It is the peculiar boon of the Naturalist that he can look back upon his life with undiluted satisfaction. Was there a day that friend Davis did not add to his store of Nature wisdom? And, more than all this, was he not always ready and eager to share his knowledge and love of Nature with others? As a spokesman for the many he helped and inspired, I beg him to accept this modest tribute as a token of gratitude and esteem.

CARNUS HEMAPTERUS NITZSCH, AN ECTOPARA-SITIC FLY OF BIRDS, NEW TO AMERICA (DIPTERA).

By J. Bequaert, Boston, Mass.

A small collection of bird parasites recently received from Mr. Malcolm J. Lerch, of Penn Yan, New York, contained several minute dealated flies, taken from a nestling flicker. They proved to belong to the genus Carnus, the single known species of which is fairly common on birds or in their nests, in parts of Europe. I have found, among the unnamed Diptera at the Museum of Comparative Zoölogy, additional specimens of the same parasite, taken many years ago in Florida from a screech owl.

As these appear to be the first American records of Carnus, I am reviewing what is known of these parasites and append a reference list of the European literature. A similar list was compiled by Bezzi in 1922, to which Eichler (1936 and 1937) added later references.

Taxonomy.—European authorities accept only one species in the genus, Carnus hemapterus Nitzsch (1818, p. 305; figured by Germar, 1822, Pls. 24 and 25), with Cenchridobia eggeri Schiner (1862, p. 436) and Carnus setosus Stobbe (1913, p. 193) as synonyms. The main character on which Stobbe based his setosus was the denser and longer vestiture of setae. No doubt this was a deceptive appearance, caused by the more shrivelled or less physogastric condition of his specimens. Similar apparent differences are noted between newly hatched and fully engorged ked-flies (Melophagus and Lipoptena). Moreover, the male of Carnus

seems to be more hirsute than the female, as its abdomen swells much less.

The taxonomic relationships of Carnus are as yet somewhat in dispute. While most recent students agree that the genus is closely related to Meoneura, some are content to leave these two genera in the Milichiidae, while others place them in a separate family, the Carnidae, first erected by Hendel (1928). In Curran's key to the North American genera of Milichiidae, which family he calls Phyllomyzidae (1934, Fam. Gen. N. Amer. Dipt., p. 334), Carnus runs out to Paramyia, both genera lacking the posterior cross-vein (m); but it is readily separated by the obsolescence of all cross-veins except the anterior (r-m) and the simple, short, swollen proboscis. It differs from its closest relative, Meoneura, in having only one cross-vein, in the fourth and fifth longitudinal veins much shortened and ending far from the hind margin, and in the short and swollen proboscis. Melander includes Carnus in his table of the genera of Milichiinae (1913, Jl. New York Ent. Soc., XXI, p. 237); but it should be noted that the wings cannot properly be called rudi-

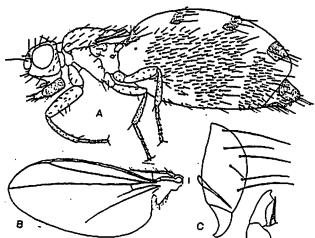


Figure 1. Carnus hemapterus Nitzsch. A, female, with retracted ovipositor, off Colaptes auratus luteus; Penn Yan, New York. B, wing of newly-hatched fly of Germany (after de Meijere). C, male external terminalia of Florida specimen, off Otus asio (from the side and below).

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mentary. As all my American specimens are dealated, I have copied de Meijere's figure of the wing of the European form (Fig. 1B), for comparison with Meoneura. The latter occurs in North America also, and some species have been bred in Europe from birds' nests, where they live as scavengers only, the adult flies never being found on the birds themselves.

I was unable to compare my American Carnus with European specimens, none of which appear to exist in any American collection. I have, however, carefully studied all published descriptions and figures, particularly those of Collin (1911), de Meijere (1913), Séguy (1930 and 1934), and Hennig (1937). I have been unable to discover reliable differences and I am forced to the conclusion that the North American flies are identical with Carnus hemapterus. The chaetotaxy of head, thorax and tergal and sternal plates of the abdomen is the same. The abdominal sclerotized plates of both sexes also agree. There is a slight difference in the distribution of the setae over the soft areas of the abdomen, if my drawing is compared with de Meijere's figure of the female (1913, fig. 2), but this is scarcely of importance. The male terminalia are practically identical. It may be noted that in my drawing the eye is relatively larger and the jowls or cheeks shorter than figured by de Meijere. I was at first inclined to regard this as a reliable difference, at least of subspecific value. Hennig's figure of the head (1937, p. 74, fig. 73) is, however, practically like my own, while Séguy's (1934, p. 632, fig. 816) shows even larger eyes. I may add that in my American specimens the eyes are of about the same relative size in

. Distribution.—In Europe, C. hemapterus seems to be fairly generally distributed and no doubt it will be found eventually in northern · Asia also: At present there are definite records from the Netherlands (de Meijere, 1928), Germany (Nitzsch, 1818; de Meijere, 1913; Nöller, 1920; Engel, 1920; Wülker, 1925; Eichler, 1936; etc.), Switzerland (Wegelin, 1933), Austria (Egger, 1854; Stobbe, 1913), Jugoslavia (Stobbe, 1913), Italy (Bezzi, 1922; Séguy, 1930), Roumania (Collin, 1911), Lithuania (de Meijere, 1928) and Finland (Frey, 1921; Nordberg, 1936).1 In America, Carnus is probably also widespread, as shown by its being known from New York (Penn Yan) and Florida (without more precise locality). Its distribution will become known only through an extensive and

¹ Bezzi (1922) includes Hungary in the range, but I have failed to trace a published record from that country. The occurrence in France is open to question, as Mercier (1928) does not state where he obtained his specimens and Seguy does not list a French locality.

systematic study of the arthropod fauna of birds' nests, a field which is almost virgin.2

Host Relations.—The following is a list of all known European hosts, arranged as to families, with the countries where they were observed in nature, either by breeding them from the nests (N) or on the birds (B). An asterisk marks hosts known to nest normally in cavities or sheltered places.

Fam. Accipitriidae: Haliaeetus albicilla (L.). Finland. N. Aquila heliaca Sav. (= imperialis Bech.). Jugoslavia. B.

Fam. FALCONIDAE: Falco peregrinus Tunst. Finland. N. * " tinnunculus L. Austria, Germany. N. B.

" cherrug D. E. Gr. (= sacer Gmel.). Roumania. B.

" sp. Italy. B.

Fam. COLUMBIDAE: *Columba livia Gm. (= domestica). Finland. N. oenas L. Finland. N.

Fam. TYTONIDAE: *Tyto alba (Scop.). Germany. N. B.

*Aegolius funereus L. [Cryptoglaux]. Finland. N.

Fam. PICIDAE: *Dryobates major L. Austria, Finland. N. B. *Picus viridis L. Germany. B.

*Dryocopus martius L. Finland. N.

Fam. Jyngidae: *Jynx torquilla L. Germany, Switzerland. B.

Fam. HIRUNDINIDAE: *Delichon urbica L. Finland. N.

Fam. CORVIDAE: Pica pica (L.). Finland. N. Corvus cornix L. Finland. N.

" corone L. Lithuania, Germany. B. *Colaeus monedula (L.). Netherlands, Finland,

Germany, N. B.

Fam. PARIDAE: *Penthestes atricapillus (L.). Finland. N.

*Parus ater L. Finland. N.

Fam. CERTHIDAE: *Certhia familiaris L. Finland. N. Fam. Turdidae: Turdus philomelus Brehm. Finland. N.

Arcenthornis musicus (L.). Finland. N.

*Phoenicurus phoenicurus L. Finland. N.

Fam. Sylviidae: Regulus regulus (L.). Finland. N. Sylvia atricabilla L. Germany. N.

² Most American papers dealing with this topic are confined to the blood-sucking maggets of Protocalliphora or (more rarely) to fleas or ticks. McAtee (1927 and 1929), Jellison and Philip (1033), and Dobroscky (1925) are the only investigators who paid attention to all arthropods found in nests.

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Fam. STURNIDAE: *Sturnus vulgaris L. Germany, Switzerland,

Italy, Finland. N, B.

Fam. PLOCEIDAE: *Passer domesticus L. Switzerland. N. Fam. FRINGILLIDAE: Fringilla coelebs L. Finland. N.

This list brings out some interesting points. In the first place, host specificity of Carnus is very slight and similar to that of many common Hippoboscidae of birds. It seems to be governed chiefly by certain features of nesting ecology and not at all by the taxonomic affinities of the hosts. Flies were bred from the nests of 24 species (of 14 families) and were taken from birds of 9 species (of 7 families). Out of a total of 29 bird hosts, 5 only have yielded them thus far from the birds as well as from the nests; but this is merely due to the method of obtaining the host records. Those known from Finland only (17 out of 29) were based entirely on a study of the contents of abandoned nests, no attempt being made at finding flies on the nestlings. For some birds the larvae of Carnus are the dominant or constant arthropods of the nests. Nordberg found them in 55 per cent of 11 nests of Turdus philomelus, 86 per cent of 7 nests of Parus ater, 67 per cent of 12 nests of Phoenicurus phoenicurus, 100 per cent of 57 nests of Colacus monedula, 91 per cent of 22 nests of Sturnus vulgaris, and 62 per cent of 13 nests of Columba oenas. A slight preference is shown for birds nesting in sheltered places, 17 (or 58 per cent) out of a total of 29 being of this type. Moreover, this group contains most of the birds in whose nests Carnus is often the dominant nidicole. The remaining 12 birds (42 per cent) all build nests in the open, but some distance above the ground, either in trees or on ledges. True ground and swamp nesting birds are completely avoided.

The only hosts known thus far in America, Colaptes auratus (L.) and Otus asio (L.), both nest in cavities or well sheltered places. Nine flies (29, 76) were taken many years ago in Florida by J. F. Whiteaves from a screech-owl (probably the race floridanus of Otus asio), but the circumstances of the find are not known. On June 25, 1939, Mr. Malcolm J. Lerch took five flies (39, 26) from the body of young flickers, bare of hair or feathers, in a nest placed in the broken stub of a dead tree, at Penn Yan, New York. No doubt the flickers were of the northern race (Colaptes auratus luteus Bangs).

Bionomics.—Our knowledge of the life-history and habits of Carnus is as yet fragmentary, some published statements being based on surmises rather than on actual observations. The adults have been bred from puparia found in birds' nests. Upon hatching,

both sexes are fully winged and able to fly,2 probably reaching new breeding places or new hosts by flight at that time, particularly when they hatch in the spring from old nests. So far as I know, however, no specimens have ever been taken on the wing in nature. Those that hatch in mid-summer, in nests occupied by young birds, probably remain there. At any rate, both sexes have been found in summer in a dealated condition on the body of nestlings, running about swiftly or hiding in the axilla. The wing breaks off some distance from the base, at the deep notch of the costa where the first longitudinal vein ends. A fairly long stump (of about 0.3 mm.) remains on the thorax. Mercier (1928) has shown that, as in the case of Lipoptena, the longitudinal thoracic muscles of flight are replaced in dealated specimens by adipocytes, which later are resorbed. Perhaps this tissue material of the thorax is used in part for the postimaginal growth of the internal organs of the abdomen, a conspicuous feature of dealated Carnus. As a result of this growth, the integument is considerably distended. The physogastric condition is less pronounced in the male than in the female, the latter eventually reaching twice the original size. The increase in size seems to call for the taking of some food by the adult fly, after it reaches the bird.

The exact nature of the diet is, I believe, far from settled. Most writers surmise or state as a fact that Carnus is a blood-sucking fly; but a careful study of the mouth-parts discloses none of the vulnerating structures of the proboscis of the true "biting" muscoid flies. There is, it is true, a swollen and heavily sclerotized basal portion; but this could scarcely pierce the skin, as it ends in soft labella, bearing only long, sensorial setae (See de Meijere, 1913, p. 8, figs. 5 A-B; Frey, 1921b, p. 151, Pl. 10, fig. 125). There appears to be none of the elaborate prestomal rods, rasps and teeth by means of which Stomoxys and Glossina cut the skin. I can find only two accounts of actual observations bearing on this subject, and they are contradictory. Nöller (1920, p. 159) describes the feeding as follows: "It is possible to keep Carnus alive without difficulty for three days in a Petri-dish, with a moist wad of cotton in the incubator at 25° C., feeding it once or twice a day in the axilla of longeared owls ["Waldohreulen," Asio otus L.] cleared of the feathers. At the close of this period it is as hungry and bloodthirsty as when it was first taken from the barn-owl. Long series of experiments

^a The reduced venation certainly does not impair flight much. The species of *Lipoptena*, in which the veins are even more reduced, are good and active fliers before they drop the wings.

were not carried out, because no birds infected with Haemobroteus were available at the time. The act of sucking blood takes only a few minutes, after some running about under the glass-container placed on the bird. It usually begins in short order particularly if the skin of the bird has been somewhat injured through scratching with a needle." Engel (1919, p. 249), on the other hand, writes: "Most of the flies remaining on the body of the birds [nestling wrynecks, killed with ether | were attached by means of the proboscis to the insertion of a feather-quill, where they probably obtain their food. This, however, could scarcely be the blood of the young birds, but consists rather only of the secretions of the skin and of the fat exuded by the feather-quills. For the mouth-parts of Carnus do not seem to me built for piercing the skin of birds. Furthermore, in none of the freshly collected flies did I see blood through the membrane of the abdominal segments, such as may always be observed in engorged culicids." The presence of avian blood in the intestinal tract of fresh flies could readily be determined by microscopic examination of the contents. Meanwhile, I am inclined to agree with Hendel (1928, p. 105) that Carnus feeds most probably on secretions of the skin, which the fly licks or sucks after the fashion of the house-fly.

The true diet of adult Carnus is of particular importance in connection with the possibility that this fly might act as a biological carrier of certain avian blood-parasites. In the case of the Haemoproteus of the European kestrel (Falco tinnunculus), von Wasielewski and Wülker (1918, p. 75) believe that Carnus hemapterus is the intermediate host and that it infects the nestling by the bite. They offer, however, no evidence to support this claim, apart from the fact that the fly was often found on infected nestlings. They were unable to experiment with it, not did they attempt to find developmental stages of the protozoon in the insect. From what is known of the transmission of the pigeon Haemoproteus, which may be identical with that of kestrel, it is more probable that a species of Pseudolynchia or a related genus of Hippoboscidae, is the carrier. Some such flies were also occasionally seen on kestrels by von Wasielewski and Wülker.

The dealated flies are most commonly observed on nestlings, before the feathers are developed or, at any rate, before the young leave the nest. I find 20 definite records from nestlings and only 4 that possibly refer to adult birds away from the nest. Several flies are usually found on one nestling and they are sometimes very numerous, making black patches on the skin. They often rest or hide in the axilla and, when disturbed, scurry about very swiftly with a hopping motion.

Probably most of the flies eventually die on the nestlings, but how long they live or whether they ever leave the bird after the wings break off, is not known. Mating and oviposition have not been observed. Brauer (1880, p. 117; and 1883, p. 60) claimed that Carnus was ovoviviparous. He gave a very brief description of the first larval instar, which, as de Meijere (1913, p. 13) points out, was based on larvae extracted from the abdomen of a gravid female. The unhatched egg, as found in the uterus of the fly, was also described by de Meijere. He surmises that several first instar larvae are voided at very short intervals. Since the puparia have been found in the nests, there can be little doubt that the several larval instars live there; but no description of them has ever been given, nor is it known what they feed on. They could be either scavengers, living off decaying organic matter, or predactious, attacking other arthropod inmates of the nest. The puparium was described and figured by de Meijere (1913, p. 17, figs. 11-12). As in all Muscoidea, it is the hardened and shrivelled integument of the last larval instar, of which it retains many of the characteristics. It is established that the insect hibernates as a puparium, perhaps the only method of surviving winter. Nordberg (1936, pp. 160-161) found in Finland that many of the flies hatched throughout July and August from starling nests after they were abandoned by the birds, but that a fair number of puparia remained to give flies next spring.

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