Vol. 85, No. 13, pp. 163–178 30 August 1972

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

PUPA OF *NEOMOCHTHERUS ANGUSTIPENNIS* (HINE), WITH NOTES ON FEEDING HABITS OF ROBBER FLIES AND A REVIEW OF PUBLICATIONS ON MORPHOLOGY OF IMMATURE STAGES (DIPTERA: ASILIDAE)

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Feeding Habits

Robber flies are one of the most taxonomically diverse and numerically abundant groups of Diptera. As far as known, the adults and some (possibly all) larvae are predators of other insects, especially phytophagous forms. Some adult asilids attack beneficial insects such as honey bees and other Hymenoptera, and some prey on harmful species, such as locusts, grasshoppers, and chafer-beetles. Although these common flies appear to be significant elements of the ecosystem and of practical importance to agriculture, surprisingly little is known about the behavior of the adults. Even less is known about the immature stages.

In addition to many isolated, single-specimen observations of prey, extensive lists of prey of adult Asilidae have been presented (among others) by Adamovic (1964) and Hobby (1930, 1933) in Europe, Bromley (1930) and Fattig (1945) in North America, Carrera and Vulcano (1961) in South America, Cuthbertson (1937) in Africa, and Iwata and Nagatomi (1962) in Japan. No adult asilids are known to be monopha-

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gous or even oligophagous. Whereas some robber flies are opportunistic predators and attack most of the abundant, slow-flying, appropriately sized and conspicuous species available (Powell and Stage, 1962), others have more limited prey preferences (Linsley, 1960; Lavigne and Holland, 1969). Apparently many species have hunting zones restricted to certain parts of the habitat (Adamovic, 1963; Lehr, 1969; Zinov'eva, 1959). As is true of most other groups of entomophagous insects, there is little quantitative data on the impact of adult robber flies on populations of their prey.

The most extensive study of the biology of Asilidae (Melin, 1923) includes much information on various aspects of all stages, especially the adults, but little specific data on the critical issues of the food and feeding behavior of the larvae. From the fragmentary data of many earlier authors (but not including the important information of Felt, 1918, and Davis, 1919) and from his own mainly circumstantial evidence, Melin concluded that asilid larvae are principally phytophagous. This opinion, made without knowledge of the complete life cycle of any species, has been repeated in many subsequent general discussions of the biology of Asilidae.

Since Melin's paper, conclusive studies of the feeding habits of larvae belonging to the genera *Hyperechia*, *Mallophora*, and *Promachus* have appeared. Adults of *Hyperechia* are well known as striking mimics of *Xylocopa* bees in the Old World Tropics, and at least the mature larvae of several species of *Hyperechia* are predators of the larvae and pupae of the xylocopid models (Poulton, 1924; Tsacas, et al., 1970). The complete development of the larvae of only three of the 5,000 known species of Asilidae (*Promachus yesonicus* Bigot, *Mallophora media* Clements and Bennett, and *M. ruficauda* (Wiedemann)) has been studied. The larvae of *Promachus yesonicus* are free-living predators of the larvae of Scarabaeidae, especially of *Anomala* spp., in Japan (Kinoshita, 1940). The larvae of *Mallophora media* were reared from larvae of a scarabaeid (*Barybas insulanus* Moser) in Trinidad by Clements and Bennett (1969). The young larva is an ectoparasite and remains in place with its anterior end buried in the in-

tegument of the grub. During later larval life it may remain with the original host or it may live free in the soil. The young larva of *M. ruficauda* is an ectoparasite of *Archohileurus vervex* (Burmeister) (Scarabaeidae); it remains with the host larva and consumes it as it matures (Copello, 1927, 1942). Less detailed reports of the behavior of the larvae of *M. ruficauda* are found in the papers of Crouzel (1965) and De Gavotto (1964).

Other reports on the food and feeding habits of asilid larvae not included in Melin's 1923 review or published subsequently are summarized below. Most of these also indicate that the larvae of Asilidae are predaceous. Felt (1918) reported that larvae of *Promachus fitchii* Osten Sacken are efficient natural enemies of larvae of *Phyllophaga fusca* (Froelich (Scarabaeidae) in New York. Davis (1919) observed free-living larvae of *Promachus vertebratus* (Say) feeding on white grubs in Wisconsin and Michigan, and he cited unpublished reports of other asilid larvae feeding on scarabaeid larvae. Irwin-Smith (1923) kept first-instar larvae of an Australian species, *Neoaratus hercules* Wiedemann, alive for more than 25 days but the larvae did not feed on, '. . . pieces of Scarabaeidae larvae . . .' or on earthworms or scraps of meat. Champlain and Knull (1923) reared adults from larvae and pupae of *Andrenosoma fulvicauda* (Say) found in pupal cells of *Chrysobothris femorata* (Olivier) (Buprestidae) in *Quercus* sp. in Pennsylvania. Osterberger (1930) reared larvae of *Triorla interrupta* (Macquart) on larvae of *Eutheola rugiceps* (LeConte) (Scarabaeidae) in Louisiana. Osterberger stated that, "The feeding (Pl. 24, fig. 1) was accomplished by the larva attaching itself to the white grub in a tender, unprotected region just back of the head. There it remained until all the body juices were sapped. . . ." Reinhard (1938) was unable to induce newly hatched larvae of *Efferia aestuans* (L.) to feed on small *Phyllophaga* grubs or on ant larvae in Illinois. Ritcher (1940) found over 40 larvae of *Diogmites discolor* Loew attacking pupae or in pupal cells containing shrivelled skins of pupae of five species of *Phyllophaga* in Kentucky. Fattig (1944) stated that, "From hundreds

FIG. 1. Larva of *Mallophora* sp. on larva of *Phyllophaga* sp.

of white grubs brought in with the larva of some insect attached . . . ," he reared the following in Georgia: *Asilus virginicus* Banks, "*Deromyia winthemi* Wiedemann," *Diogmites discolor* Loew, *D. ternatus* Loew, *Efferia aestuans* (L.), *E. pogonias* (Wiedemann), "*Erax barbatus* Fabricius," "*Erax interruptus* (L.)," "*Proctacanthus brevipennis* Wiedemann," *P. longus* (Wiedemann), *P. rufus* Williston, *Promachus rufipes* (Fabricius), and *Tolmerus notatus* Wiedemann. Stower, et al., (1958) found larvae of *Scylaticus* sp. in egg-pods of *Schistocerca gregaria* (Forskål) in Eritrea. Greathead (1963) recorded larvae of *Scylaticus* sp., *Stenopogon* sp., and *Trichardis* sp. from egg-pods of *S. gregaria* in East Africa. Daniels (1966) found larvae (1–1.5 inches long) of an unidentified species of Asilidae in soil with larvae of *Phyllophaga koehleriana* (Saylor) in Texas: the asilid larvae killed and ate the scarabaeid larvae during laboratory rearings. Ecipenko (1967) collected a larva of *Eutolmus rufibarbis* Meigen, ". . . that was

sucking out a larva of the beetle *Maladera japonica* Motschulsky [Scarabaeidae] through a puncture in the head capsule." During laboratory rearings, Ecipenko saw a larva of *E. rufibarbis* kill and eat a larva of *Machimus* sp. (Asilidae), and he also observed cannibalism in a culture of *E. rufibarbis*. Weinberg (1968) obtained hatching of eggs of *Dysmachus fuscipennis* (Meigen) in Romania. The larvae lived for 11 days in containers of different kinds of soil. Weinberg did not state that the larvae fed, although she did mention that some of the larvae molted to the second instar.

The sites and manner of attachment of young *Mallophora* larvae are very similar to those of the larvae of certain tiphiid wasps that are also ectoparasites of scarabaeid larvae. The presence of a pair of bristles on each thoracic segment and of four pairs of elongate, fine bristles on the last body segment and the absence of lateral abdominal spiracles readily distinguish asilid larvae from tiphiid larvae. Figure 1 shows a larva of *Phyllophaga* sp. (Scarabaeidae) (determined by D. M. Anderson) parasitized by young asilid larvae, possibly of the genus *Mallophora*. Several scarabaeid larvae infested in this manner were sent to the Systematic Entomology Laboratory, USDA, for determination by L. Castenada, Salvadorian Coffee Research Institute, San Salvador. The specimens were collected during September 1968, at El Sunza, Dept. Sonsonate, San Salvador. The asilid larvae closely match the description of *Mallophora media* (Clements and Bennett, 1969) and *M. ruficauda* (Copello, 1927, 1942). Mr. A. N. Clements (personal communication), who has seen the specimens, agrees that they are Asilidae, possibly of the genus *Mallophora*. There are seven specimens of *Mallophora ruficauda* in the National Museum of Natural History, Smithsonian Institution, pinned with pupal skins and labeled as follows: 1♂, So. Amer. Par. Labo., Uruguay, near Montevideo, No. 1013, XII.22, H. L. Parker col., Host, Scarabaeidae. 2♀, as above except 1♀ XII. 20, P. A. Berry col. and 1♀ XII.26, P. A. Berry col. 1♀, So. Amer. Paras. Lab., Montevideo, No. 561.9, XII.21, Host, Scarabaeidae, Parker and Silveira. 1♀, as above except No. 5618. 1♀, So. Amer. Paras. Lab., Seriano, Uruguay, No. 6262, XII.17,

in soil, Silveira. 1♀ Canelones, Uruguay, pred. Scarabaeidae, 16.I.1942, 561.11, Lot No. 42–8967, H. L. Parker.

Morphology of Immature Stages

Only about 2 percent of the approximately 5,000 world species of Asilidae are known in any immature stage. Of some 400 total genera, there is information on the immature stages of only 41. Of the 856 species and 82 genera known from North America, immature stages of only 25 and 12, respectively, have been described. Papers on the morphology and biology of immature stages of Asilidae, published to 1918, were listed by Irwin-Smith (1923). Hennig (1952) summarized descriptive data on the immature stages of 64 species in 30 genera. Information on the morphology of immature stages that has been published since Hennig's and Irwin-Smith's summaries (and earlier papers not included by them) is listed in Table 1.

Pupa of *Neomochtherus angustipennis* (Hine) and Features of the Adults

Neomochtherus Osten-Sacken is a typical example of the paucity of information available on the immature stages of Asilidae. In his revision of the genera of Asilidae of the world, Hull (1962) listed 49 species belonging to this genus. The Old World fauna has been studied intensively recently by Tsacas (1968, 1969), who treated 120 Palearctic and Ethiopian species. Apparently only the first-instar larva and pupa of *N. perplexus* Becker (= *N. hungaricus rossicus* Engel?) (Zinov'eva, 1959) and the egg of *N. kivuensis* Tsacas (Tsacas, 1969) have been described. In the Smithsonian Institution there is a male of the rare *N. angustipennis* (Hine) pinned with a pupal skin, which is described below.

Neomochtherus angustipennis (Hine)

Pupa, Figures 2-5.

Greatest length, 14.0 mm; greatest width of thorax, 3.5 mm; greatest width of abdomen, 3.5 mm, tapering to 1.5 mm at greatest width of last abdominal segment. Subshining straw-yellow, spines and processes glistening reddish brown. Head with a pair of terminal anterior antennal

TABLE 1. Recently published descriptions and figures of the immature stages of Asilidae.

	LEPTOGASTRINAE		
Leptogaster cylindrica De Geer	E, IL, P[1]	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Leptogaster salvia Martin	E	Wyoming, U.S.A.	Lavigne, 1963
	LAPHRIINAE		
Andrenosoma atra Séguy	P	France	Musso, 1967
Andrenosom bayardi Séguy	P	France	Musso, 1967
Andrenosoma fulvicauda (Say)	L	Ohio, U.S.A.	Peterson, 1957
Hyperechia bomboides (Loew)	L, P	Senegal	Tsacas, et al., 1970
Laphria sp.	L	Ohio, U.S.A.	Peterson, 1957
Laphria flava L.	L	England	Brindle, 1962
Laphria gilva L.	E	Germany	Wichmann, 1956
Laphria gilva L.	E	South Dakota, U.S.A.	Schmid, 1969
Laphria gilva L.	L	England	Brindle, 1962
Laphria gilva L.	P	France	Quentin, 1948
	DASYPOGONINAE		
?*Dioctria oelandica* (L.)	L	Westmoreland, England	Brindle, 1969
Dioctria rufipes (De Geer)	L	England	Brindle, 1962
Dioctria rufipes (De Geer)	L, P	Cheshire, England	Brindle, 1968
Diogmites angustipennis Loew	E	Wyoming, U.S.A.	Lavigne and Holland, 1969
Diogmites basalis (Walker) (as *Deromyia umbrina* Loew)	E	Indiana, U.S.A.	Davis, 1919
Diogmites discolor Loew	L, P	Kentucky, U.S.A.	Ritcher, 1940

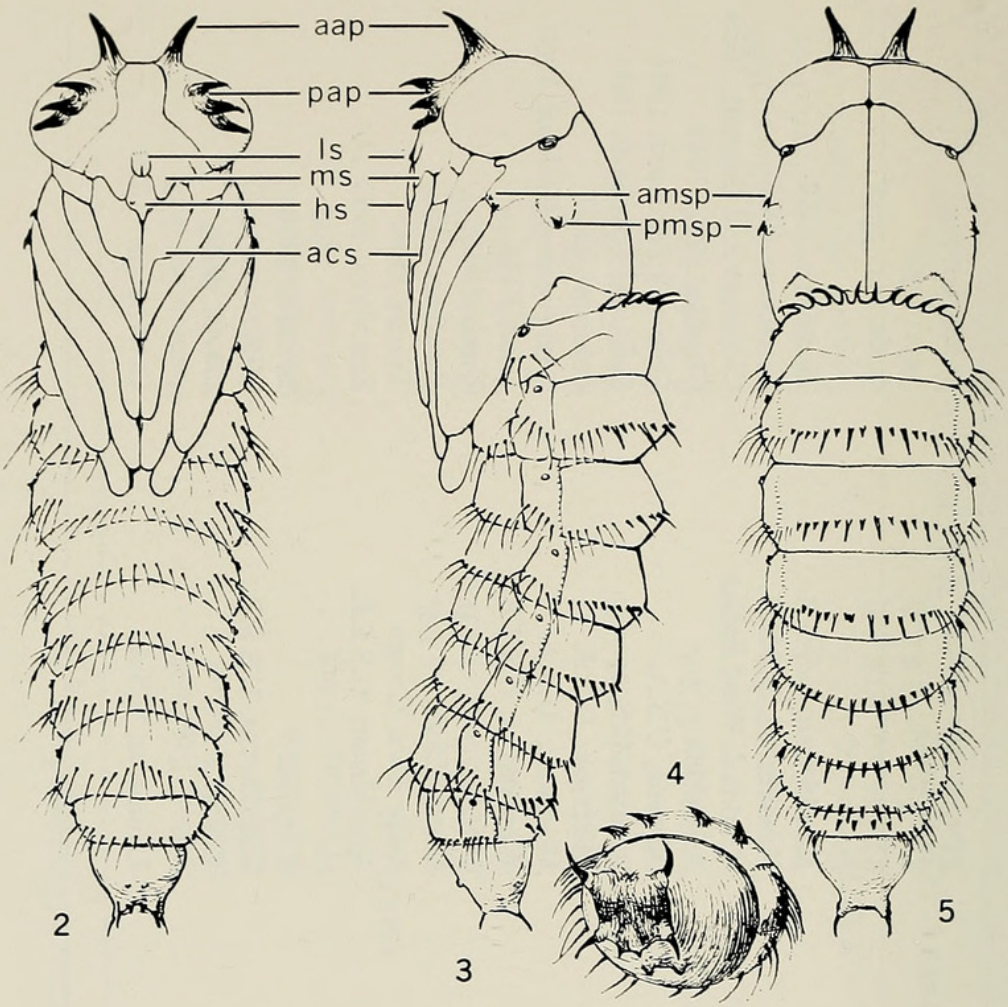
[1] E = egg, L = Mature larva only, unless otherwise indicated, P = pupa.

TABLE 1 (Continued)

Leptarthrus brevirostris Meigen	P	Sussex, England	Parmenter, 1952
Leptarthrus brevirostris Meigen	E	Surrey, England	Stubbs, 1970
Pritchardia hirtipes (Macquart)	E	Chile	Artigas, 1970
Scylaticus sp.	L, P	East Africa	Greathead, 1963
Stenopogon coyote Bromley	E	Wyoming, U.S.A.	Lavigne, 1963
		ASILINAE	
Apoclea helvipes Loew	E, IL	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Astochia caspica Hermann	E, IL	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Dysmachus sp.	L	Germany	Brauns, 1954a
Dysmachus fuscipennis (Meigen)	E, I, II L	Rumania	Weinberg, 1968
?*Dysmachus trigonus* Meigen	P	Germany	Brauns, 1954b
Echthistus rufinervis Meigen	E, IL, P	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Eccritosia rubriventris (Macquart)	P	Chile	Artigas, 1970
Efferia helene (Bromley) (as *E. bicaudata* (Hine))	E	Wyoming, U.S.A.	Lavigne, 1964
" "	E	Wyoming, U.S.A.	Lavigne and Holland, 1969
Efferia pallidula (Hine)	E	Wyoming, U.S.A.	Lavigne and Holland, 1969
Efferia staminea (Williston)	E	Wyoming, U.S.A.	Lavigne and Holland, 1969
Eremisca vernalis Zinov'eva	E, L	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Eutolmus implacidus Loew	E	Kazakhstan, U.S.S.R.	Lehr, 1962
Eutolmus rufibarbus Meigen	L, P	Khabarovsk Region, U.S.S.R.	Ecipenko, 1967

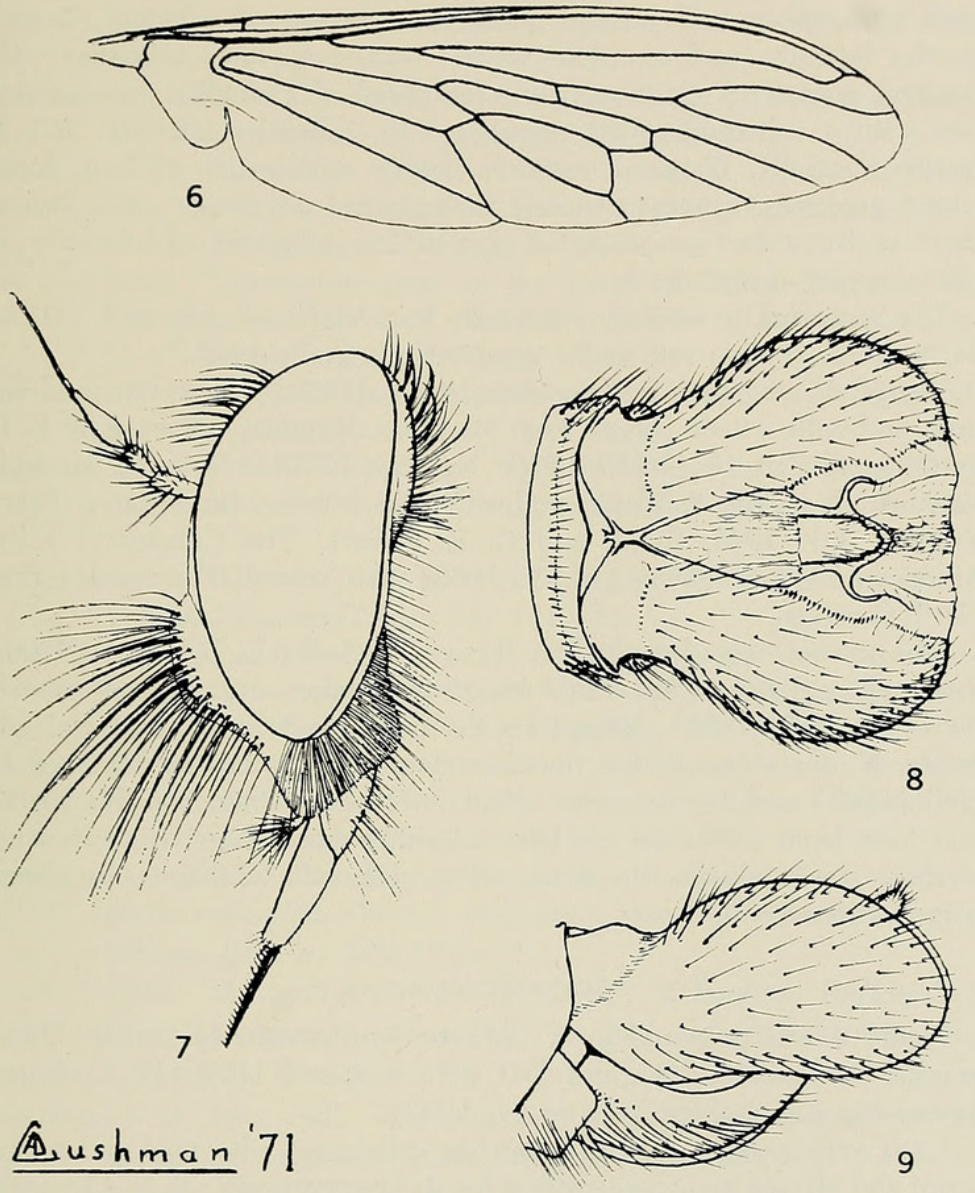
TABLE 1. (Continued)

	ASILINAE		
Machimus atricapillus Fallén	P	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Machimus gonatistes Zeller	E, L, P	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Mallophora media Clements and Bennett	I–IV L, P	Trinidad, West Indies	Clements and Bennett, 1969
Mallophora ruficauda (Wiedemann)	E, I–IV L, P	Argentina	Copello, 1927, 1942
Mallophorina frustra Pritchard	E	Arizona, U.S.A.	Cole and Pritchard, 1964
Mallophorina pulchra Pritchard	E	Arizona, U.S.A.	Cole and Pritchard, 1964
Promachus bastardii (Macquart)	L	Michigan, U.S.A.	Peterson, 1957
Promachus dimidiatus (Curran)	E	Wyoming, U.S.A.	Lavigne and Holland, 1969
Promachus leontochlaenus Loew	E	Kazakhstan, U.S.S.R.	Lehr, 1958
Promachus vertebratus (Say)	L, P	U.S.A.	Davis, 1919
Promachus sp., prob. *vertebratus* (Say)	L	Ohio, U.S.A.	Peterson, 1957
Neomochtherus kivuensis Tsacas	E	Lake Kivu, Congo	Tsacas, 1969
Neomochtherus perplexus Becker (= *N. hungaricus rossicus* Engel ?)	E, IL, P	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Philonicus albiceps (Meigen)	L	England	Brindle, 1962
Satanas gigas Eversmann	E, IL, P	Kazakhstan, U.S.S.R.	Zinov'eva, 1959
Triorla interrupta (Macquart) (as *Erax maculatus* Macquart)	L	U.S.A.	Davis, 1919
Triorla interrupta (Macquart) (as *Erax interruptus* Macquart)	L, P	Louisiana, U.S.A.	Osterberger, 1930



FIGS. 2–5. *Neomochtherus angustipennis* (Hine); pupal skin: 2, ventral view; 3, lateral view; 4, posterolateral view of last abdominal segment; 5, dorsal view. aap, anterior antennal process; acs, anterior coxal sheath; amsp, anterior mesothoracic spines; hs, hypopharyngeal sheath; ls, labral sheath; ms, maxillary sheath; pap, posterior antennal process; pmsp, posterior mesothoracic spine.

processes (aap) not joined at base and a group of 3 basally fused posterior antennal processes (pap) located ventrolaterally on either side, the 2 outermost processes fused basally for a greater distance and thus appearing shorter than the innermost process. Outermost process rounded apically, the 2 innermost processes acute. Labral sheath (ls) with a slight keel apically that is rugulose on either side. Hypopharyngeal sheath (hs) with a minute tubercle on either side. Maxillary (ms) and anterior coxal sheaths (acs) entirely smooth. Paired prothoracic spiracles elongate-oval, surrounded by a ring of thickened cuticle basally, situated midlaterally at anterior margin of thorax. A pair of anterior mesothoracic spines (amsp), 1 short and blunt, the other long and sharply curved,



Figs. 6–9. *Neomochtherus angustipennis* (Hine): 6, Wing; 7, Head; 8, Male terminalia, dorsal view; 9, Same, lateral view.

on either side of thorax above bases of sheaths of second pair of legs. A short, dull posterior mesothoracic spine (pmsp) on tubercle at base of each wing sheath. No rugulose area on thorax above wing sheaths. Sheaths of third pair of legs reaching slightly beyond middle of abdominal segment 3. First abdominal segment with a transverse row of 10 long, subequal, apically recurved spines dorsally along anterior margin and 4 yellowish bristles behind lateral spiracle, venter obscured. Second segment with a median transverse row of alternate long and short, straight spines dorsally, a short row of 4 or 5 bristles dorsolaterally, 4 to 7 bristles behind the lateral spiracle, and a mesally interrupted row of bristles ventrally. Third through seventh abdominal segments similar,

each with spines and bristles dorsally as on second segment, 5 or 6 bristles laterally, and complete ventral transverse row of bristles. Abdominal segment 8 (last segment) composed of a ringlike anterior portion with 4 subequal spines dorsally, 6 or 7 bristles laterally, and 12 bristles ventrally. Tapered posterior portion with a pair of long dorsolateral processes, a pair of shorter ventrolateral processes, and a pair of short ventromedian processes. A pair of low tubercles midventrally on posterior part of segment 8.

The specimen is labeled, "Barcroft, Va., VIII.1.34, emerged VIII.13.34, pupa in surface soil under pine tree, J. C. Bridwell."

The adult compares exactly with Hine's (1909) description and figures, and with a male cotype from St. Elmo, Virginia, collected by F. C. Pratt, September 13 (USNM Type Number 12648). There is an additional adult in the Smithsonian Institution, a male, from Camp Peary, Virginia, July 1943, R. M. and G. E. Bohart. The Catalog of North American Diptera (Stone, et al., 1965) also records the species from North Carolina.

This species was described in the genus *Asilus* L. by Hine (1909), listed under *Asilus* in the North American Catalog, and under *Neomochtherus* by Hull (1962). Except for the rather well-developed facial gibbosity, *N. angustipennis* has the characters of the genus as discussed by Hull (1962) and Tsacas (1963, 1968). The only figures of this species that have been published are Hine's (1909) rather superficial drawings of the male terminalia; the head, wing, and male terminalia are shown here in Figures 6–9.

Acknowledgments

Figure 1 was prepared by V. Krantz, Smithsonian Institution Photographic Services, and Figures 2–9 were prepared by A. D. Cushman, Systematic Entomology Laboratory, USDA.

I am very grateful to the following colleagues who read the manuscript and offered many suggestions for its improvement: A. N. Clements, Woodstock Agricultural Research Centre; R. J. Lavigne, University of Wyoming; H. Oldroyd, British Museum (N. H.); and L. Tsacas, Museum National d'Histoire Naturelle, Paris.

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