of head. 11 X; FIG. 6.—Closeup of empty *S. adersi* cocoon shown in Fig. 5. 23 X. The foreshortened view is into the cocoon aperture.

bers among the respiratory filaments of *Simulium* spp., finding shelter and feeding on detritus and algae deposited among the filaments, and occasionally gnawing at the latter. Steffan (1967) regarded these Orthocladiinae, probably *Cardiocladius*, as being partly commensal. Thienemann (1932, 1939) described *Cardiocladius* larvae which not only were sheltered and protected among blackfly larvae and pupae, but also fed on them. Steffan regarded this behavior as ectoparasitism involving

a special kind of paroecy, or side-by-side relationship.

SUMMARY. Three 23 mm nymphs of the dragonfly *Zygonyx torrida* Kirby were found at blackfly attachment sites in northern Ghana with *Simulium* pupae attached. In the Red Volta River at Nangodi, near Bolgatanga, two nymphs were found: one with a complete pupa of *S. adersi* Pomeroy on the right outer wing pad, and the other with an empty *S. adersi* cocoon at the left side of the head. On the dam spillway of the dam at Nalerigu, east of Gambaga, a third nymph was found with a deteriorated, silt-covered pupa of *S. hargreavesi* Gibbins attached to the right outer wing pad. The three phoretic attachments are illustrated by photographs. Phoresy involving *Simulium* spp. aquatic stages attached to mayfly and dragonfly nymphs is reviewed and discussed, and summarized in a comprehensive table.

ACKNOWLEDGMENT. We wish to thank Dr. Oliver S. Flint, U.S. National Museum, Smithsonian Institution, Washington, D.C. for identifying the dragonfly nymphs described in this paper.

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